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Léa Kervroëdan

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Effets des traits et de la diversité fonctionnelle des plantes sur le ruissellement et la rétention des sédiments

Application pour le contrôle de l'érosion des sols dans les bassins versants agricoles tempérés

Soutenue le 17 Décembre 2018 après avis des rapporteurs, devant le jury d'examen :

M^{me} Alexia STOKES – Directeur de recherche INRA	**Rapporteur**
M. Charles BIELDERS – Professeur	**Rapporteur**
M. Olivier CHABRERIE – Maître de conférences HDR	**Examinateur**
M. Grégory MAHY – Professeur	**Examinateur**
M. Julien TOURNEBIZE – Ingénieur de recherche IRSTEA	**Membre invité**
M. Jean-François OUVRY – Directeur de l'AREAS	**Membre invité**
M. Romain ARMAND – Enseignant-Chercheur	**Co-encadrant**
M. Michel-Pierre FAUCON – Directeur de recherche HDR	**Directeur**

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by

Léa Kervroëdan

to obtain the degree of Doctor from the University of Picardie Jules Verne

Plant traits and functional diversity effects on runoff and sediment retention

Application to soil erosion control in temperate agricultural catchments

Defended on the 17th of December 2018, after the reviewer's opinion, in front of the examination jury:

Ms Alexia STOKES – Head of Research INRA	**Reviewer**
Mr Charles BIELDERS – Professor	**Reviewer**
Mr Olivier CHABRERIE – Lecturer (HDR)	**Examiner**
Mr Grégory MAHY – Professor	**Examiner**
Mr Jean-François OUVRY – Director of AREAS	**Guest member**
Mr Julien TOURNEBIZE – Research engineer IRSTEA	**Guest member**
Mr Romain ARMAND – Associate Professor	**Co-supervisor**
Mr Michel-Pierre FAUCON – Head of Research (HDR)	**Supervisor**

AVANT-PROPOS

Cette thèse a débuté en Janvier 2016 et s'inscrit dans une collaboration CIFRE (Convention Industrielle de Formation par la Recherche) – subventionnée par l'ANRT (Association Nationale de la Recherche et de la Technologie) – entre l'AREAS (Association de Recherche sur le Ruissellement, l'Érosion et l'Aménagement du Sol), basée à Saint Valéry en Caux (France), et l'équipe de recherche AGHYLE (Agroécologie, Hydrogéochimie, Milieux et Ressources) d'UniLaSalle (rattachée à l'Université Picardie Jules Verne), basée à Beauvais (France).

Cette thèse fait partie du projet HHAE2 (Haies Herbacées Anti-Erosives 2) de l'AREAS, rendu possible par les subventions accordées par la Région Normandie et l'Agence de l'Eau Seine-Normandie. Ce projet fait suite à HHAE 1 qui avait permis de démontrer la faisabilité et l'intérêt des haies herbacées. HHAE2, en confrontant les résultats d'HHAE1, a pour but de définir (1) les modalités techniques d'implantation et de gestion ; (2) les conditions optimales d'utilisation par la modélisation ; (3) l'effet de la diversité fonctionnelle des haies herbacées ; (4) l'effet des haies herbacées sur les transferts de pesticides ; et (5) l'apport des haies herbacées à la biodiversité dans le paysage.

Le manuscrit de thèse est rédigé en anglais, afin de le rendre plus accessible, et sous forme d'une thèse sur articles. Le premier chapitre a été publié dans un journal international, le deuxième est soumis dans un journal international et le dernier est en finalisation avant soumission. Une liste des publications est disponible à la fin du manuscrit, ainsi qu'un résumé étendu du manuscrit en français.

FOREWORD

This PhD research started in January 2016 and is a CIFRE collaboration (Industrial research training agreements) – funded by the ANRT (National Association of Research and Technology) – between AREAS, located in St Valéry en Caux (France), and the research unit AGHYLE from UniLaSalle (attached to Université Picardie Jules Verne), located in Beauvais (France).

This PhD is part of an AREAS' project: HHAE2; funded by "Région Normandie" and "Agence de l'eau Seine-Normandie". This project follows HHAE1, which demonstrated the feasibility and the interest of herbaceous hedges. HHAE2, notably by comparing the results obtained in HHAE1, aims to define (1) the technical methods of implementation and management; (2) the optimal conditions of use, using modelling; (3) the effect of the functional diversity of herbaceous hedges on runoff and soil erosion reduction; (4) the effects of herbaceous hedges on pesticide transfers; and (5) the contribution of herbaceous hedges to biodiversity enhancement in the landscape.

The PhD thesis is written in English, to make it more accessible, and in the form of a PhD on articles. The first chapter has been published in an international journal, the second is submitted in an international journal and the last one is being finalised before submission. A list of the publications is provided at the end of the manuscript, as well as an extended summary of the thesis in French.

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Je vous aimais, je vous aime et je vous aimerai…

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF SUPPLEMENTARY MATERIALS

INTRODUCTION

1. INTRODUCTION

1.1. Implications of plant functional ecology into plant-soil processes in ecosystems

The search for understanding how plant communities affect ecosystem processes has existed for centuries. The characterisation of vegetation using a functional approach, rather than taxonomical, was introduced by Theophrastus in 300 B.C., by using plant height and stem density to classify the vegetation (Weiher et al. 1999). From the 19th century, there has been an increasing interest in classifying plant communities following their characters and functions, to arrive at the characterisation of functional ecology (Calow 1987; Laureto et al. 2015). Plant functional ecology focuses on the understanding of ecosystem processes and community dynamics in response to environmental factors (Calow 1987; Keddy 1992).

Understanding how plant functions determine plant distribution but also the ecosystem and community structures and dynamics has been increasingly at the centre of attention for the past decades (Pugnaire and Valladares 1999; Lavorel and Garnier 2002). A number of functions (e.g. plant growth, photosynthesis, respiration) have been targeted in order to understand the plant and community responses to changing environments as well as their effects on ecosystem processes and properties (e.g. productivity, decomposition rates, nutrient cycling) (Loreau et al. 2001; Lavorel and Garnier 2002).

Functional ecology allows to deepen the comprehension of a number of questions related to the relationship between plant and ecosystem processes, such as the organism functioning and its response to the environment; the identification of the rules driving the community assembly; or the impact of the organisms' functioning on ecosystem processes (Grime 1998; Pugnaire and Valladares 1999; Loreau et al. 2001; Lavorel and Garnier 2002; Mcgill et al. 2006; Díaz et al. 2007b; Garnier and Navas 2012).

1.1.1. Plant functional traits approach in ecosystem processes

What is a trait?

Using plant features, as a measure of their functions in ecosystem structure and processes, was integrated in conceptual vegetation models in order to predict the effects of changes in ecosystem processes (Lavorel and Garnier 2002). Indeed, these plant features were found to have stronger relationships towards ecosystem processes than species and their number (Díaz and Cabido 2001; Lavorel and Garnier 2002; Cadotte et al. 2011). Rather than using the plant taxonomical identity, these models thus focussed on the plant biological characteristics called "functional traits". A trait is defined as "any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organisation" (Figure 1) (Violle et al. 2007).

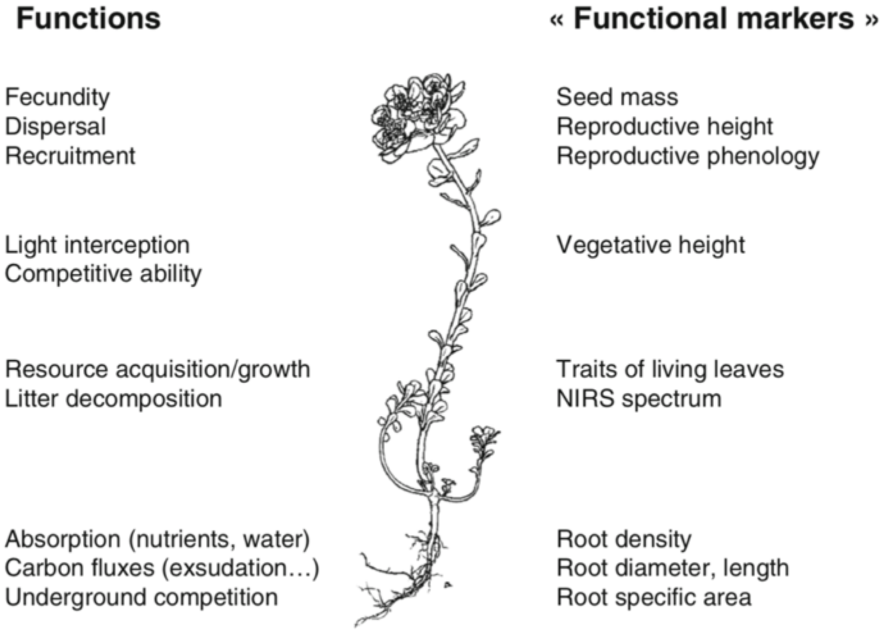


Figure 1. Examples of plant functions and functional traits. Hand drawing of *Euphorbia helioscopia* by Baptiste Testi (Garnier and Navas 2012).

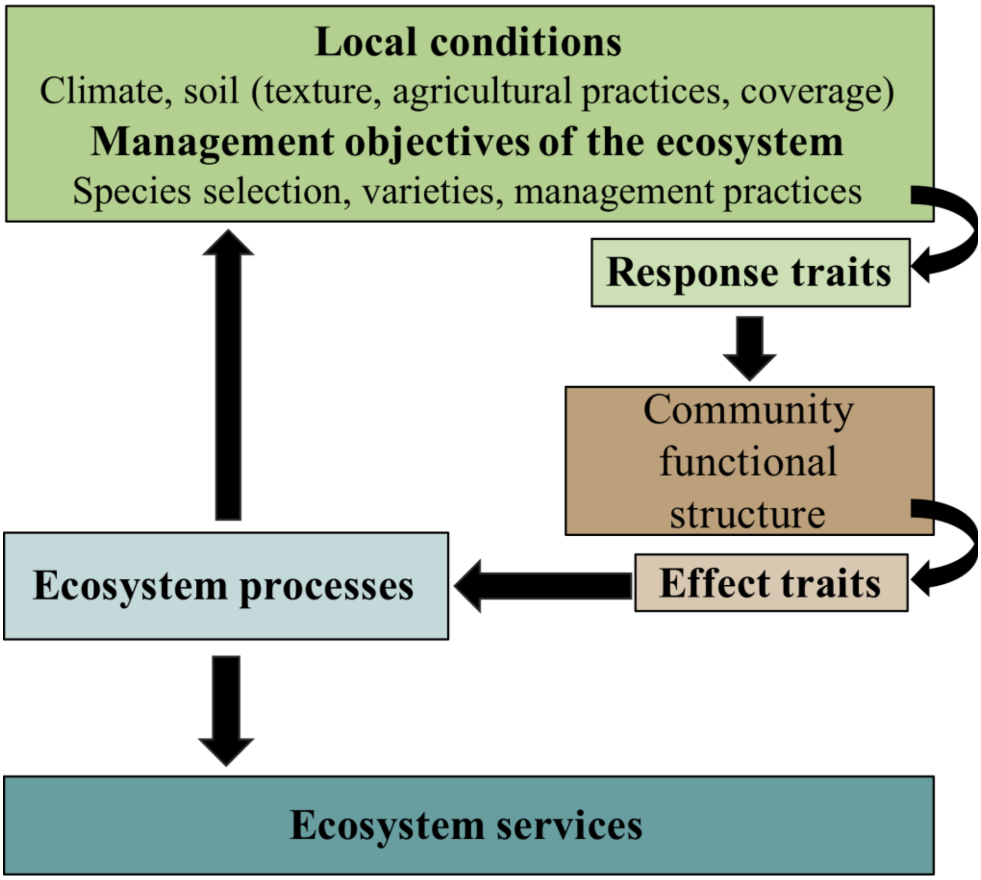
When measuring a trait, its value or modality is called an "attribute" which corresponds to a specific population for a given space and time and is susceptible to change along environmental gradients or through time (Lavorel et al. 2007; Violle et al. 2007). A functional trait is characterised as a functional marker which directly influences the individual performance (vegetative biomass, the reproductive output and the plant survival) and indirectly, the fitness (growth, reproduction and survival) (Mcgill et al. 2006; Lavorel et al. 2007; Violle et al. 2007; Garnier and Navas 2012). The functional trait approach allows to investigate the effects of plants on ecosystem processes and properties without being restricted to a given phyto-geographical territory with a specific species composition and thus be limited in the interpretation and spreading of the results.

Interactions with the environment: response and effect traits

Using the functional trait-based approach allows to predict the adaptive response to environmental variations (notably of soil conditions) and the effects of environmental changes on ecosystem. However, interactions with the environment induce effects on the community structure and ecosystem functioning (Lavorel and Garnier 2002).

Two notions are derived from both habitat filtering and the plant community structure: the response and effect traits (Figure 2) (Keddy 1992; Lavorel and Garnier 2002; Garnier et al. 2016). Indeed, Keddy (1992) developed the concept of environmental filters that would select the traits with specific attributes suitable to persist in the community (response traits). A response trait is thus defined as "a trait whose values respond to variation in environmental conditions, whether these be biotic or abiotic in nature" (Garnier et al. 2016).

Although environmental changes would then select the traits within a community and thus define the community structure, when scaling up to ecosystem processes, the traits in the community impact the ecosystem properties and more especially its functioning and/or structure (effect traits) (Lavorel and Garnier 2002; Garnier and Navas 2012; Garnier et al. 2016). However, the community structure, and thus the effect traits, are influenced by the functional trait diversity within the community and its behaviour toward the environmental factors.



Local conditions

Climate, soil (texture, agricultural practices, coverage)

Management objectives of the ecosystem

Species selection, varieties, management practices

Response traits

Community functional structure

Effect traits

Ecosystem processes

Ecosystem services

Figure 2. Conceptual framework of the effect and response traits in ecosystem dynamics (Faucon 2015).

Functional traits effects on plant-soil processes in ecosystems

Plant-soil processes are driven and influenced by plant functional traits in vegetation communities through their effects on soil properties (i.e. biological, physical and chemical properties) (Lavorel et al. 1997; Cadotte et al. 2011; Mariotte et al. 2017; Faucon et al. 2017). By influencing ecosystem processes, plant functional traits also play a key role in the management of ecosystem services (Figure 3), defined as an ecosystem process presenting benefits to humans, directly or indirectly (Faucon et al. 2017). The effects of functional traits on soil properties (e.g. soil nutrient cycles, soil microbial community, soil structure) need to be fully understood in order to define and achieve the related ecosystem services provided by plant communities (e.g. productivity, soil fertility, soil and water conservation, nutrient cycling).

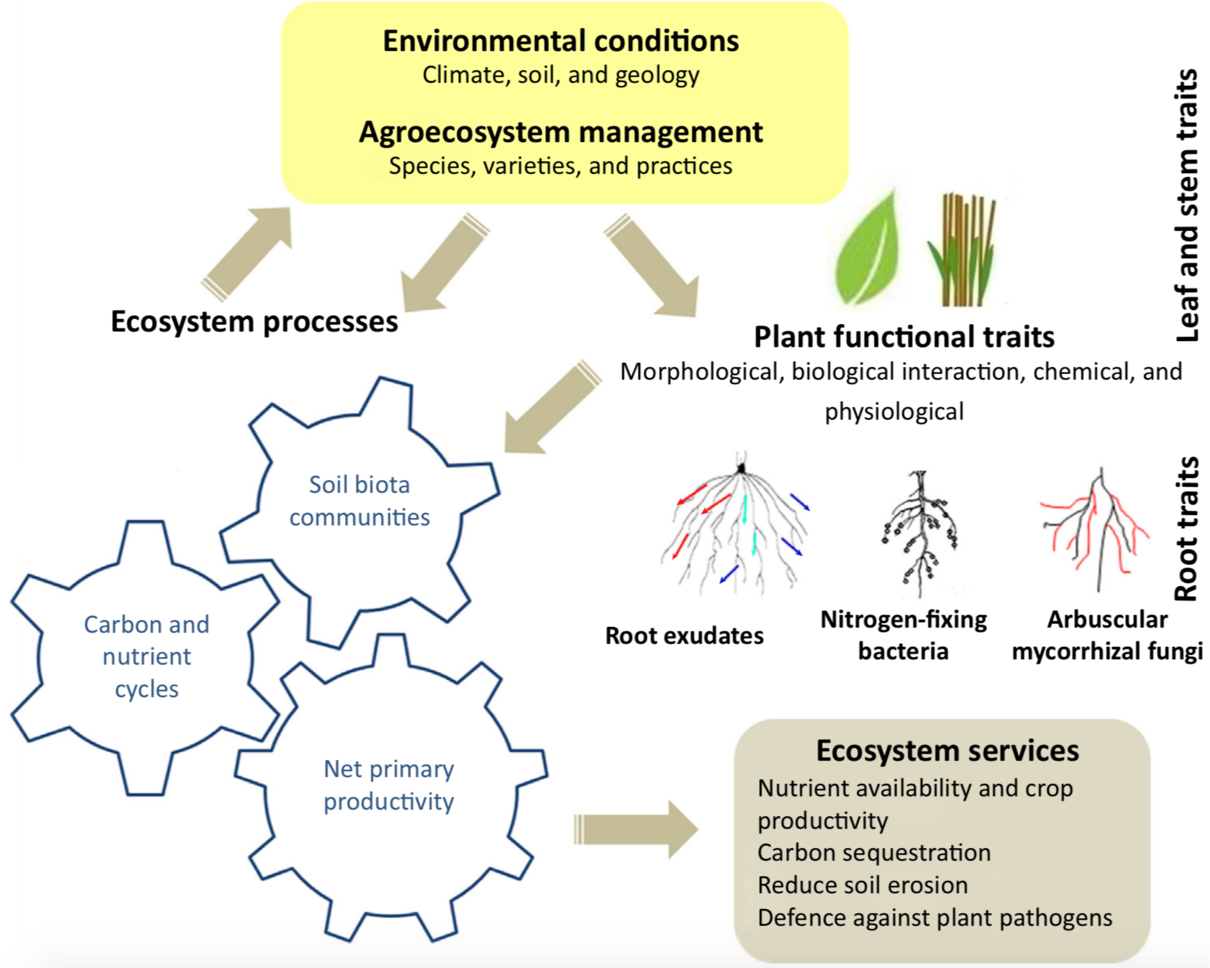


Figure 3. Relationships between functional traits, ecosystem processes and services (Faucon et al. 2017).

Plant trait effects on soil biological and chemical properties have been the most studied effects using the trait-based approach. Regarding nutrient cycling, most of the studies focussed on nitrogen and phosphorus, highlighting plant traits involved in both nutrient acquisition and conservation strategies (e.g. specific leaf area, leaf nitrogen concentration, leaf dry matter, specific root length, root nitrogen concentration, root length density, root area and root hair cylinder volume) (Grime et al. 1997; Eissenstat et al. 2000; Craine et al. 2001; Díaz et al. 2004; Roumet et al. 2006; Kidd et al. 2016; Wendling et al. 2016). Plant trait effects on soil biological properties were also investigated, notably soil microbial activity driven by aboveground and belowground traits (e.g. leaf C:N ratio, leaf dry matter content, root soluble carbon concentration, root concentration of non-soluble carbon, shoot biomass) (Wardle 2002; Wardle et al. 2004; Valé et al. 2005; Deyn et al. 2008; Bardgett et al. 2008; Orwin et al. 2010; de Vries et al. 2012; Grigulis et al. 2013; Schlesinger and Bernhardt 2013; Legay et al. 2014; Bardgett 2017; Sayer et al. 2017). Relationships between plant functional traits and soil physical properties have been the least studied, especially regarding processes involved in soil erosion which were mostly focussed on root traits effects on soil stabilisation. Plant root traits, by furthering microbial activity, influence the stability of soil aggregates and enhance soil structure (Amézketa 1999; Stokes et al. 2014). Aggregate stability represents the percent of stable aggregate left after water immersion for a set period (Le Bissonnais et al. 1996). Soil aggregation is mediated by plant traits and soil biota, as well as their interactions (Rillig et al. 2015). Focussing on plant traits, aggregate stability is enhanced by high root length density, important root biomass, large root diameter and root exudates (Amézketa 1999; Gyssels et al. 2005; Fattet et al. 2011). Root trait effects on the formation and stabilisation of soil aggregates play a critical role in the enhancement of soil structure, carbon storage, resistance to soil erosion and water infiltration (García- Orenes et al. 2012; Rillig et al. 2015). Although research has been done on soil physical properties related notably to soil erosion, work is still needed to fully understand the effects of traits on these processes.

While identifying the relationship between plant traits and soil properties is a major tool to understand the effects of vegetation on ecosystem processes, the understanding of how plant communities presenting a diversity of traits affect these ecosystem processes is the next step to fully characterise vegetation effects. The complexity of plant communities and their effects on ecosystem processes requires the use of the trait-based approach at the community scale to evaluate the effects of functional diversity.

1.1.2. Plant functional traits to community structure: functional diversity

Concepts of functional diversity: dominance or complementarity?

Compared to species diversity, functional diversity was found to explain better the variation observed in ecosystem properties as ecosystem processes are driven by functional traits rather than by species richness (Lavorel et al. 1997; Díaz and Cabido 2001; Díaz et al. 2007a; Cadotte et al. 2011). Functional diversity is defined as “the value, range, and relative abundance of plant functional traits in a given ecosystem” (Tilman 2001b; Díaz et al. 2007a). It characterises the variation in the degree of functions at different spatial and temporal levels of organization from organism to system (Garnier et al. 2016). By impacting and being impacted by environmental conditions, functional diversity has generated an increasing number of studies on the effects of functional diversity on ecosystem processes over the past decades, emphasising contrasting effects on ecosystem functioning. The community constitution (functional diversity) follows two non-exclusive hypotheses (Figure 4) on the relationship between the community structure and ecosystem properties, led by the dominance or by the divergence of the traits of the individuals in the community (Garnier and Navas 2012).

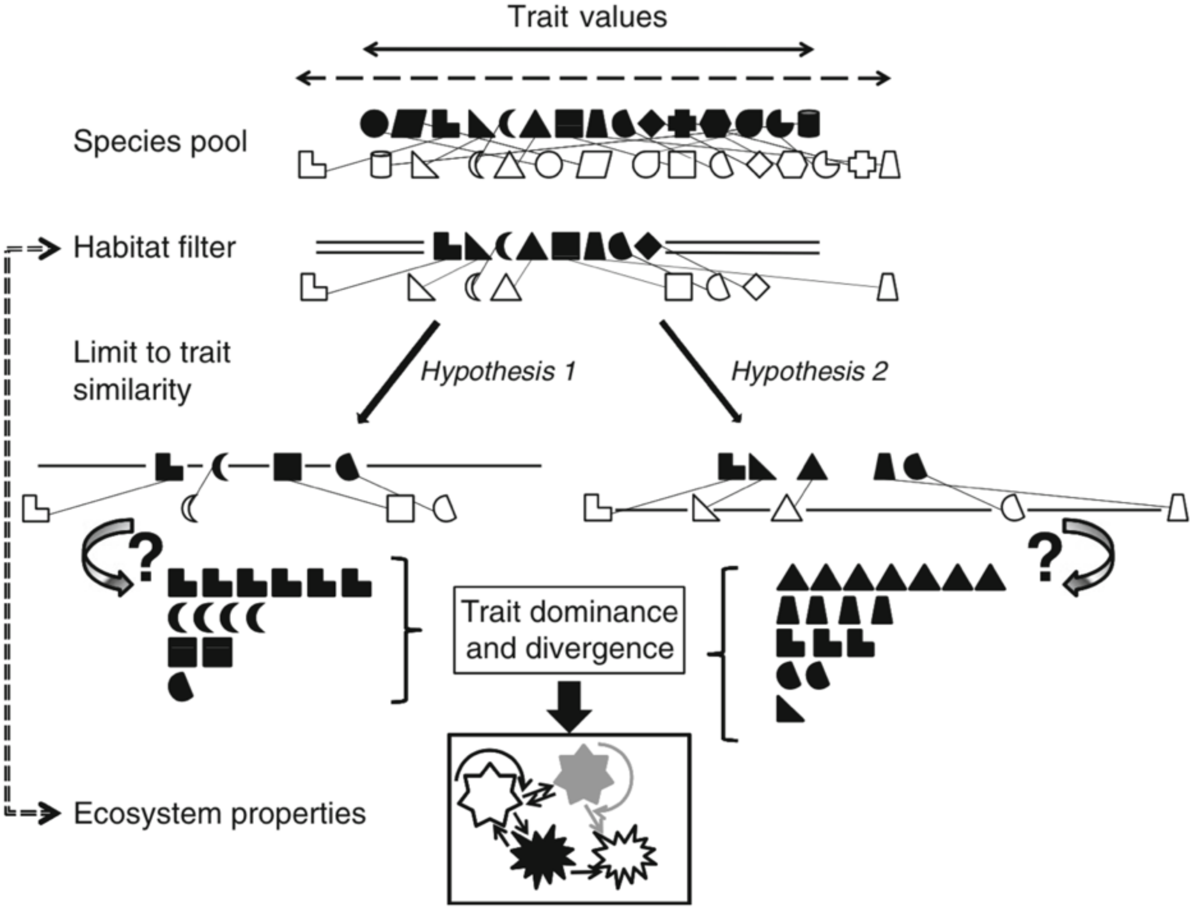


Figure 4. Response and effect framework representing the filtering and selection processes of the community structure and the effects on ecosystem processes, from Garnier and Navas (2012).

The first hypothesis, the "mass-ratio hypothesis" developed by Grime (1998), stipulates that the ecosystem properties (structure and functioning) are driven by the traits of the dominant (i.e. most abundant) species in the community. Following this hypothesis, the ecosystem properties could be represented by the community-weighted mean traits of the dominant species (Díaz et al. 2007b). The community-weighted traits, community-level features, characterise the abundance-weighted traits mean value in the community (Figure 5; Table 1) (Violle et al. 2007).

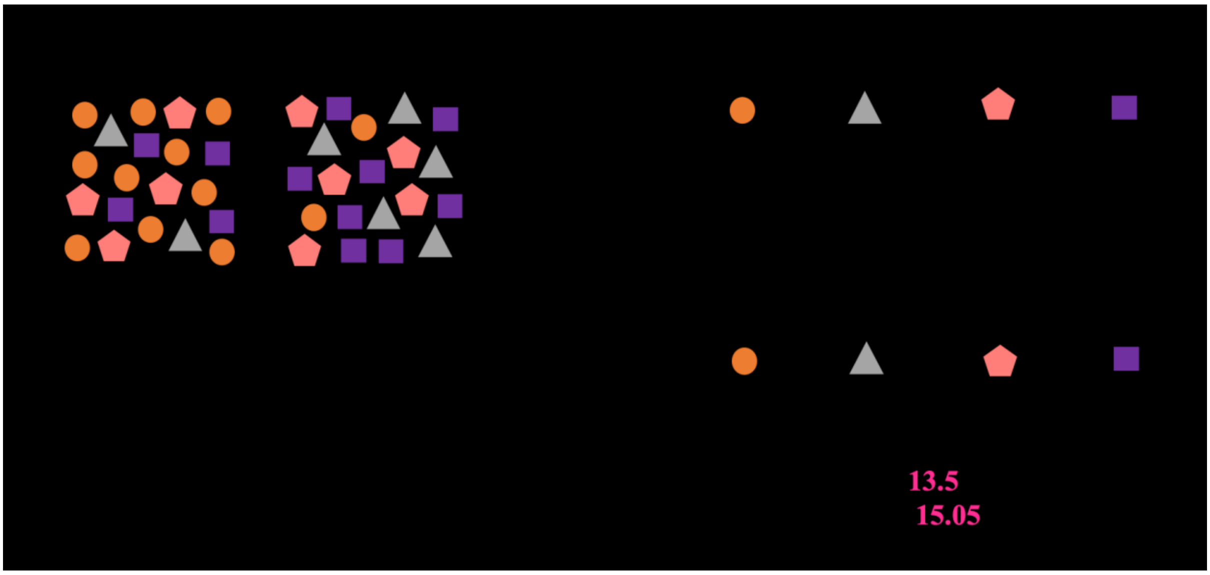


Figure 5. Illustration of the determination of the community-weighted specific leaf area (SLA) for two distinctive communities.

The second hypothesis, the diversity hypothesis (also called "niche complementarity" hypothesis) stipulates that the ecosystem properties are driven by the diversity of traits composing the community, leading to non-additive effects among the species through complementarity effects or facilitation (Tilman et al. 1997a; Petchey 2003; Petchey and Gaston 2006). With an increase in functional diversity in the community there would be a higher dissimilarity in traits and niche differentiation (Cadotte et al. 2011), which would lead to a more complete use of the resources (Loreau and Hector 2001; Petchey and Gaston 2006; Cadotte 2017). The ecosystem properties would then be represented by functional diversity indices (Table 1), notably the functional divergence ("degree of overlap in trait values within the community") (Rao 1982; Mason et al. 2003, 2005; Botta-Dukát 2005; Violle et al. 2007; Díaz et al. 2007b; Villéger et al. 2008; Laliberté and Legendre 2010). However, these two hypotheses are not mutually exclusive and can simultaneously influence the ecosystem properties (Díaz et al. 2007b; Garnier et al. 2016).

Table 1. List of the functional diversity indices (inspired from Mouchet et al. (2010)).

Index name		Definition	Description	Formula	Dimension	Hypothesis
Community-weighted trait (Violle et al. 2007; Díaz et al. 2007b)	CWT	Mean trait value in the community	Sum of the abundance-weighted trait values	$CWT_i = \sum_{k=1}^{N} A_{k,i}\, T_{k,i}$	Uni-dimensional	Mass-ratio
Functional variance (Mason et al. 2003; Botta-Dukát 2005)	FDvar	Variance of the trait values of the species in the community	Variance of the log-transformed abundance-weighted trait values	$FDvar = \frac{2}{\pi}\, arctan\left[5 \sum_{i=1}^{N}\left[\left(\ln T_{k,i} - \overline{\ln x}\right)^2 A_{k,i}\right]\right]$	Uni-dimensional	Diversity
Functional richness (Villéger et al. 2008)	FRic	Functional space volume occupied by the community	Convex hull volume: volume filled in the dimensional space by the community	Quickhull algorithm (Barber)	Multi-dimensional	Diversity
Functional divergence (Villéger et al. 2008)	FDiv	Distance between high abundant species and the centre of the functional space	Species deviance from the mean distance to the centre of gravity weighted by relative abundance	$FDiv = \frac{\Delta d + \overline{dG}}{\Delta \lvert d \rvert + dG}$	Multi-dimensional	Diversity
Functional evenness (Villéger et al. 2008)	FEve	Degree of regularity abundance-weighted traits are displayed within the multidimensional functional space	Sum of MST branch length weighted by relative abundance	$FEve = \frac{\sum_{i=1}^{S-1} \min\left(PEW_i\, , \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$	Multi-dimensional	Diversity
Rao's quadratic entropy (Rao 1982; Botta-Dukát 2005)	RaoQ FDQ	Index of functional dissimilarity of the trait in the community	Sum of pairwise distances between species weighted by relative abundance	$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij}\, p_i\, p_j$	Multi-dimensional	Diversity
Functional dispersion (Laliberté and Legendre 2010)	FDis	Mean distance to the centre of the multidimensional functional space	Ratio between the sum of abundance-weighted mean distances to the centroid and the sum of species abundance	$FDis = \frac{\sum A_{k,i}\, z_k}{\sum A_{k,i}}$	Multi-dimensional	Diversity

N: the number of species in the community i. $A_{k,i:}$ the relative abundance of the species k in the community i. Tk,i the trait value of the species k in the community i. ln x: the abundance-weighted logarithmic mean of the trait value of the species k in the community i. Δd: sum of abundance-weighted deviances. dG: mean distance to the centre of gravity. Δ|d|: absolute abundance-weighted deviances from the centre of gravity. PEW: partial weighted evenness. S: the total species richness. dij: dissimilarity between species (or functional unit) i and j. pi: relative abundance of species i. pj: relative abundance of species j. zk: the distance of species k to the weighted centroid c.

Impacts of functional diversity on plant-soil processes in ecosystems

The relationships between functional diversity and ecosystem functioning have been studied for decades – understanding if they were driven by dominant species composing the community or to non-additive effects among the species – to evaluate the effects of species loss on ecosystem processes and properties (Naeem et al. 1994; Lavorel et al. 1997; Grime 1998; Lavorel and Garnier 2002; Díaz et al. 2007b; Song et al. 2014; Faucon et al. 2017; Cadotte 2017). Through the years, numerous studies have tested the dominance and the complementarity hypotheses, by incorporating both hypotheses but also by only considering one, on various plant-soil ecosystem processes such as biomass net productivity, biochemical cycle components (e.g. litter decomposition, soil carbon storage, nutrients cycle, dry matter digestibility) or soil water content (Tilman et al. 1997a, 2014; Loreau and Hector 2001; Cardinale et al. 2007; Cortez et al. 2007; Díaz et al. 2007b; Mouillot et al. 2011; Mueller et al. 2013; Ebeling et al. 2014; Garnier et al. 2016; Mariotte et al. 2017; Faucon et al. 2017; Cadotte 2017). Contradictory relationships between functional diversity and the studied ecosystem processes have been found, sometimes finding a dominant effect of the traits on the process or a complementary effect, or both. Moreover, different responses are also observed on a temporal scale, showing settling and growing complementarity effects on ecosystem processes through time (Cardinale et al. 2007; Isbell et al. 2018).

While stronger supports of the dominance hypothesis on the previously cited processes are emphasised, positive effects of functional diversity through traits' complementarity are also found (Lavorel 2013; Garnier et al. 2016). The effects of functional diversity on ecosystem processes have been a lot focussed on plant biomass productivity – as it represents a simple feature to measure which expresses ecosystem functioning – and showed that both mechanisms can positively drive biomass productivity (Loreau and Hector 2001; Tilman 2001a; Mokany et al. 2008; Klumpp and Soussana 2009; Zuo et al. 2016a; Cadotte 2017; Xu et al. 2018). However, functional diversity can also negatively affect the biomass productivity (Mokany et al. 2008; Xu et al. 2018). Considering other processes such as carbon and nutrient cycling, positive effects of functional diversity were found on carbon sequestration and nitrogen accumulation (Fornara and Tilman 2008; Klumpp and Soussana 2009; Lange et al. 2015) as well as a combined effect of dominance and complementarity on the nitrogen use efficiency in herbaceous semi-arid grassland (Zuo et al. 2016b). Studies also focussed on soil biology, showing a positive effect of functional diversity on soil microbial community (Lange et al.

2015). Regarding soil fungal diversity, a strong positive effect of dominant plant community-weighted traits were found in grassland, while indirect negative effects of functional diversity on fungal diversity were highlighted (Zuo et al. 2016a).

A number of soil-plant processes have been studied in order to understand the effects of functional diversity and controverting results were found. However, there are numerous other processes involving plant-soil interactions for which the effects of functional diversity are little known, especially processes related to soil physical properties. Focussing future research on functional diversity effects on physical soil processes would allow to widen the range of studied processes and deepen the knowledge of how functional diversity affects soil biogeochemical processes. For instance, water soil erosion is a global process driving soil degradation and leading to major economic and environmental damages. Plant communities are a key feature to control runoff and soil erosion, but the identification of plant functional trait effects is lacking data for a number of related regulating processes (i.e. hydraulic resistance, sediment retention). How functional traits and diversity impact these regulating processes could lead to the determination of useful tools to control and reduce concentrated runoff and soil erosion.

1.2. Plant trait effects on soil water erosion

1.2.1. Soil erosion processes

Soil erosion by water, main process leading to soil degradation, is composed of sub-processes impacted by functional traits in plant communities. It is a natural and frequently observed hazard in tropical, Mediterranean and temperate areas and is accentuated by anthropogenic factors, especially by agricultural practices. Soil degradation by water erosion leads to long-term effects on soil fertility and productivity, but also to wider environmental damages through runoff and sediment transport such as eutrophication, muddy floods and pollutant leaching in water bodies (Le Bissonnais et al. 2004; Morgan 2005; Boardman et al. 2006; Rekolainen et al. 2006; Evrard et al. 2010; Verstraeten et al., 2006).

Soil erosion by water is composed of two steps: soil particle detachment and sediment transport (Morgan 2005; Boardman and Poesen 2006). In the absence of concentrated flows, the soil detachment rates are mainly influenced by rainsplash: the raindrops falling on the soil surface will detach the soil particles due to their kinetic energy (Leguédois 2003). Runoff will also play a role in the detachment process by ripping the particles of the soil.

Soil erosion is a general process which refers to specific mechanisms (Figure 6):

(1) overland flow, characterised as uniform superficial shallow flow with an infinite width, is the first form of surface runoff that would transport soil particles and are defined as interrill erosion. Interrill erosion is often caused by soil degradation processes (i.e. soil compaction, surface sealing and crusting) which generate runoff (Morgan 2005; Boardman and Poesen 2006).

(2) The flows then concentrate and form small rills in which the velocity and the transport capacity increase. These flows are defined under the terms “rill erosion” or “gully erosion” depending on the dimensions of the channels formed, and also represent a powerful

erosive agent due to high velocities and flow concentration (Poesen 1989; Poesen et al. 2003; Morgan 2005; Boardman and Poesen 2006).

(3) The last mechanism is characterised as “torrential erosion”, with a high concentration of sediments forming mud flows and is mainly encountered in mountainous regions (Poesen and Hooke 1997; Descroix and Mathys 2003; Morgan 2005).

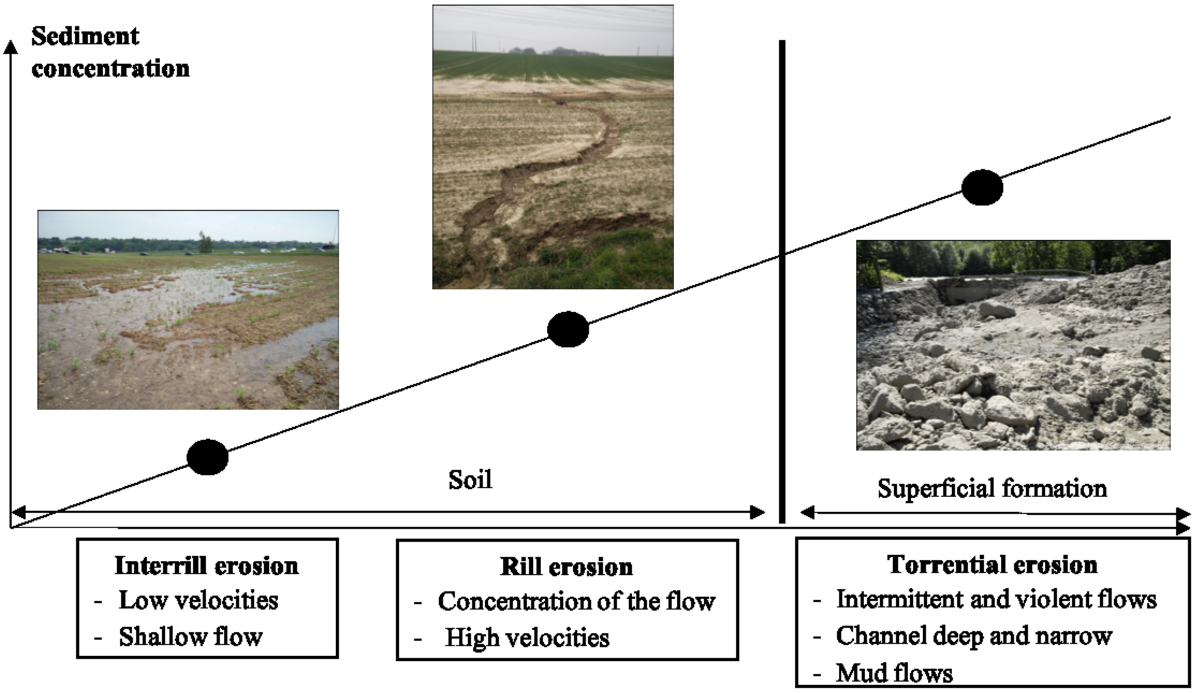


Figure 6. The different erosion types involved in sediment transport in soil erosion processes. Photos: Léa Kervroëdan (both photos on the left) and IRMA/Gominet (2010) (photo on the right).

The water erosion rate of a soil depends on the combination of a number of initiating factors (Wischmeier and Smith 1978; Dunne et al. 1991; Haan et al. 1994; Agassi 1995; Le Bissonnais et al. 1996, 2001; Morgan 2005; Boardman and Poesen 2006; Durán Zuazo and Rodríguez Pleguezuelo 2008), being:

- the soil surface conditions, influenced by the soil characteristics such as the soil moisture, texture (silt and fine sand), aggregate stability, porosity and organic matter content. These parameters play an important role on the soil erodibility (i.e. resistance of the soil to the erosion steps: detachment and transport) and especially on the crusting and surface sealing of the soil, which lead to a decrease of the infiltration capacity and trigger runoff generation.

- the topography at both field and landscape scales, by the length and the steepness of the slopes and the presence of water concentration bottom lines (i.e. thalwegs, ditches) which will influence the runoff concentration and intensity as well as the rate of erosion.

- the land use and cover, especially due to the impact of the intensity of agricultural practices on the soil. The absence of vegetation covering the soil during erosive rainfall episodes (e.g. winter in oceanic climates) due to monocultures, as well as tillage or overgrazing are factors furthering the soil erosion rates.

- the climate, through the effects of rainfalls, with the detaching action of the raindrops on the soil surface and the water input into the runoff, as well as their seasonality (depending on the vegetation growth form). Both prolonged low intensity (e.g. in oceanic climates) and short intense (e.g. Mediterranean climates) rainfall events will lead to runoff and erosion, by saturation of the soil profile or by overcoming the infiltration capacity of the top soil layer (Hortonian runoff), respectively.

From all the initiating factors, only the land use and cover can be manipulated in order to reduce soil erosion rates. For example, in cultivated areas with annual crops, a tillage reduction would reduce soil erosion rates (Knapen et al. 2007). The presence of vegetation provides greater services towards runoff and soil erosion dynamics (Figure 7). Both the aboveground and belowground parts of the vegetation provide protection against the different sub-processes involved in soil erosion (i.e. soil detachment, transport) by limiting the impacts of raindrops and furthering the resistance and mechanical strength of the soil (Haan et al. 1994; Morgan and Rickson 1995; Gyssels et al. 2005).

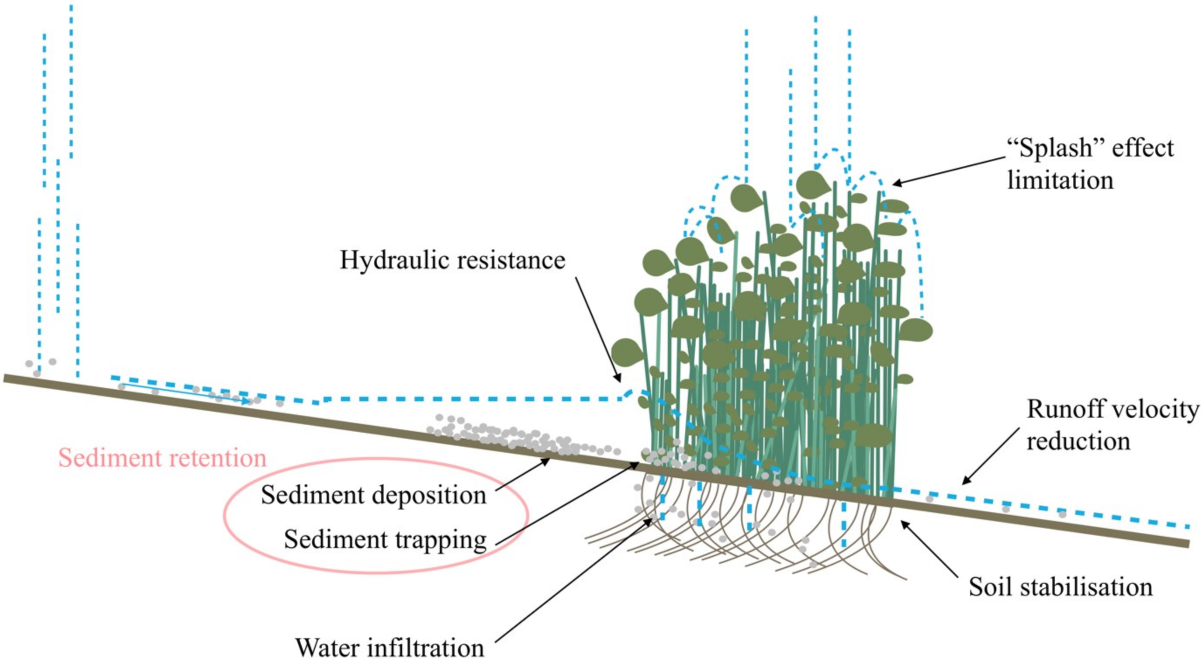


Figure 7. Vegetation effects on runoff and soil erosion processes.

1.2.2. Effects of plant traits on runoff pre-generation processes

Rainfall interception

The first direct effect of the vegetation on soil erosion is the interception of rainfall by the aboveground biomass. This interception leads to the reduction of the "splash" erosion, by absorbing the kinetic energy of the raindrops which limit the soil detachment and particles transport (Haan et al. 1994; Styczen and Morgan 1995; Bochet et al. 2002; Morgan 2004; Boardman and Poesen 2006). The intercepted drops are either (1) collected into the leaves and stems and will be later evaporated or (2) flow along the stems (stemflow) or the leaves (leaf drainage) and get to the ground. Due to the interception of the water, the vegetation also limits soil crusting and sealing, which improves the infiltration capacity underneath the vegetation. However, the plant efficiency to raindrop interception is highly dependent on the vegetation density, morphology and height, as well as the presence of litter (Bochet et al. 2002; Morgan 2004). Grasses and small shrubs are found to be the most efficient to intercept raindrops, due to their leaf and stem densities and low height. Morgan (2004) highlighted that positive effects of vegetation on splash erosion are found for vegetation of 1m height or less. Vegetation higher than 1m might trigger negative effects on the splash erosion by an increase of drops' kinetic energy from leaf drainage.

Infiltration

Water infiltration, one of the main processes influencing the runoff generation, depends on soil properties and is improved by the presence of vegetation. The presence of roots increases the soil permeability by the creation of macropores, enhancing the water flow within the soil and the infiltration capacity (Styczen and Morgan 1995; Gyssels et al. 2005; Dosskey et al. 2010; Ghestem et al. 2011). Dense fibrous root systems, with a root diameter smaller than 1mm, are positively correlated with the soil permeability (Li et al. 1992). The effects of the root channel diameter and the root channel area on the efficiency of the infiltration rates have also been emphasised (Wu et al. 2017).

The infiltration rates associated to the vegetation depends on the type (i.e. grass, shrub, tree) and the species present (Dunne et al. 1991; Christen and Dalgaard 2013; Clark and Zipper 2016). While grasses create a higher number of flow paths in the near-surface soil (<10 cm); tree root systems reach deeper layers of the soil and create a high flow-path continuity in the soil sub-surface (Clark and Zipper 2016). Concerning the effect of herbaceous plants, the infiltration capacity is influenced by the root biomass, the root weight density (i.e. the weight of living roots divided by the soil sample volume, expressed in $kg.m^{-3}$), the root length density and the root surface area density (Li et al. 2013; Liu et al. 2016; Wu et al. 2016).

Once runoff has been generated, the infiltration is also furthered by the hydraulic roughness of the vegetation, especially by the slowing down of the flow and the creation of a backwater area. Indeed, the cumulated infiltration is increased by the longer contact between the water and the soil surface in the backwater area (Dunne et al. 1991; Gilley et al. 2000; Dosskey et al. 2010).

1.2.3. Effects of plant traits on rill and inter-rill erosions

Once runoff is generated, a number of sub-processes amplified through rill and inter-rill erosion, linked mostly with the runoff velocity, will trigger an increase of the soil erosion.

Soil stabilisation and resistance

Soil erodibility is dependant of a number of soil properties such as the organic matter content, texture, aggregate stability and shear strength all being influenced by the hydrological and mechanical effects of plant roots (Gyssels et al. 2005; De Baets et al. 2006; Stokes 2007; Durán Zuazo and Rodríguez Pleguezuelo 2008; Stokes et al. 2014). The structural stability and erosion resistance of the soil are enhanced by the roots, especially by the presence of monocotyledonous plants which comprise fine dense root system (Gyssels et al. 2005; De Baets et al. 2006; Burylo et al. 2012b). The root density, length density and root tensile strength (i.e. strength of the root against a tension) were found to positively influence the soil erosion resistance (De Baets et al. 2006; Burylo et al. 2012b). Soil erosion resistance is improved by the presence of roots which induce (1) mechanical effects affecting soil shear strength (or soil cohesion) and (2) physicochemical effects impacting soil aggregate stability (Styczen and Morgan 1995; Gyssels et al. 2005; Stokes et al. 2014).

Soil shear strength represent the frictional resistance of the soil particles under a sliding energy forcing them to slide against one another or move out of interlocking positions (Morgan 2005). The mechanical effects of roots on soil shear strength provide a protection against shearing forces (i.e. gravity, moving fluids and mechanical loads) by binding the soil particles and increase soil cohesion (Morgan 2005; Gyssels et al. 2005). The enhancement of the soil shear strength results on the soil-root matrix, which is the best trade-off between the compression strength of the soil and the tension strength of the roots (Simon and Collison 2002).

The aggregate stability is notably increased by the presence of monocotyledons species, especially grasses, due to their large root biomass with exudates that bind fine particles into stable aggregates (Amézketa 1999; Gyssels et al. 2005). The exudates produced by the roots stimulate the microbial activity in the soil that will increase aggregate stability by physico-chemical activities (i.e. production of extracellular polysaccharides and hydrophobic substances) (Stokes et al. 2014).

Thus, through a number of characteristics, the roots reduce the soil sensitivity to rill and inter-rill erosion mainly by reinforcing the soil against the shear action of the runoff flows and stabilising the soil aggregates (Gyssels et al. 2005).

Hydraulic resistance: effects on the hydraulic roughness, flow velocity and sediment retention

One of the most important effects of vegetation on the flow transport capacity and particle detachment rate, both influenced by the flow velocity and energy, is the hydraulic roughness created by the plants in contact with the flow (Haan et al. 1994; Styczen and Morgan 1995; Järvelä 2002; Akram et al. 2014; Cantalice et al. 2015; Cao et al. 2015). The hydraulic roughness is defined as the frictional resistance that the contact of vegetation creates on a water flow. The presence of vegetation has positive impacts on hydraulic roughness, as it reduces flow velocity and increases backwater depth (Hussein et al. 2007; Akram et al. 2014; Cantalice et al. 2015). Due to the linear relationship between backwater depth and sediment transport capacity, vegetation also decreases the later by furthering sediment retention (Dabney et al. 1995; Meyer et al. 1995; Hussein et al. 2007).

Most of the studies focussed on trait effects on sediment retention rather than hydraulic roughness, and both stem and leaf traits have been identified for the past decades as efficient for triggering sediment retention. Considering the leaf traits, the leaf density, the leaf area and specific leaf area are involved in sediment retention (Graff et al. 2005; Burylo et al. 2012a; Lambrechts et al. 2014). The stem density and diameter are two of the main traits influencing sediment retention (Hayes et al. 1978; Temple 1982; Meyer et al. 1995; Bochet et al. 2000; Isselin-Nondedeu and Bédécarrats 2007; Morgan and Duzant 2008; Mekonnen et al. 2016).

The efficiency of the stems on runoff depends on the stem density, the stem diameter, the slope and the type of soil. Indeed, on 20% slopes of silty soils, vegetation with a stem density of 7500 stems.m^{-2} would reduce the flow velocity by 90.6%; while on a 10% slope 2500 stems.m^{-2} would reduce the velocity by 91.9% compared to bare soil (Morgan 2004).

However, negative effects of the vegetation can also be found depending on the vegetation density, type or arrangement (Styczen and Morgan 1995; Morgan 2004, 2005; Bautista et al. 2007; Erktan et al. 2013). Morgan (2004) and Styczen and Morgan (1995) highlighted the importance of the vegetation uniformity and density in the mitigation of soil erosion related to hydraulic roughness, as a localised increase of the runoff velocity (and associated detachment and transport capacities) can be found within heterogeneous and scattered vegetation. Moreover, Erktan et al. (2013) found that the high presence of shrubs and trees would create preferential flow paths, leading to a decrease of the vegetation efficiency against soil erosion. However, the hydraulic roughness of dense and homogeneous vegetation leads to a decrease of the flow velocity, with an increase of the infiltration rates by the increase of the residence time of the water, as well as the sediment retention by the reduction of the transport capacity (Dunne et al. 1991; Styczen and Morgan 1995; Dosskey et al. 2010).

1.3. The necessity to develop trait-based ecological engineering from herbaceous vegetation to control soil erosion

1.3.1. State of art of ecological engineering for soil erosion mitigation

Soil erosion can be mitigated in agricultural catchments by (1) increasing the soil cover by vegetation (i.e. growing cover crops during winter which will also increase crop residues quantity on the soil surface), (2) changing the agricultural practices (reduced tillage or no tillage) and (3) maintaining crop diversity at the watershed scale (Van Oost and Govers 2006; Knapen et al. 2007). An additional solution to reduce inter-rill, rill and ephemeral gully erosion is the use of vegetation-based measures, following the principle of ecological engineering. Mitsch and Jørgensen (2003) defined ecological engineering as “the design of sustainable ecosystems that integrate human society with its natural environment for the benefit of both”. It characterises the restoration of disturbed ecosystems, as well as the creation of new ones, that would generate a sustainable value, both ecological and economical. Regarding soil erosion mitigation in loamy agricultural catchments, planting vegetative buffers and/or barriers (i.e. fascines, herbaceous hedges) across the thalweg has already been proven to efficiently reduce the on and off-site impacts of soil erosion (Dabney et al. 1995; Van Dijk et al. 1996; Le Bissonnais et al. 2004; Richet et al. 2017; Frankl et al. 2018). Within the vegetative barriers used to control runoff and soil erosion, two types are highlighted: (1) objects mainly composed of dead materials and (2) objects composed of alive materials possessing a number of functional traits limiting runoff and soil erosion.

Vegetative objects composed of dead materials

Fascines are thin linear vegetative barriers made of dead or alive wooden posts holding bunches of stems (Figure 8) and have been used for centuries in riverbank stabilisation as well as for mountainous torrential erosion mitigation (Rey 2005; Evette et al. 2009). It is only recently that fascines have been used to control runoff and soil erosion in agricultural catchments (Ouvry et al. 2012; Degré et al. 2013; Richet et al. 2017; Frankl et al. 2018). The fascines are placed across a concentrated flow path (within or on the field border or across a thalweg) to mitigate rill and gully erosion, by furthering the reduction of runoff velocity and sediment deposition by increasing the hydraulic roughness. Ouvry et al. (2012) highlighted sediment retention efficiencies of fascines varying from 77 to 99%; with the highest trapping efficiencies of 90% to 99% being for particles larger than 125µm and the lowest ones (77 to 90%) for finer particles. Frankl et al. (2018) also showed the positive effects of fascines on gully length reduction.

However, through time and depending on the design and maintenance of the fascines, their effects change due to the deterioration of the bundles or the changes in the gully and rill pathways (Richet et al. 2017; Frankl et al. 2018). Fascines, being static objects, become inefficient when the sediment deposition area upstream gets higher through time. In addition to the regular bundle changing, either the fascines will have to be re-installed after a few years to avoid being buried by the sediments, or the deposited area would have to be excavated regularly, leading to additional costs. Vegetative objects composed of living vegetation would limit those costs and maintenance due to the sustainability of the plant community.

Figure 8. Fascine implanted in the field across the thalweg (Richet et al. 2017).

Vegetative objects composed of living materials

The effects of the functional traits in herbaceous communities composing vegetative barriers and buffers have been found to efficiently influence runoff and soil erosion (Temple 1982; Haan et al. 1994; Meyer et al. 1995; Van Dijk et al. 1996; Burylo et al. 2012a). There are two main types of these vegetative objects: vegetative filter strips (as vegetative buffer) and herbaceous hedges (as vegetative barrier), each being efficient for different concentration of erosional episodes.

- **Vegetative filter strips**

Vegetative filter strips (also buffer strips, grass strips, retention/detention basin, riparian buffer or grass waterways) are wide bands (> 5m width) of homogeneous vegetation (Figure 9), usually placed (1) along the field contours, (2) downslope a field close to a waterbody in order to protect it from nutrients, pollutants and sediment contaminations or (3) within a field, along the thalweg in order to limit the rill and gully formation (Dillaha et al. 1986, 1989; Haan et al. 1994; Van Dijk et al. 1996; Le Bissonnais et al. 2004).

Figure 9. Vegetative filter strips along: A –a stream; B - the thalweg's bottom line ; C – an agricultural field and D – a ditch (Billy et al. 2017).

They are constituted of perennial species, usually grasses due to their fast establishment capacity, their deep and fine root systems and a dense and homogeneous cover. The purpose of a grass strip is too limit runoff and sediment loss by enhancing infiltration and sedimentation, (Dillaha et al. 1989; Haan et al. 1994; Van Dijk et al. 1996). The efficiency of the strips depends on five parameters: (1) the strip width, (2) the vegetation density and height, (3) the sediment concentration in the flow, (4) the flow velocity and (5) the level of the vegetation submergence

(Temple 1982; Dillaha et al. 1989; Haan et al. 1994; Van Dijk et al. 1996). However, under concentrated flows, grass strips are found inefficient both for trapping pollutants, nutrients and sediments and for reducing the runoff flow velocity (Dillaha et al. 1989; Meyer et al. 1995; Van Dijk et al. 1996). In the case of rill and gully erosion, vegetative barriers are found efficient against concentrated flows and should be preferred to grass strips (Meyer et al. 1995; Richet et al. 2017; Frankl et al. 2018).

- Herbaceous hedges

Herbaceous hedges (also grass hedges, stiff-grass hedges) are narrow vegetative barriers (from 0.5m) made with tall, dense, erect and stiff perennial vegetation placed across concentrated flow paths (Figure 10) (Dabney et al. 1995; Meyer et al. 1995). They have been used for decades in various areas such as in the United States, tropical or semi-arid areas (Dabney et al. 1995; Meyer et al. 1995; Gilley et al. 2000; Wu et al. 2010; Xiao et al. 2012; Mekonnen et al. 2016).

These hedges are used to mitigate not only interrill erosion but also concentrated erosion processes, by retarding the flow velocity and furthering sediment retention. The stiffness of the vegetation provides a better reduction of erosion rates than buffer strips, as the vegetation does not get submerged nor bend under the flow (Dillaha et al. 1989; Meyer et al. 1995). Herbaceous hedges are also more sustainable than fascines due to (1) the limitation of changes in gully and rill pathways by the constant growth of the hedge vegetation on the deposited sediments and (2) the limited maintenance needed through time, and thus maintenance costs, as only a cutting would be needed every two/three years to limit the development of tree and shrub species within the hedge.

Herbaceous hedges are thus a great compromise between grass strips and fascines, corresponding to a small implementation area with a high efficiency in sediment retention and runoff control in concentrated flow paths. In order to design efficient hedges, it is important to identify the aboveground plant traits influencing the hydraulic roughness and sediment retention to select the most suitable plant species.

Figure 10. Herbaceous hedge of *Miscanthus sacchariflorus* (AREAS).

1.3.2. Plant functional traits: a tool in ecological engineering for soil erosion control

Trait effects on the hydraulic roughness: flow velocity and sediment retention

In order to create efficient herbaceous hedges to reduce runoff and soil erosion, a good understanding of the relationship between the plant functional traits with the hydraulic roughness is needed, being the main reducing process at the vegetation patch scale (Styczen and Morgan 1995). However, most of the studies about vegetation impacts on soil erosion focussed on the impacts of aboveground functional traits on sediment retention. The hydraulic roughness being the main process inducing sediment retention once the soil is at saturation, the functional traits influencing sediment retention should directly influence the hydraulic roughness.

Both stem and leaf traits are emphasised as impacting sediment retention and thus, hydraulic roughness: leaf density, leaf area and specific leaf area, as well as stem diameter and density represent the main traits involved in sediment retention (Hayes et al. 1978; Temple 1982; Meyer et al. 1995; Bochet et al. 2000; Graff et al. 2005; Isselin-Nondedeu and Bédécarrats 2007; Morgan and Duzant 2008; Burylo et al. 2012a; Lambrechts et al. 2014; Mekonnen et al. 2016). The stem stiffness have also been found to induce sediment retention (Meyer et al. 1995), although contrasting results are found in the literature (Burylo et al. 2012a). These contrasting results could be explained by the differences in the discharges used, as with higher discharges (from 11 to 43.7 $l.s^{-1}.m^{-1}$) an effect of the stem stiffness was found compared to smaller discharges (1.6 $l.s^{-1}.m^{-1}$). Moreover, a changing response of the leaf structure, stem density, diameter and stiffness on hydraulic roughness and sediment retention was also found depending on the discharges. At low discharges, the hydraulic roughness was dependent on the vegetation density (Temple et al. 1987; Van Dijk et al. 1996); while at higher discharges, with flow depths higher than the deflecting vegetation height, the hydraulic roughness was found primarily influenced by the stem density, diameter and stiffness, and less by the leaf structure (Temple et al. 1987; Meyer et al. 1995). However, due to the differences in hydraulic and erosion processes, as well as in the vegetation types, found in temperate phytogeographic territories (i.e. north-west Europe) compared to the territories in the cited studies (Mediterranean territories, mountainous, semi-arid ecosystems, etc.), the traits influencing hydraulic roughness and sediment retention might be different. Thus, there is still work needed to identify the traits specific to the indigenous vegetation and directly influencing hydraulic roughness and sediment retention in temperate oceanic climates.

The traits showing significant effects on sediment retention referenced above combined negatively associated traits: (1) leaf area and density and (2) stem diameter and density. This stresses that using a combination of contrasting and efficient traits would have a better effect on hydraulic roughness and sediment retention. Understanding the effects of trait complementarity and functional diversity on hydraulic roughness and sediment retention could allow to create efficient herbaceous hedges to reduce runoff and soil erosion.

Complementarity effects on hydraulic roughness and sediment retention

As previously stated, some traits impacting the hydraulic roughness and sediment retention are found negatively associated (i.e. stem density and diameter; and leaf area and density), which suggests that using communities comprising contrasting traits could reach better effects on the hydraulic roughness and sediment retention. The effects of multi-species communities on soil erosion processes have been studied for decades, although the analysis was most often based on taxonomical characterisation of the communities (Meyer et al. 1995; Fullen 1998; Bautista et al. 2007; Turnbull et al. 2008; Pohl et al. 2009; Martin et al. 2010; Zhang et al. 2015; Berendse et al. 2015; Hou et al. 2016). A number of these studies focussed on the effects of non-herbaceous plant roots on soil stabilisation and vegetation patch pattern impact on erosion rates showing that an increase of diversity led to a better soil resistance and stabilisation (Gyssels et al. 2005; Balvanera et al. 2006), as well as an increase of sediment retention in heterogeneous vegetation pattern (Hou et al. 2016).

A number of studies focused on the effects of functional groups, marking a first step into the use of a functional ecology characterisation of the effects on runoff and soil erosion processes. The results showed complementarity effects on runoff, soil erosion and soil aggregation capacity (Pohl et al. 2009; Martin et al. 2010; Zhang et al. 2015).

In order to understand the effects of vegetation on runoff and soil erosion processes using a functional trait-based approach and fully illustrate these effects for multi-specific communities, it is necessary to characterise the effects of functional diversity. Indeed, traits drive the effects of vegetation communities on ecosystem processes, and more especially runoff and soil erosion. The taxonomical approach, by the use of species diversity as an index of diversity, does not consider the functional properties of vegetation on runoff and soil erosion. Functional diversity, by taking into account the aspects of diversity that might impact community structure and functions, was highlighted as a better predictor to characterise the effects of plant diversity on ecosystem processes (Cadotte et al. 2011). Identify the effects of functional diversity on runoff and soil erosion processes would be the key to deepen the knowledge fully understand how plant communities affect these processes.

Functional diversity effects on the hydraulic roughness and sediment retention

Only few studies have focussed on the functional diversity effects on soil erosion, with contentious results (Erktan et al. 2013; Zhu et al. 2015). In semi-arid grassland, the functional divergence explained up to 40% of the variation of the erosion rates, due to a greater niche differentiation within the tested communities (Zhu et al. 2015). However, when focusing on effects of functional type mixtures in Mediterranean mountainous ecosystems, no effect of the functional diversity on sediment retention were found, due to areas of least resistance to the flow created by the individual shrubs and trees (Erktan et al. 2013).

Although the results found for these erosion processes are contentious, using herbaceous species comprising a range of identified efficient traits, could lead to a better understanding of the functional diversity effect types on hydraulic roughness and sediment retention. Research is thus still needed to characterise the effects of functional diversity on runoff and soil erosion processes, and more specifically on the hydraulic roughness and sediment retention.

REFERENCES

Agassi (1995) Soil Erosion, Conservation, and Rehabilitation. CRC Press

Akram S, Yu B, Ghadiri H, et al (2014) The links between water profile, net deposition and erosion in the design and performance of stiff grass hedges. J Hydrol 510:472–479. doi: 10.1016/j.jhydrol.2014.01.001

Amézketa E (1999) Soil Aggregate Stability: A Review. J Sustain Agric 14:83–151. doi: 10.1300/J064v14n02_08

Balvanera P, Pfisterer AB, Buchmann N, et al (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services: Biodiversity and ecosystem functioning/services. Ecol Lett 9:1146–1156. doi: 10.1111/j.1461-0248.2006.00963.x

Bardgett RD (2017) Plant trait-based approaches for interrogating belowground function. Biol Environ Proc R Ir Acad 117B:1–13. doi: 10.3318/bioe.2017.03

Bardgett RD, Freeman C, Ostle NJ (2008) Microbial contributions to climate change through carbon cycle feedbacks. ISME J 2:805–814. doi: 10.1038/ismej.2008.58

Bautista S, Mayor ÁG, Bourakhouadar J, Bellot J (2007) Plant Spatial Pattern Predicts Hillslope Runoff and Erosion in a Semiarid Mediterranean Landscape. Ecosystems 10:987–998. doi: 10.1007/s10021-007-9074-3

Berendse F, van Ruijven J, Jongejans E, Keesstra S (2015) Loss of plant species diversity reduces soil erosion resistance. Ecosystems 18:881–888. doi: 10.1007/s10021-015-9869-6

Billy C, Carluer N, Grimaldi C, et al (2017) Guide d'aide à l'implantation des zones tampons pour l'atténuation des transferts de contaminants d'origine agricole

Boardman J, Poesen J (eds) (2006) Soil Erosion in Europe. John Wiley & Sons, Ltd

Boardman J, Verstraeten G, Bielders C (2006) Muddy Floods. In: Boardman J, Poesen J (eds) Soil Erosion in Europe. John Wiley & Sons, Ltd, pp 743–755

Bochet E, Poesen J, Rubio JL (2002) Influence of plant morphology on splash erosion in a Mediterranean matorral. Z Geomorph N F 46:223–243

Bochet E, Poesen J, Rubio JL (2000) Mound development as an interaction of individual plants with soil, water erosion and sedimentation processes on slopes. Earth Surf Process Landf 25:847–867

Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J Veg Sci 16:533–540

Burylo M, Rey F, Bochet E, Dutoit T (2012a) Plant functional traits and species ability for sediment retention during concentrated flow erosion. Plant Soil 353:135–144. doi: 10.1007/s11104-011-1017-2

Burylo M, Rey F, Mathys N, Dutoit T (2012b) Plant root traits affecting the resistance of soils to concentrated flow erosion. Earth Surf Process Landf 37:1463–1470. doi: 10.1002/esp.3248

Cadotte MW (2017) Functional traits explain ecosystem function through opposing mechanisms. Ecol Lett 20:989–996. doi: 10.1111/ele.12796

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. J Appl Ecol 48:1079–1087. doi: 10.1111/j.1365-2664.2011.02048.x

Calow P (1987) Towards a Definition of Functional Ecology. Funct Ecol 1:57–61. doi: 10.2307/2389358

Cantalice JRB, Melo RO, Silva YJAB, et al (2015) Hydraulic roughness due to submerged, emergent and flexible natural vegetation in a semiarid alluvial channel. J Arid Environ 114:1–7. doi: 10.1016/j.jaridenv.2014.10.012

Cao L, Zhang Y, Lu H, et al (2015) Grass hedge effects on controlling soil loss from concentrated flow: A case study in the red soil region of China. Soil Tillage Res 148:97–105. doi: 10.1016/j.still.2014.12.009

Cardinale BJ, Wright JP, Cadotte MW, et al (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. Proc Natl Acad Sci 104:18123–18128

Christen B, Dalgaard T (2013) Buffers for biomass production in temperate European agriculture: A review and synthesis on function, ecosystem services and implementation. Biomass Bioenergy 55:53–67. doi: 10.1016/j.biombioe.2012.09.053

Clark EV, Zipper CE (2016) Vegetation influences near-surface hydrological characteristics on a surface coal mine in eastern USA. CATENA 139:241–249. doi: 10.1016/j.catena.2016.01.004

Cortez J, Garnier E, Pérez-Harguindeguy N, et al (2007) Plant traits, litter quality and decomposition in a Mediterranean old-field succession. Plant Soil 296:19–34. doi: 10.1007/s11104-007-9285-6

Craine JM, Froehle J, Tilman DG, et al (2001) The Relationships among Root and Leaf Traits of 76 Grassland Species and Relative Abundance along Fertility and Disturbance Gradients. Oikos 93:274–285

Dabney SM, Meyer LD, Harmon WC, et al (1995) Depositional patterns of sediment trapped by grass hedges. Trans ASAE 38:1719–1729

De Baets S, Poesen J, Gyssels G, Knapen A (2006) Effects of grass roots on the erodibility of topsoils during concentrated flow. Geomorphology 76:54–67. doi: 10.1016/j.geomorph.2005.10.002

de Vries FT, Manning P, Tallowin JRB, et al (2012) Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. Ecol Lett 15:1230–1239. doi: 10.1111/j.1461-0248.2012.01844.x

Degré A, Pineux N, Vincent C, et al (2013) Estimation of the fascine efficiency in terms of runoff infiltration and sediments deposition. pp EGU2013-11378

Descroix L, Mathys N (2003) Processes, spatio-temporal factors and measurements of current erosion in the French Southern Alps: a review. Earth Surf Process Landf 28:993–1011. doi: 10.1002/esp.514

Deyn GBD, Cornelissen JHC, Bardgett RD (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol Lett 11:516–531. doi: 10.1111/j.1461-0248.2008.01164.x

Díaz S, Hodgson JG, Thompson K, et al (2004) The Plant Traits That Drive Ecosystems: Evidence from Three Continents. J Veg Sci 15:295–304

Díaz S, Lavorel S, Chapin FS, et al (2007a) Functional Diversity — at the Crossroads between Ecosystem Functioning and Environmental Filters. In: Canadell JG, Pataki DE, Pitelka LF (eds) Terrestrial Ecosystems in a Changing World. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 81–91

Díaz S, Lavorel S, de Bello F, et al (2007b) Incorporating plant functional diversity effects in ecosystem service assessments. Proc Natl Acad Sci 104:20684–20689. doi: 10.1073/pnas.0704716104

Dillaha TA, Reneau RB, Mostaghimi S, Lee D (1989) Vegetative filter strips for agricultural nonpoint source pollution control. Trans ASAE 32:513–0519

Dillaha TA, Sherrard JH, Lee D (1986) Long-term effectiveness and maintenance of vegetative filter strips

Díaz S, Cabido M (2001) Vive la différence: Plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655. doi: 10.1016/S0169-5347(01)02283-2

Dosskey MG, Vidon P, Gurwick NP, et al (2010) The role of riparian vegetation in protecting and improving chemical water quality in streams. J Am Water Resour Assoc 1–18. doi: 10.1111/j.1752-1688.2010.00419.x

Dunne T, Zhang W, Aubry BF (1991) Effects of rainfall, vegetation, and microtopography on infiltration and runoff. Water Resour Res 27:2271–2285. doi: 10.1029/91WR01585

Durán Zuazo VH, Rodríguez Pleguezuelo CR (2008) Soil-erosion and runoff prevention by plant covers. A review. Agron Sustain Dev 28:65–86. doi: 10.1051/agro:2007062

Ebeling A, Pompe S, Baade J, et al (2014) A trait-based experimental approach to understand the mechanisms underlying biodiversity–ecosystem functioning relationships. Basic Appl Ecol 15:229–240. doi: 10.1016/j.baae.2014.02.003

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Research View: Building Roots in a Changing Environment: Implications for Root Longevity. New Phytol 147:33–42

Erktan A, Cécillon L, Roose E, et al (2013) Morphological diversity of plant barriers does not increase sediment retention in eroded marly gullies under ecological restoration. Plant Soil 370:653–669. doi: 10.1007/s11104-013-1738-5

Evette A, Labonne S, Rey F, et al (2009) History of bioengineering techniques for erosion control in rivers in western Europe. Environ Manage 43:972. doi: 10.1007/s00267-009-9275-y

Evrard O, Nord G, Cerdan O, et al (2010) Modelling the impact of land use change and rainfall seasonality on sediment export from an agricultural catchment of the northwestern European loess belt. Agric Ecosyst Environ 138:83–94. doi: 10.1016/j.agee.2010.04.003

Fattet M, Fu Y, Ghestem M, et al (2011) Effects of vegetation type on soil resistance to erosion: Relationship between aggregate stability and shear strength. CATENA 87:60–69. doi: 10.1016/j.catena.2011.05.006

Faucon M-P (2015) Ecologie et biogéochimie des interactions sol-plante et leurs implications en conservation de la biodiversité, ingénierie écologique et agroécologie. Université de Picardie Jules Verne

Faucon M-P, Houben D, Lambers H (2017) Plant functional traits: soil and ecosystem services. Trends Plant Sci 22:385–394. doi: 10.1016/j.tplants.2017.01.005

Fornara DA, Tilman D (2008) Plant functional composition influences rates of soil carbon and nitrogen accumulation. J Ecol 96:314–322. doi: 10.1111/j.1365-2745.2007.01345.x

Frankl A, Prêtre V, Nyssen J, Salvador P-G (2018) The success of recent land management efforts to reduce soil erosion in northern France. Geomorphology 303:84–93. doi: 10.1016/j.geomorph.2017.11.018

Fullen MA (1998) Effects of grass ley set-aside on runoff, erosion and organic matter levels in sandy soils in east Shropshire, UK. Soil Tillage Res 46:41–49

García- Orenes F, Roldán A, Mataix-Solera J, et al (2012) Soil structural stability and erosion rates influenced by agricultural management practices in a semi-arid Mediterranean agro-ecosystem. Soil Use Manag 28:571–579. doi: 10.1111/j.1475-2743.2012.00451.x

Garnier E, Navas M-L (2012) A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. Agron Sustain Dev 32:365–399

Garnier E, Navas M-L, Grigulis K (2016) Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties. Oxford University Press

Ghestem M, Sidle RC, Stokes A (2011) The Influence of Plant Root Systems on Subsurface Flow: Implications for Slope Stability. BioScience 61:869–879. doi: 10.1525/bio.2011.61.11.6

Gilley JE, Eghball B, Kramer LA, Moorman TB (2000) Narrow grass hedge effects on runoff and soil loss. J Soil Water Conserv 55:190–196

Gominet S (2010) Lave torrentielle dans la Combe de la Chambre d'Ane

Graff CD, Sadeghi AM, Lowrance RR, Williams RG (2005) Quantifying the sensitivity of the riparian ecosystem management model (REMM) to changes in climate and buffer characteristics common to conservation practices. Trans ASAE 48:1377–1387

Grigulis K, Lavorel S, Krainer U, et al (2013) Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. J Ecol 101:47–57. doi: 10.1111/1365-2745.12014

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910. doi: 10.1046/j.1365-2745.1998.00306.x

Grime JP, Thompson K, Hunt R, et al (1997) Integrated Screening Validates Primary Axes of Specialisation in Plants. Oikos 79:259–281. doi: 10.2307/3546011

Gyssels G, Poesen J, Bochet E, Li Y (2005) Impact of plant roots on the resistance of soils to erosion by water: A review. Prog Phys Geogr 29:189–217. doi: 10.1191/0309133305pp443ra

Haan CT, Barfield BJ, Hayes JC (1994) Design Hydrology and Sedimentology for Small Catchments. Academic Press

Hayes JC, Barfield BJ, Barnhisel RI (1978) Evaluation of grass characteristics related to sediment filtration. ASAE 78–2513:21

Hou J, Wang H, Fu B, et al (2016) Effects of plant diversity on soil erosion for different vegetation patterns. CATENA 147:632–637. doi: 10.1016/j.catena.2016.08.019

Hussein J, Yu B, Ghadiri H, Rose C (2007) Prediction of surface flow hydrology and sediment retention upslope of a vetiver buffer strip. J Hydrol 338:261–272

Isbell F, Cowles J, Dee LE, et al (2018) Quantifying effects of biodiversity on ecosystem functioning across times and places. Ecol Lett 21:763–778. doi: 10.1111/ele.12928

Isselin-Nondedeu F, Bédécarrats A (2007) Influence of alpine plants growing on steep slopes on sediment trapping and transport by runoff. Catena 71:330–339. doi: 10.1016/j.catena.2007.02.001

Järvelä J (2002) Flow resistance of flexible and stiff vegetation: A flume study with natural plants. J Hydrol 269:44–54

Keddy PA (1992) A pragmatic approach to functional ecology. Funct Ecol 6:621–626

Kidd DR, Ryan MH, Haling RE, et al (2016) Rhizosphere carboxylates and morphological root traits in pasture legumes and grasses. Plant Soil 402:77–89. doi: 10.1007/s11104-015-2770-4

Klumpp K, Soussana J-F (2009) Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect trait approach. Glob Change Biol 15:2921–2934. doi: 10.1111/j.1365-2486.2009.01905.x

Knapen A, Poesen J, Govers G, et al (2007) Resistance of soils to concentrated flow erosion: A review. Earth-Sci Rev 80:75–109. doi: 10.1016/j.earscirev.2006.08.001

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Lambrechts T, François S, Lutts S, et al (2014) Impact of plant growth and morphology and of sediment concentration on sediment retention efficiency of vegetative filter strips: Flume experiments and VFSMOD modeling. J Hydrol 511:800–810. doi: 10.1016/j.jhydrol.2014.02.030

Lange M, Eisenhauer N, Sierra CA, et al (2015) Plant diversity increases soil microbial activity and soil carbon storage. Nat Commun 6:. doi: 10.1038/ncomms7707

Laureto LMO, Cianciaruso MV, Samia DSM (2015) Functional diversity: an overview of its history and applicability. Nat Conserv 13:112–116. doi: 10.1016/j.ncon.2015.11.001

Lavorel S (2013) Plant functional effects on ecosystem services. J Ecol 101:4–8. doi: 10.1111/1365-2745.12031

Lavorel S, Díaz S, Cornelissen JHC, et al (2007) Plant Functional Types: Are We Getting Any Closer to the Holy Grail? In: Canadell JG, Pataki DE, Pitelka LF (eds) Terrestrial Ecosystems in a Changing World. Springer, Berlin, Heidelberg, pp 149–164

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Funct Ecol 16:545–556

Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol Evol 12:474–478. doi: 10.1016/S0169-5347(97)01219-6

Le Bissonnais Y, Benkhadra H, Gallien E, et al (1996) Genèse du ruissellement et de l'érosion diffuse sur sols limoneux : analyse du transfert d'échelle du m2 au bassin versant élémentaire agricole/Runoff and interrill erosion on silty loamy soils: analysis of scale tranfer from m2 to small cultivated catchments. Géomorphologie Relief Process Environ 2:51–64. doi: 10.3406/morfo.1996.885

Le Bissonnais Y, Lecomte V, Cerdan O (2004) Grass strip effects on runoff and soil loss. Agronomie 24:129–136

Le Bissonnais Y, Montier C, Jamagne M, et al (2001) Mapping erosion risk for cultivated soil in France. CATENA 46:207–220

Legay N, Baxendale C, Grigulis K, et al (2014) Contribution of above- and below-ground plant traits to the structure and function of grassland soil microbial communities. Ann Bot 114:1011–1021. doi: 10.1093/aob/mcu169

Leguédois S (2003) Mécanismes de l'érosion diffuse des sols. Modélisation du transfert et de l'évolution granulométrique des fragments de terre érodés. PhD, Université d'Orléans

Li J, He B, Chen Y (2013) Root features of typical herb plants for hillslope protection and their effects on soil infiltration. Acta Ecol Sin 33:1535–1544. doi: 10.5846/stxb201205170737

Li Y, Xu XQ, Zhu XM, Tian JY (1992) Effectiveness of plant roots on increasing the soil permeability on the Loess Plateau. Chin Sci Bull 37:1735–1738

Liu Y-J, Hu J-M, Wang T-W, et al (2016) Effects of vegetation cover and road-concentrated flow on hillslope erosion in rainfall and scouring simulation tests in the Three Gorges Reservoir Area, China. CATENA 136:108–117. doi: 10.1016/j.catena.2015.06.006

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76. doi: 10.1038/35083573

Loreau M, Naeem S, Inchausti P, et al (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. science 294:804–808

Mariotte P, Mehrabi Z, Bezemer TM, et al (2017) Plant–Soil Feedback: Bridging Natural and Agricultural Sciences. Trends Ecol Evol

Martin C, Pohl M, Alewell C, et al (2010) Interrill erosion at disturbed alpine sites: Effects of plant functional diversity and vegetation cover. Basic Appl Ecol 11:619–626. doi: 10.1016/j.baae.2010.04.006

Mason NWH, MacGillivray K, Steel JB, Wilson JB (2003) An index of functional diversity. J Veg Sci 14:571–578. doi: 10.1111/j.1654-1103.2003.tb02184.x

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118

Mcgill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends Ecol Evol 21:178–185. doi: 10.1016/j.tree.2006.02.002

Mekonnen M, Keesstra SD, Ritsema CJ, et al (2016) Sediment trapping with indigenous grass species showing differences in plant traits in northwest Ethiopia. Catena 147:755–763. doi: 10.1016/j.catena.2016.08.036

Meyer LD, Dabney SM, Harmon WC (1995) Sediment-trapping effectiveness of stiff-grass hedges. Am Soc Agric Eng 38:809–815

Mitsch WJ, Jørgensen SE (2003) Ecological engineering: A field whose time has come. Ecol Eng 20:363–377. doi: 10.1016/j.ecoleng.2003.05.001

Mokany K, Ash J, Roxburgh S (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland: Determinants of ecosystem processes. J Ecol 96:884–893. doi: 10.1111/j.1365-2745.2008.01395.x

Morgan RPC (2005) Soil Erosion and Conservation, 3rd ed. Blackwell Pub, Malden, MA

Morgan RPC (2004) Vegetative-Based Technologies for Erosion Control. In: Stokes A, Spanos I, Norris JE, Cammeraat E (eds) Eco- and Ground Bio-Engineering: The Use of Vegetation to Improve Slope Stability. Springer, Dordrecht, The Netherlands, pp 265–272

Morgan RPC, Duzant JH (2008) Modified MMF (Morgan–Morgan–Finney) model for evaluating effects of crops and vegetation cover on soil erosion. Earth Surf Process Landf 33:90–106. doi: 10.1002/esp.1530

Morgan RPC, Rickson RJ (1995) Slope Stabilization and Erosion Control: A Bioengineering Approach

Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules: Functional diversity measures. Funct Ecol 24:867–876. doi: 10.1111/j.1365-2435.2010.01695.x

Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional Structure of Biological Communities Predicts Ecosystem Multifunctionality. PLoS ONE 6:e17476. doi: 10.1371/journal.pone.0017476

Mueller KE, Tilman D, Fornara DA, Hobbie SE (2013) Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. Ecology 94:787–793

Naeem S, Thompson LJ, Lawler SP, et al (1994) Declining biodiversity can alter the performance of ecosystems. Nature 368:734–737. doi: 10.1038/368734a0

Orwin KH, Buckland SM, Johnson D, et al (2010) Linkages of plant traits to soil properties and the functioning of temperate grassland: Links of plant traits to soil properties. J Ecol 98:1074–1083. doi: 10.1111/j.1365-2745.2010.01679.x

Ouvry J-F, Richet J-B, Bricard O, et al (2012) Fascines et Haies pour réduire les effets du ruissellement érosif : Caractérisation de l'efficacité et conditions d'utilisation. AREAS, St Valéry en Caux, France

Petchey OL (2003) Integrating methods that investigate how complementarity influences ecosystem functioning. Oikos 101:323–330

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9:741–758. doi: 10.1111/j.1461-0248.2006.00924.x

Poesen J, Nachtergaele J, Verstraeten G, Valentin C (2003) Gully erosion and environmental change: importance and research needs. Catena 50:91–133

Poesen JWA (1989) Conditions for gully formation in the Belgian loam belt and some ways to control them. In: Schwertmann U, Rickson RJ, Auerswald K (eds) Soil erosion protection measures in Europe: proceedings of the European community workshop on soil erosion protection, Freising, FR Germany, May 24-26, 1988. CATENA VERLAG, Cremlingen-Destedt, Germany, pp 39–52

Poesen JWA, Hooke JM (1997) Erosion, flooding and channel management in Mediterranean environments of southern Europe. Prog Phys Geogr 21:157–199. doi: 10.1177/030913339702100201

Pohl M, Alig D, Körner C, Rixen C (2009) Higher plant diversity enhances soil stability in disturbed alpine ecosystems. Plant Soil 324:91–102. doi: 10.1007/s11104-009-9906-3

Pugnaire F, Valladares F (1999) Handbook of Functional Plant Ecology. CRC Press

Rao CR (1982) Diversity and dissimilarity coefficients: A unified approach. Theor Popul Biol 21:24–43. doi: 0040-5809/82/010024-2OSO2.00/0

Rekolainen S, Ekholm P, Heathwaite L, et al (2006) Off-Site Impacts of Erosion: Eutrophication as an Example. In: Boardman J, Poesen J (eds) Soil Erosion in Europe. John Wiley & Sons, Ltd, pp 775–789

Rey F (2005) Efficacité des ouvrages de génie biologique pour le piégeage des sédiments dans des ravines incisées dans des marnes (Alpes du Sud, France). Géomorphologie Relief Process Environ 11:21–30. doi: 10.4000/geomorphologie.222

Richet J-B, Ouvry J-F, Saunier M (2017) The role of vegetative barriers such as fascines and dense shrub hedges in catchment management to reduce runoff and erosion effects: Experimental evidence of efficiency, and conditions of use. Ecol Eng 103:455–469. doi: 10.1016/j.ecoleng.2016.08.008

Rillig MC, Aguilar- Trigueros CA, Bergmann J, et al (2015) Plant root and mycorrhizal fungal traits for understanding soil aggregation. New Phytol 205:1385–1388. doi: 10.1111/nph.13045

Roumet C, Urcelay C, Diaz S (2006) Suites of root traits differ between annual and perennial species growing in the field. New Phytol 170:357–368. doi: 10.1111/j.1469-8137.2006.01667.x

Sayer EJ, Oliver AE, Fridley JD, et al (2017) Links between soil microbial communities and plant traits in a species- rich grassland under long- term climate change. Ecol Evol 7:855–862. doi: 10.1002/ece3.2700

Schlesinger WH, Bernhardt ES (2013) Biogeochemistry: An Analysis of Global Change. Academic Press

Simon A, Collison AJC (2002) Quantifying the mechanical and hydrologic effects of riparian vegetation on streambank stability. Earth Surf Process Landf 27:527–546. doi: 10.1002/esp.325

Song Y, Wang P, Li G, Zhou D (2014) Relationships between functional diversity and ecosystem functioning: A review. Acta Ecol Sin 34:85–91. doi: 10.1016/j.chnaes.2014.01.001

Stokes A (ed) (2007) Eco- and ground bio-engineering: the use of vegetation to improve slope stability: proceedings of the First International Conference on Eco-Engineering, 13-17 September 2004. Springer, Dordrecht

Stokes A, Douglas GB, Fourcaud T, et al (2014) Ecological mitigation of hillslope instability: ten key issues facing researchers and practitioners. Plant Soil 377:1–23. doi: 10.1007/s11104-014-2044-6

Styczen ME, Morgan RPC (1995) Engineering properties of vegetation. In: Morgan RPC, Rickson RJ (eds) Slope Stabilization and Erosion Control: A Bioengineering Approach. E & FN SPON, London, pp 4–60

Temple DM (1982) Flow Retardance of Submerged Grass Channel Linings. Trans ASAE 25:1300–1303. doi: 10.13031/2013.33717

Temple DM, Robinson KM, Ahring RM, Davis AG (1987) Stability Design of Grass-Lined Open Channels. U.S. Department of Agriculture, Washington, D.C.

Tilman D (2001a) Diversity and Productivity in a Long-Term Grassland Experiment. Science 294:843–845. doi: 10.1126/science.1060391

Tilman D (2001b) Functional Diversity. In: Levin SA (ed) Encyclopedia of Biodiversity. Elsevier, New York, pp 109–120

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and Ecosystem Functioning. Annu Rev Ecol Evol Syst 45:471–493. doi: 10.1146/annurev-ecolsys-120213-091917

Tilman D, Knops J, Wedin D, et al (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Turnbull L, Wainwright J, Brazier RE (2008) A conceptual framework for understanding semi-arid land degradation: ecohydrological interactions across multiple-space and time scales. Ecohydrology 1:23–34. doi: 10.1002/eco.4

Valé M, Nguyen C, Dambrine E, Dupouey J (2005) Microbial activity in the rhizosphere soil of six herbaceous species cultivated in a greenhouse is correlated with shoot biomass and root C concentrations. Soil Biol Biochem 37:2329–2333. doi: 10.1016/j.soilbio.2005.04.014

Van Dijk PM, Kwaad FJPM, Klapwijk M (1996) Retention of water and sediment by grass strips. Hydrol Process 10:1069–1080. doi: 10.1002/(SICI)1099-1085(199608)10:8<1069::AID-HYP412>3.0.CO;2-4

Van Oost K, Govers G (2006) Tillage Erosion. In: Boardman J, Poesen J (eds) Soil Erosion in Europe. John Wiley & Sons, Ltd, pp 599–608

Verstraeten G, Bazzoffi P, Lajczak A, et al (2006) Reservoir and pond sedimentation in Europe. In: Boardman J, Poesen J (eds) Soil erosion in Europe. John Wiley & Sons, Ltd, West

Villéger S, Mason NW, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301

Violle C, Navas M-L, Vile D, et al (2007) Let the concept of trait be functional! Oikos 116:882–892. doi: 10.1111/j.2007.0030-1299.15559.x

Wardle DA (2002) Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press

Wardle DA, Bardgett RD, Klironomos JN, et al (2004) Ecological Linkages Between Aboveground and Belowground Biota. Science 304:1629–1633. doi: 10.1126/science.1094875

Weiher E, Werf A van der, Thompson K, et al (1999) Challenging Theophrastus: A common core list of plant traits for functional ecology. J Veg Sci 10:609–620. doi: 10.2307/3237076

Wendling M, Büchi L, Amossé C, et al (2016) Influence of root and leaf traits on the uptake of nutrients in cover crops. Plant Soil 409:419–434. doi: 10.1007/s11104-016-2974-2

Wischmeier WH, Smith DD (1978) Predicting rainfall erosion losses — a guide to consevation planning. US Department of Agriculture, Washington, DC

Wu G-L, Liu Y, Yang Z, et al (2017) Root channels to indicate the increase in soil matrix water infiltration capacity of arid reclaimed mine soils. J Hydrol 546:133–139. doi: 10.1016/j.jhydrol.2016.12.047

Wu G-L, Yang Z, Cui Z, et al (2016) Mixed artificial grasslands with more roots improved mine soil infiltration capacity. J Hydrol 535:54–60. doi: 10.1016/j.jhydrol.2016.01.059

Wu JY, Huang D, Teng WJ, Sardo VI (2010) Grass hedges to reduce overland flow and soil erosion. Agron Sustain Dev 30:481–485. doi: 10.1051/agro/2009037

Xiao B, Wang Q, Wang H, et al (2012) The effects of grass hedges and micro-basins on reducing soil and water loss in temperate regions: A case study of Northern China. Soil Tillage Res 122:22–35. doi: 10.1016/j.still.2012.02.006

Xu Z, Li M-H, Zimmermann NE, et al (2018) Plant functional diversity modulates global environmental change effects on grassland productivity. J Ecol 106:1941–1951. doi: 10.1111/1365-2745.12951

Zhang L, Wang J, Bai Z, Lv C (2015) Effects of vegetation on runoff and soil erosion on reclaimed land in an opencast coal-mine dump in a loess area. CATENA 128:44–53. doi: 10.1016/j.catena.2015.01.016

Zhu H, Fu B, Wang S, et al (2015) Reducing soil erosion by improving community functional diversity in semi-arid grasslands. J Appl Ecol 52:1063–1072. doi: 10.1111/1365-2664.12442

Zuo X, Wang S, Lv P, et al (2016a) Plant functional diversity enhances associations of soil fungal diversity with vegetation and soil in the restoration of semiarid sandy grassland. Ecol Evol 6:318–328. doi: 10.1002/ece3.1875

Zuo X, Zhang J, Lv P, et al (2016b) Plant functional diversity mediates the effects of vegetation and soil properties on community-level plant nitrogen use in the restoration of semiarid sandy grassland. Ecol Indic 64:272–280. doi: 10.1016/j.ecolind.2016.01.012

OBJECTIVES

2. PhD OBJECTIVES

This PhD research aims to deepen the knowledge regarding the effects of plant functional traits on concentrated runoff and sediment retention processes, as well as understand the effects of functional diversity on these processes, in order to evaluate the efficiency and design of herbaceous hedges to reduce the impacts of soil erosion in loamy European agricultural catchments. This thesis is composed of three chapters corresponding to the three main objectives of the study (Figure 11).

Chapter 1 characterises the effects of aboveground functional traits on the hydraulic roughness, main process favouring runoff velocity reduction and sediment retention, using a trait-based ecohydrology approach. The aims of this chapter are (1) to identify the traits influencing the hydraulic roughness for concentrated runoff processes found in north-west European agricultural catchments and (2) investigate the effects of these concentrated flow processes, using different discharges, on the relationship between the traits and the hydraulic roughness. These objectives would lead to an improved understanding of the relationship between functional traits and runoff and soil erosion process in order to select candidate species and create efficient herbaceous hedges for north-west Europe.

Chapter 2 focusses on the complementarity effects of traits on hydraulic roughness and sediment retention, using an in-situ experiment with a multi-specific condition comprising three species presenting contrasting traits involved in hydraulic roughness. This chapter aims to understand if the complementarity effect of the traits drives the hydraulic roughness and sediment retention efficiency due to a better resources and space use. The findings in this chapter would lead to a better comprehension of the influence of trait diversity on runoff and sediment transport processes.

Chapter 3 examines the relationship between aboveground functional structure and the hydraulic roughness using three levels of functional diversity and four discharges. This chapter aims to improve the understanding of functional diversity effects on hydraulic roughness and identify if the effects are driven by a dominance or an additive effect of the traits in the community.

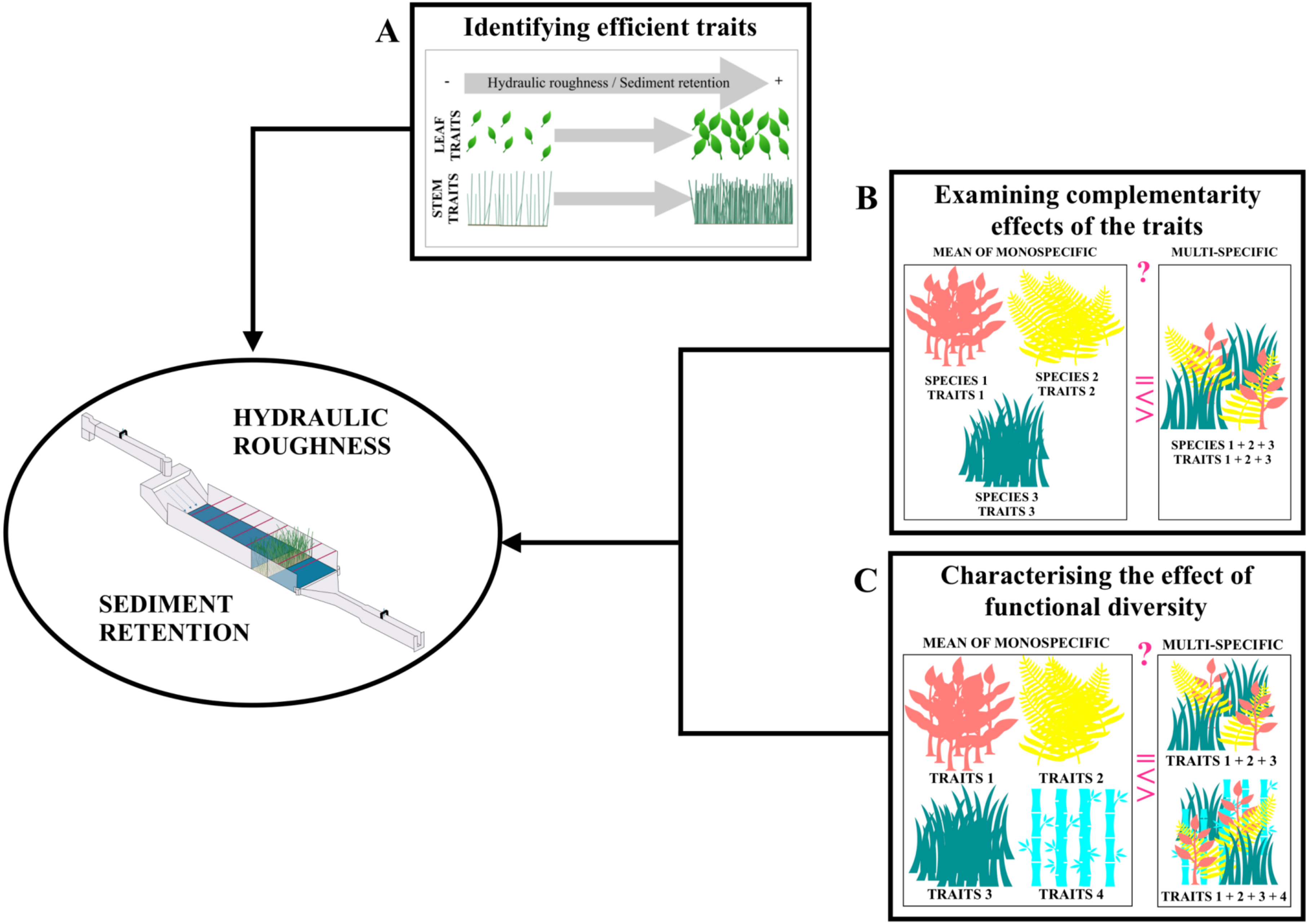


Figure 11. Objectives of the PhD research

PhD METHODS

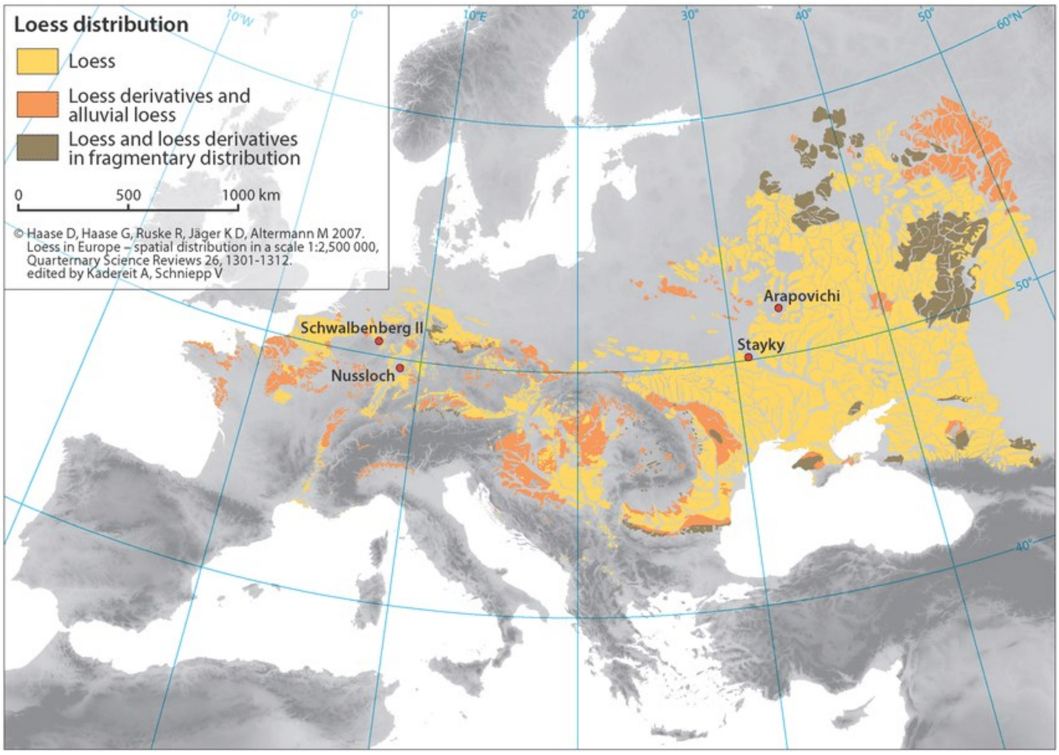
3. APPROACH TO METHODS

This PhD research aims at understanding and characterising the water-plant interactions between a community and concentrated runoff and sediment retention processes in order to increase hydraulic roughness and sediment retention upstream of the vegetation (Figure 11). To answer these objectives, the analyses and experiments were performed at the vegetation scale for the functional ecology side of the study, and at the concentrated flow scale for the hydraulic side.

Trait responses towards runoff and soil erosion processes depend on the context and processes occurring in phytogeographical territories, which emphasises the need to select a phytogeographic area for the present research.

3.1. Contextual framework of north-west Europe

Soil erosion induces major soil degradation impacting the soil fundamental functions (e.g. productivity, water and nutrients cycling, provision of habitats). The understanding of the importance of soil erosion in north-west Europe (especially in the European loss belt area (Figure 12)), has started from the 70's (Morgan 2005). This late interest and realisation was due to the characterisation of the north-west European soils as non-sensitive to soil erosion, mainly due to the slope gradients lower than 5% (Remy and Le Bissonnais 1998).



© Haase D, Haase G, Ruske R, Jäger K D, Altermann M 2007. Loess in Europe – spatial distribution in a scale 1:2,500 000, Quarternary Science Reviews 26, 1301-1312. edited by Kadereit A, Schniepp V

Figure 12. European loess belt and loess distribution (Kadereit and Wagner 2014; based on Haase et al. (2007)).

However, the land consolidation of intensively cultivated loamy soils, with a disappearance of the linear landscape elements (i.e. hedges, ditches) in the landscapes regulating erosion after WWII has led to the appearance and the increase of soil erosion in north-western European agricultural catchments (Remy and Le Bissonnais 1998; Boardman and Poesen 2006). Cerdan et al. (2010) estimated the overall soil loss in European arable lands by rill and inter-rill erosion at circa 3.6 t.ha^{-1}.year^{-1}. The consequences of soil erosion in agricultural catchments are grouped into two categories, both being short and long-term impacts: the on-site and off-site effects. The on-site effects of soil erosion are mainly related to the soil loss, that induce crop yield losses, crop damage, the reduction of topsoil thickness and the loss of organic matter (Morgan 2005; Boardman and Poesen 2006). The off-site effects comprise the transfer of pollutants (e.g. fertilizers, herbicides) and sediments into water bodies (i.e. rivers, streams, ditches, marsh, ponds, reservoirs) which can lead to (1) the increase the flooding risk and the damages of infrastructures and habitations, (2) the eutrophication of those water bodies by the increase of nitrogen and phosphorus concentrations, (3) the pollution of drinking water and (4) the release of the soil sequestrated carbon into the atmosphere (Morgan 2005; Boardman et al. 2006; Boardman and Poesen 2006; Rekolainen et al. 2006; Schuler et al. 2006; Verstraeten et al. 2006).

3.2. Selection of candidate species using functional types to study herbaceous hedges role in the control soil erosion

The selection of potential candidate species to design efficient vegetation to increase the hydraulic roughness and sediment retention requires the identification of the influencing functional types and selective criteria (Figure 13) (Villarroel 2015). A plant functional type can be defined as a group of plant species sharing similar functioning at the organismic level, similar responses to environmental factors and/or similar roles in ecosystems (Lavorel and Garnier 2002).

For a specific phytogeographical territory under temperate climates, indigenous perennial herbaceous species under the Raunkiaer's life-form categories "herbaceous chamaephytes", "hemicryptophytes" and "geophytes" would provide an effective soil cover through all seasons and limit runoff, sediment detachment and improve sediment retention. Within these life-form categories, caespitose and non-caespitose types allow a constant ground cover with fresh or dry biomass in winter, when soil erosion is observed at its highest in temperate climates, and would thus protect the soil from sediment detachment and control the flow velocity (Boardman and Poesen 2006). Species favouring vegetative reproduction, with the presence of tillers, rhizomes or stolon would ensure a homogeneous cover to limit the presence of preferential flow paths within the vegetation. Indeed, tillers, rhizomes and stolon guarantee a lateral spreading growth pattern, with a maximum ground cover (100%), and a burying tolerance towards sedimentation. Herbaceous hedges are efficient against concentrated flows as long as they do not get submerged. Vegetative height defined by the water maximal level constitutes a major trait to reduce runoff and increase sediment retention. In addition to these plant functional types and selective criteria, the species' ecological niche should also be considered, as to choose species with broad ecological niches enabling them to grow in several loamy cultivated soils presenting contrasting edaphic conditions. Moreover, in order to avoid the vegetation spreading in the crops, only non-weed species should be selected.

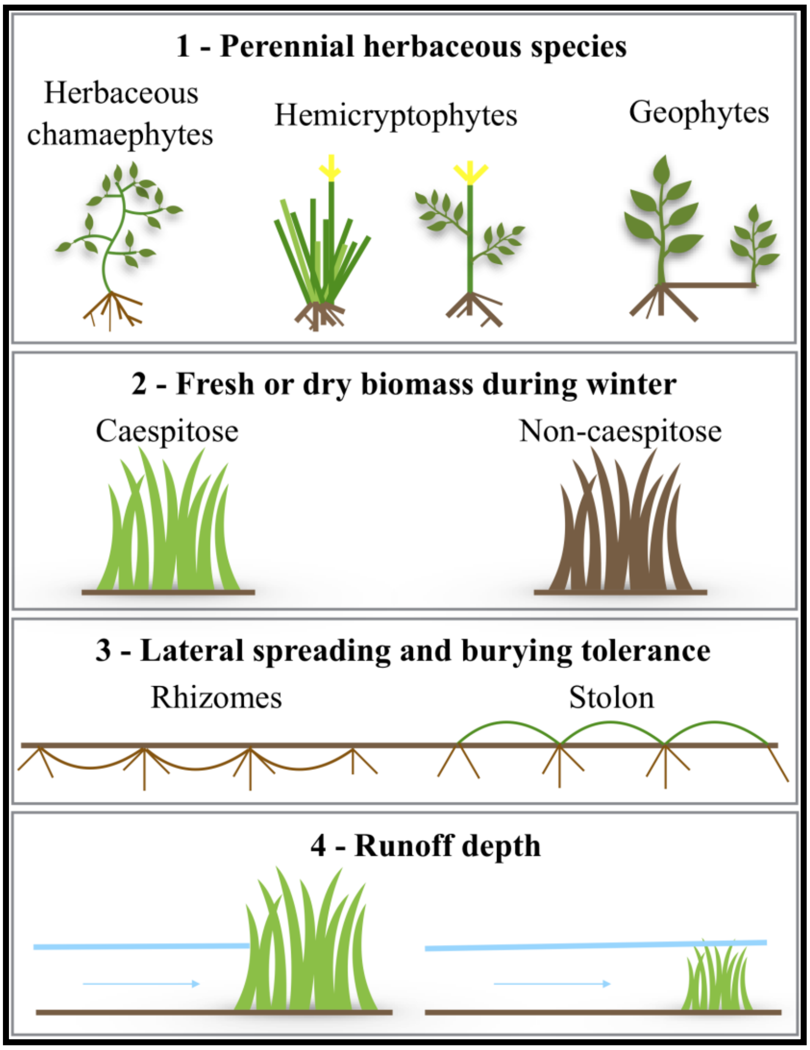


Figure 13. Functional types and selective criteria to determine a list of potential candidates to control soil erosion

Considering north-west Europe as the phytogeographical area of study, the list of criteria is applied to the 3,500 indigenous spermaphyte species this territory is composed of (Lambinon et al. 2012). The peak discharges and their frequencies have been measured depending on the catchment size in north-west European agricultural territories (Table 2). The maximal water depth found in north-west European thalwegs being 20 cm, only plants with a minimum vegetative height of 20 cm or higher are chosen.

Table 2. Peak discharges depending on catchment sizes and their frequency (Richet et al. 2017).

Frequency (year)	Peak flow rate (L.s^{-1}) 50 ha catchment	20 ha catchment	5 ha catchment
0.5	50.2	24.1	8
1	150	72.5	23.9
2	251.3	120.8	39.8
5	384.4	184.7	60.9
10	484.9	233	76.9
20	585.5	281.3	92.8

After the application of the filters on the 3,500 species, only 76 potential candidate species are highlighted (Table 3). However, in order to finalise the selection, a final filter considering the traits involved in hydraulic roughness and sediment retention increase should be developed.

Table 3. The 76-candidate species list potentially able to mitigate soil erosion in the north-west European loess belt. The minimum vegetative heights are represented under the median value (Quartile 1; Quartile 4) of the data obtained from Hegi, 1906; Jauzein and Nawrot, 2011; Lambinon et al., 2012; Mansion et al., 1989; Rothmaler and Jäger, 2009; Bugnon, 1995 In Université de Bourgogne (UFR Science de la vie), 2018).

Family	Species name	Life form	Minimum vegetative height (cm)
Adoxaceae	*Sambucus ebulus*	Hemicryptophyte	55 (50; 80)
Apiaceae	*Anthriscus sylvestris*	Hemicryptophyte	45 (40; 80)
	Bupleurum falcatum	Hemicryptophyte	30 (20; 50)
	Heracleum sphondylium	Hemicryptophyte	50 (30; 50)
Asteraceae	*Achillea ptarmica*	Hemicryptophyte	20 (20; 30)
	Artemisia verlotiorum	Hemicryptophyte	70 (67.5; 150)
	Artemisia vulgaris	Hemicryptophyte	60 (52.5; 60)
	Aster laevis	Hemicryptophyte	60 (60; 60)
	Aster salignus	Hemicryptophyte	80 (72.5; 90)
	Eupatorium cannabinum	Hemicryptophyte	55 (50; 80)
	Hieracium piloselloides	Hemicryptophyte	20 (20; 20)
	Senecio jacobaea	Hemicryptophyte	30 (30; 40)
	Tanacetum corymbosum	Hemicryptophyte	30 (30; 50)
	Tanacetum parthenium	Hemicryptophyte	30 (30; 30)
	Tanacetum vulgare	Hemicryptophyte	55 (42.5; 60)
Caryophyllaceae	*Saponaria officinalis*	Hemicryptophyte	30 (30; 30)
Clusiaceae	*Hypericum perforatum*	Hemicryptophyte	27.5 (21.25; 30)
Cyperaceae	*Carex acutiformis*	Hemicryptophyte	50 (35; 50)
	Carex binervis	Caespitose hemicryptophyte	30 (30; 30)
	Carex brizoides	Hemicryptophyte	25 (25; 30)
	Carex canescens	Hemicryptophyte	20 (20; 25)
	Carex otrubae	Hemicryptophyte	30 (30; 30)
	Carex diandra	Hemicryptophyte	20 (20; 30)
	Carex distans	Hemicryptophyte	22.5 (20; 30)
	Carex divulsa	Caespitose hemicryptophyte	20 (20; 30)
	Carex elongata	Caespitose hemicryptophyte	30 (30; 30)
	Carex flacca	Hemicryptophyte	20 (10; 20)
	Carex flava	Hemicryptophyte	20 (20; 30)
	Carex paniculata	Caespitose hemicryptophyte	40 (40; 50)
	Carex pendula	Caespitose hemicryptophyte	50 (50; 60)
	Carex pilosa	Hemicryptophyte	20 (20; 30)
	Carex pseudocyperus	Caespitose hemicryptophyte	40 (40; 50)
	Carex remota	Caespitose hemicryptophyte	30 (22.5; 30)
	Carex spicata	Caespitose hemicryptophyte	20 (10; 30)
	Carex strigosa	Caespitose hemicryptophyte	35 (22.5; 50)
	Carex sylvatica	Caespitose hemicryptophyte	20 (12.5; 30)
	Carex vulpina	Caespitose hemicryptophyte	30 (30; 40)
Lamiaceae	*Calamintha nepeta*	Hemicryptophyte	30 (27.5; 30)
	Clinopodium vulgare	Hemicryptophyte	25 (20; 30)
	Mentha longifolia	Hemicryptophyte	40 (30; 50)
	Mentha spicata	Hemicryptophyte	35 (27.5; 50)
	Mentha suaveolens	Hemicryptophyte	25 (16.25; 40)
	Origanum vulgare	Chamaephyte; Hemicryptophyte	25 (20; 40)
Linaceae	*Linum perenne*	Hemicryptophyte	25 (22.5; 30)

Papaveraceae	*Meconopsis cambrica*	Hemicryptophyte	30 (25; 40)
Poaceae	*Agrostis gigantea*	Hemicryptophyte	30 (30; 40)
	Arrhenatherum elatius	Hemicryptophyte	60 (50; 70)
	Brachypodium pinnatum	Hemicryptophyte	40 (32.5; 60)
	Brachypodium sylvaticum	Hemicryptophyte	50 (50; 60)
	Bromus erectus	Hemicryptophyte	30 (30; 30)
	Bromus inermis	Hemicryptophyte	30 (30; 50)
	Bromus ramosus	Hemicryptophyte	70 (45; 100)
	Calamagrostis arundinacea	Caespitose hemicryptophyte	60 (60; 60)
	Calamagrostis epigejos	Hemicryptophyte	60 (45; 60)
	Calamagrostis varia	Hemicryptophyte	40 (40; 50)
	Calamagrostis villosa	Hemicryptophyte	60 (45; 60)
	Cynosurus cristatus	Hemicryptophyte	20 (20; 30)
	Dactylis glomerata	Hemicryptophyte	20 (20; 50)
	Deschampsia cespitosa	Hemicryptophyte	30 (30; 50)
	Deschampsia flexuosa	Caespitose hemicryptophyte	25 (20; 30)
	Festuca arundinacea	Hemicryptophyte	60 (40; 70)
	Festuca gigantea	Hemicryptophyte	55 (50; 60)
	Festuca heteropachys	Caespitose hemicryptophyte	27.5 (23.75; 40)
	Festuca heterophylla	Caespitose hemicryptophyte	40 (40; 60)
	Festuca longifolia	Caespitose hemicryptophyte	20 (20; 30)
	Festuca marginata	Caespitose hemicryptophyte	20 (18.75; 20)
	Festuca polesica	Caespitose hemicryptophyte	20 (20; 20)
	Festuca pratensis	Hemicryptophyte	30 (30; 40)
	Festuca rubra	Geophyte with rhizomes	30 (20; 40)
	Koeleria pyramidata	Hemicryptophyte	20 (20; 45)
	Melica ciliata	Hemicryptophyte	22.5 (20; 30)
	Melica nutans	Hemicryptophyte	30 (22.5; 30)
	Melica uniflora	Hemicryptophyte	25 (20; 30)
	Milium effusum	Hemicryptophyte	55 (50; 80)
	Phalaris arundinacea	Hemicryptophyte	50 (50; 80)
Rosaceae	*Filipendula ulmaria*	Rosette hemicryptophyte	50 (50; 100)

3.3. Assessment of the hydraulic roughness of the herbaceous vegetation

The concentrated runoff flow was recreated using a runoff simulator that allowed the measurement of the water depths resulting from the vegetation (Figure 14). The simulator comprised three main parts: two Venturi channels with flowmeter probes placed on both ends of the main channel; and a flow range of 0.06 $L.s^{-1}$ to 6 $L.s^{-1}$. The ultrasound probes on the Venturi channels allowed to measure the water levels of the inflow and outflow with a precision of ± 1.26 mm and transpose these level values into discharges. This system was manufactured by ISMA, France (Richet et al. 2017). The central channel was made of galvanised iron and comprised levelled spacers along the channel. Each spacer was levelled and their elevations were measured and used as elevation-known baselines for the water level measurements. The spacers were used to measure the topography of the channel bed and the water levels in the backwater area upstream the plot.

The water depths were then used to characterise the hydraulic roughness associated with each vegetation plot. There are different indices that can be used to characterise the hydraulic roughness. The most commonly used indices are the Manning (1) and the Darcy-Weisbach (2) hydraulic roughness coefficients, both calculated using the hydraulic radius and the flow velocity; although the Darcy-Weisbach coefficient also includes the gravitational acceleration (Gilley et al. 1988). The Darcy-Weisbach coefficient characterises the head losses of the flow. The Manning coefficient is widely used in runoff simulation models at the catchment scale (e.g. VFS-MOD, LISEM, SWAT); however, the application of this index to characterise the hydraulic roughness of surface runoff in the present experimental conditions is debatable, due to the non-uniform conditions of the flow (Richet et al. 2017). The equations of these two indices are as follow:

$$V = \frac{1}{n} R_h^{2/3} \sqrt{S} \quad (1)$$

Where V is the mean velocity; n is the Manning coefficient; Rh is the hydraulic radius and S is the slope.

$$\Delta h = f \frac{L}{D_h} \frac{V^2}{2g} \quad (2)$$

Where Δh is the head loss; f is the friction coefficient; L is the channel length (m); Dh is the hydraulic diameter (m); V is the velocity of the flow ($m.s^{-1}$) and g is the gravitational acceleration ($m.s^{-2}$).

The index used through the experiments in this research is the unit stream power (USP), defined as the "energy dissipation per unit of time and per unit of weight of the flow" (Govers 1992), and used as a sediment transport capacity index (Yang 1972; Govers 1992):

$USP = V.S$

where V is the mean flow velocity and S the slope.

The choice of the USP as the hydraulic roughness index lied in (1) its easy characterisation and application for the experimental scale (vegetation) and (2) the threshold value from which soil is most likely to erode for loamy soils in the European loess belt which allows a critical value to select species according to their traits. This value of 0.004 $m.s^{-1}$ was determined for bare loess soils for slopes varying from 1° to 8°, discharges from 0.2 to 10 $L.s^{-1}.m^{-1}$ and sediment particle D_{50} from 58 µm to 218 µm (Govers 1990).

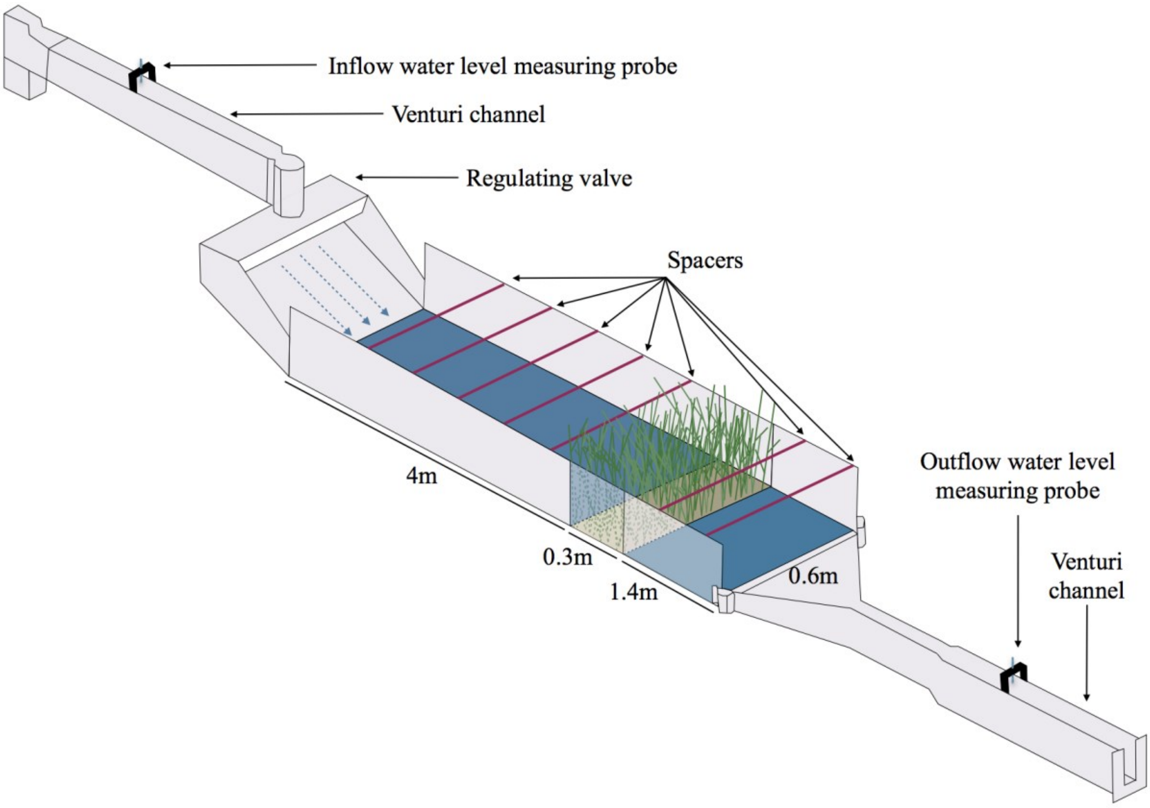


Figure 14. Runoff simulator used for the experiments

3.4. Plant morphological trait measurements

The eight measured traits comprised leaf traits (area, density and specific area) and stem traits (density, projected area, specific density, dry matter content and diameter), all supposedly involved in the increase of hydraulic roughness and sediment retention. The leaf density, the stem projected area, the stem diameter and the stem specific density were measured at three levels along the stem (0 and 5 cm; 0 and 10 cm; 0 and 20 cm) in order to analyse the effects of the traits depending on their position along the stem related to the variation to the water depth. All the traits measurements were done within 10 x 10 cm quadrats, using three representative and mature stems and leaves per quadrat. Only the first 20 cm of the stems were sampled in order to determine the stem traits values for each level.

Regarding the leaf traits, the leaf density (number of leaves.dm^{-2}) was determined by counting all the leaves, fresh and dry, within each level along the stems. The leaf area (mm^{2}) was measured by scanning the fresh sampled leaves using a scanner with a 600 dpi resolution. The images were then processed through the software Gimp 2.8 to count the pixels representing the leaf and determine the leaf area. The sampled leaves were then dried at 70°C for 72h and weighted to calculate the specific leaf area (division of the leaf area by the oven-dry mass of the leaf; mm^{2}.mg^{-1}).

The stem density (number of stems.dm^{-2}) was measured by counting all the stems within the quadrat, including pseudoculms for sedges species and tillers for grass species as stems. The stem diameter (mm) was measured three times on each level along fresh stems using an electronical calliper. The stem diameter was used in the rectangle area formula to calculate the projected stem area (mm^{2}), which represented the area of contact between the stem and the flow. The stems were then dried at 70°C for 72h and weighted to determine the oven-dry mass of the stems to calculate the specific stem density and the stem dry matter content. The stem specific density (mg.mm^{-3}) represented the structural strength of the stem and was used as a proxy of the plant resistance against the water flow (Burylo et al. 2012). It was calculated from the ratio of the oven-dry mass of the first 20cm of the stem (assuming that the density along each level was homogeneous) and the fresh stem volume (triangular prism volume formula for sedges and cylindrical volume formula for the other species). Finally, the stem dry matter content was estimated by dividing the oven-dry mass by the fresh mass of the stem.

In order to examine the vegetation effects on hydraulic roughness and sediment retention, density-weighted traits of the leaf area, the stem diameter and the stem projected area were calculated. This weighting consisted on multiplying the leaf density by the leaf area; the stem density by the stem diameter and the stem density by the stem projected area.

3.5. Characterisation of functional traits involved in the increase of hydraulic roughness and sediment retention

Functional traits are functional markers that directly influence the individual performance within the ecosystem. The identification of the traits' effect on the ecosystem properties, focussing here on the increase of the hydraulic roughness and sediment retention, allows to classify the plant species depending on their performance to reduce soil loss and runoff and design efficient herbaceous hedges (Figure 11.A).

The relationship between aboveground functional traits and the hydraulic roughness was characterised using 13 species from the 76-species list (table 1), one exotic species (*Miscanthus sinensis*) and a runoff simulator in *ex-situ* experiments. The chosen species present a wide range of trait values so the traits impacting the hydraulic roughness would be identified. The addition of the exotic species *Miscanthus sinensis* was to accentuate this trait-efficiency gradient, as it is recognised as a model plant for soil erosion and runoff reduction (Dabney et al. 2009).

The concentrated flow was created using the runoff simulator at four discharges: 2, 4, 8 and 11 $L.s^{-1}.m^{-1}$ (± 7%), observed approximately every 0.5, 1, 2 and 5 years respectively, in 5 ha catchments in the European loess belt with a 5 m-wide thalweg (Richet et al. 2017). The channel was 4 m long and 0.60 m wide upstream of the plot, with a channel bed slope of 5%. Five spacers were placed every 0.75 m from each other and started at 0.27 m from the plot to measure the water level within the backwater area.

However, some of the traits influencing the hydraulic roughness are found negatively associated when in monospecific plant communities. Creating multi-species communities presenting contrasting traits involved in the increase of the hydraulic roughness could present a better interest regarding herbaceous hedges design and reduction of soil loss and runoff intensity.

3.6. Analysing the complementarity effect of traits on the hydraulic roughness and sediment retention

The effects of plant species diversity in plant communities on ecosystem processes are driven by either a selection or a complementarity effect of the traits (Loreau and Hector 2001). The examination of the complementarity effect on hydraulic roughness and sediment retention was performed using a multi-specific condition comprising three species presenting contrasting and efficient traits (Figure 11.B). This mixture was compared to the three species placed in monospecific communities, in order to analyse if their traits presented a better performance towards hydraulic roughness and sediment retention when aggregated.

The flow was recreated on a 4m by 0.90m central channel and was implemented with a homogenous input of sediments for a concentration of 11 g.L^{-1} at 3.6 L.s^{-1}.m^{-1} (± 0.06 L.s^{-1}.m^{-1}). The channel was 4 m long and 0.90 m wide upstream the plot, with an adjusted bed slope of 4.90% (± 0.13%). The slope was adjusted by excavating the soil underneath the channel and using wooden planks to stabilise the channel during the experiments. Six spacers were placed along the channel to measure the water level within the backwater area. The closest spacer from the plot was located at 0.13 m away, the next two were spaced by 0.25 m, the forth spacer was 0.5 m away from the third and the last two were spaced by 0.75 m. The sediment retention capacity by the sediment quantity upstream, within and downstream the vegetation. The quantity downstream was estimated using a sequential calculation method based on samples taken every 15sec in the outflow.

The complementarity effect of the multi-specific communities was characterised using two indices: the land equivalent ratio (LER) and the complementarity effect index. The first metric represents the relative area of monoculture required so the productivity is the same as when the species is in multi-specific conditions (Mead and Willey 1980):

$$LER = pLER_A + pLER_B = \frac{T_{A,multi-specific}}{T_{A,monospecific}} + \frac{T_{B,multi-specific}}{T_{B,monospecific}}$$

with $pLER_A$ and $pLER_B$ being the partial LERs for the species A and B; $T_{A,\text{multi-specific}}$ and $T_{B,\text{multi-specific}}$ being the trait values of the species A and B in the multi-specific conditions; and

$T_{A,monospecific}$ and $T_{B,monospecific}$ being the trait values of the species A and B in their respective monospecific conditions.

The second metric designates the result of species in multi-specific condition compared in monospecific condition as an increase or decrease in traits values (Loreau and Hector 2001; Darch et al. 2018):

$$CEI_A = n \times \left(pLER_A - \left(\frac{1}{n}\right)\right) \times T_{A,monospecific}$$

where n is the number of species, pLER is the partial LER of the species A and $T_{A,monospecific}$ is the trait value of the species A when in monospecific condition.

This first step in the understanding of plant species diversity behaviour allows to examine the complementarity effects of traits on hydraulic roughness and sediment retention. However, work is still needed to fully understand these effects, especially on a functional diversity approach rather than a specific diversity one. Using communities with different functional diversities would allow to characterise the direct effects of functional traits on hydraulic and sediment transport processes.

3.7. Investigating functional diversity effect on the hydraulic roughness

Functional diversity impacts ecosystem properties and processes for soil erosion mitigation, however results on what drives these effects are contentious. On the one hand, these effects could be driven by the dominance of a species in the community, represented by its community-weighted traits (Grime 1998; Díaz et al. 2007b). On the other hand, the effects could be driven by the diversity in traits composing the community (leading to dissimilarity in traits and niche differentiation), represented by functional diversity indices such as the functional divergence or evenness (Tilman et al. 1997a; Mason et al. 2005; Díaz et al. 2007b; Cadotte 2017).

The effect of functional diversity was analysed only on the hydraulic roughness here (being directly correlated to sediment retention), using three levels of functional diversity (four monospecific and two multi-specific conditions). The first multi-specific condition was composed of three species and the second was composed of four species, all comprising contrasting functional traits involved in the increase of the hydraulic roughness. The experiments were carried out using a runoff simulator with the same four discharges as the one used in 3.5. The hydraulic roughness was characterised by the unit stream power. The functional diversity was characterised by the functional variance of the traits, the Rao's quadratic entropy and the community-weighted traits in both multi-specific conditions. In order to identify the type of effect (dominance or diversity), the mean of the monospecific condition was compared to each multi-specific condition regarding their performance on the hydraulic roughness (Figure 11.C): (1) no difference means an absence of functional diversity effect and that the functional traits depends on the relative abundance or the contribution to the total biomass of dominant species; (2) if the mean of the monospecific is lower than the multi-specific, there is a positive effect of the functional diversity due to complementary use of the resources between the plant species or the canopy architecture and (3) if the mean of the monospecific is higher than the multi-specific, there is a negative effect of the functional diversity due to opposite processes of the ones that are positively affected (e.g. mobilisation/immobilisation, competition for light).

These results allow to deepen the knowledge on functional diversity effect on runoff and sediment transport processes, as well as the design of multi-functional herbaceous hedges.

REFERENCES

Boardman J, Poesen J (eds) (2006) Soil Erosion in Europe. John Wiley & Sons, Ltd

Boardman J, Verstraeten G, Bielders C (2006) Muddy Floods. In: Boardman J, Poesen J (eds) Soil Erosion in Europe. John Wiley & Sons, Ltd, pp 743–755

Bugnon F (1995) Nouvelle flore de Bourgogne, tome II : clés de détermination, Edition hors-série. Bulletin scientifique de Bourgogne, Dijon, France

Burylo M, Rey F, Bochet E, Dutoit T (2012) Plant functional traits and species ability for sediment retention during concentrated flow erosion. Plant Soil 353:135–144. doi: 10.1007/s11104-011-1017-2

Cadotte MW (2017) Functional traits explain ecosystem function through opposing mechanisms. Ecology Letters 20:989–996. doi: 10.1111/ele.12796

Cerdan O, Govers G, Le Bissonnais Y, et al (2010) Rates and spatial variations of soil erosion in Europe: A study based on erosion plot data. Geomorphology 122:167–177. doi: 10.1016/j.geomorph.2010.06.011

Dabney SM, McGregor KC, Wilson GV, Cullum RF (2009) How management of grass hedges affects their erosion reduction potential. Soil Science Society of America Journal 73:241. doi: 10.2136/sssaj2007.0434

Darch T, Giles CD, Blackwell MSA, et al (2018) Inter- and intra-species intercropping of barley cultivars and legume species, as affected by soil phosphorus availability. Plant and Soil 427:125–138. doi: 10.1007/s11104-017-3365-z

Díaz S, Lavorel S, de Bello F, et al (2007) Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences 104:20684–20689. doi: 10.1073/pnas.0704716104

Govers G (1992) Relationship between discharge, velocity and flow area for rills eroding loose, non-layered materials. Earth surface processes and landforms 17:515–528

Govers G (1990) Empirical relationships for the transport capacity of overland flow. IAHS 189:45–63

Gilley JE, Finkner SC (1988) Hydraulic roughness coefficients as affected by random roughness. Biological Systems Engineering: Papers and Publications

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of ecology 86:902–910. doi: 10.1046/j.1365-2745.1998.00306.x

Haase D, Fink J, Haase G, et al (2007) Loess in Europe—its spatial distribution based on a European Loess Map, scale 1:2,500,000. Quaternary Science Reviews 26:1301–1312. doi: 10.1016/j.quascirev.2007.02.003

Hegi G (1906) Illustrierte Flora von Mitteleuropa. Band I - VI, 1st edn. Lehmanns Verlag München, Munich, Germany

Jauzein P, Nawrot O (2011) Flore d'Ile-de-France. QUAE, Versailles, France

Kadereit A, Wagner GA (2014) Geochronological reconsideration of the eastern European key loess section at Stayky in Ukraine. Climate of the Past 10:783–796. doi: 10.5194/cp-10-783-2014

Lambinon J, Delvosalle L, Duvigneaud J (2012) Nouvelle flore de la Belgique, du G.-D. de Luxembourg, du nord de la France et des régions voisines, 6th edn.

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Functional ecology 16:545–556

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76. doi: 10.1038/35083573

Mansion D, Dume G, Rameau JC (1989) Flore Forestière Française : Guide Ecologique Illustré. Institut pour le développement forestier, Paris

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118

Mead R, Willey RW (1980) The Concept of a 'Land Equivalent Ratio' and Advantages in Yields from Intercropping. Experimental Agriculture 16:217–228. doi: 10.1017/S0014479700010978

Morgan RPC (2005) Soil Erosion and Conservation, 3rd ed. Blackwell Pub, Malden, MA

Rekolainen S, Ekholm P, Heathwaite L, et al (2006) Off-Site Impacts of Erosion: Eutrophication as an Example. In: Boardman J, Poesen J (eds) Soil Erosion in Europe. John Wiley & Sons, Ltd, pp 775–789

Remy J-C, Le Bissonnais Y (1998) Comparaison des phénomènes d'érosion entre le nord et le sud de l'Europe : ampleur des problèmes et nature des mécanismes. IRD, Montpellier

Richet J-B, Ouvry J-F, Saunier M (2017) The role of vegetative barriers such as fascines and dense shrub hedges in catchment management to reduce runoff and erosion effects: Experimental evidence of efficiency, and conditions of use. Ecological Engineering 103:455–469. doi: 10.1016/j.ecoleng.2016.08.008

Rothmaler W, Jäger EJ (2009) Rothmaler - Exkursionsflora von Deutschland. Bd. 3: Gefäßpflanzen: Atlasband, 11th edn. Sperktrum Akademischer Verlag, Berlin, Germany

Schuler J, Kächele H, Müller K, et al (2006) Economic Frame for Soil Conservation Policies. In: Boardman J, Poesen J (eds) Soil Erosion in Europe. John Wiley & Sons, Ltd, pp 791–803

Tilman D, Knops J, Wedin D, et al (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Université de Bourgogne (UFR Science de la vie) (2018) Nouvelle Flore de Bourgogne - Tome II Clés de détermination. In: Flore de Bourgogne. http://serres.u-bourgogne.fr/flore/rubrique.php3?id_rubrique=1. Accessed 26 Mar 2018

Verstraeten G, Bazzoffi P, Lajczak A, et al (2006) Reservoir and pond sedimentation in Europe. In: Boardman J, Poesen J (eds) Soil erosion in Europe. John Wiley & Sons, Ltd, West

Villarroel B (2015) Influence des traits morphologiques des végétaux herbacés sur l'érosion et le ruissellement des sols cultivés du nord-ouest de l'Europe. MSc Thesis, AgoParisTech

Yang CT (1972) Unit stream power and sediment transport. ASCE Journal of the Hydraulics Division 98:1805–1826

CHAPTER 1

4. PLANT FUNCTIONAL TRAIT EFFECTS ON RUNOFF TO DESIGN HERBACEOUS HEDGES FOR SOIL EROSION CONTROL

Léa Kervroëdan, Romain Armand, Mathieu Saunier, Jean-François Ouvry and Michel-Pierre Faucon

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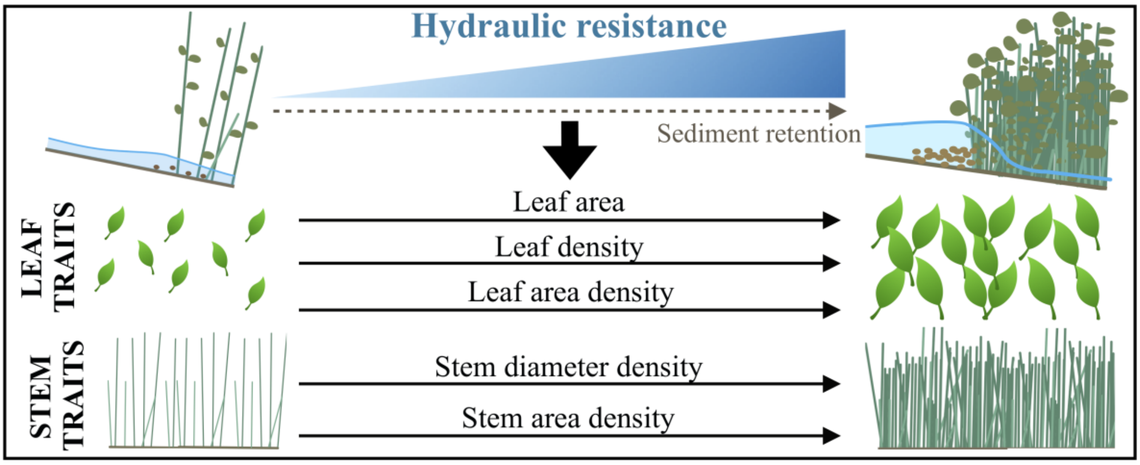
Abstract

Vegetation controls concentrated runoff and erosion in the European loess belt by increasing hydraulic roughness and sediment retention. Studies of plant effects on runoff velocity are usually based on a taxonomical characterisation and do not consider the effects of aboveground plant functional traits in attempts to understand soil erosion by water. This trait-based plant study investigates aboveground plant functional trait effects of herbaceous hedges on the hydraulic roughness to understand soil erosion. Eight aboveground functional traits were measured on fourteen indigenous and perennial plant species (caespitose or comprising dry biomass in winter) from north-west Europe with a high morphological variability. For each trait, density-weighted traits were calculated. The effects of functional traits and density-weighted traits were examined using a runoff simulator with four discharges. The leaf density and area, as well as density-weighted stem and leaf areas, stem diameter and specific leaf area were positively correlated with the hydraulic roughness. Generalised linear models defined the best combinations of traits and density-weighted traits: (1) leaf density and leaf area, (2) density-weighted leaf area and density-weighted projected stem area, and (3) density-weighted leaf area and density-weighted stem diameter. Moreover, the effects of leaf density, leaf area and density-weighted specific leaf area, varied depending on the discharge. This study is one of the first characterisation of aboveground trait effects on hydraulic roughness and highlights that vegetation with important stem density, diameter and leaf area plays a significant role in minimising soil erosion. The selection of plant species can derive from these plant trait effects to design reconstructed herbaceous hedges to minimise soil erosion.

Graphical abstract



Key-words

Aboveground functional traits; ecohydrological processes; hydraulic roughness; plant-runoff interaction; sediment retention; soil erosion control

4.1. Introduction

Soil erosion by water is influenced by precipitation, soil texture and structure, slopes that can generate intense discharges, and plant and litter covers which vary according to cultural practices in cultivated areas. Intense runoff and soil erosion are frequently found in north-western European catchments where the sloping loamy soils are intensively tilled and cultivated with annual crops (Gobin et al. 2003; Boardman and Poesen 2006). In the European loess belt, erosion can be mitigated by both (1) tillage reduction and the establishment of cover crops during sensitive seasons which increase the crop residue quantity on the soil surface and thus, reduce rill and inter-rill soil erosion (Knapen et al. 2007), and (2) establishment of vegetative barriers across the thalweg to mitigate rill and ephemeral gully erosion (Richet et al. 2017). Richet et al. (2017) demontrated the effects of fascines (i.e. vegetative barriers made of bundles of stems) on hydraulic roughness and soil erosion mitigation. However, their short lifetime and high cost represent a main limitation. Herbaceous hedges, defined as narrow strips of dense and stiff perennial vegetation, are of major interest to develop vegetative barriers with a high efficiency on the reduction of soil erosion at lower cost against concentrated flows (Dabney et al. 1995; Yuan et al. 2009). Besides, herbaceous hedges composed of indigenous plant species could offer other ecosystem services than regulating services such as the provision of habitats and their ecological connectivity in these catchments (Ouin and Burel 2002; Smith et al. 2008).

The effect of herbaceous vegetation on runoff and soil erosion, has been studied over the past decades (Temple et al. 1987; Haan et al. 1994; Ludwig et al. 2005; Lambrechts et al. 2014). Le Bissonnais et al. (2005), Blanco-Canqui et al. (2006), Dosskey et al. (2010), Ruiz-Colmenero et al. (2013), Lambrechts et al. (2014) and Stokes et al. (2014) noted the direct effects of vegetation cover on splash detachment and inter-rill erosion reduction. The impact of plant roots on infiltration capacity and resistance of soils to erosion by water has been well documented (Gyssels et al. 2005; De Baets et al. 2006; Isselin-Nondedeu and Bédécarrats 2007; Dabney et al. 2009; De Baets and Poesen 2010; Lambrechts et al. 2014; Berendse et al. 2015). The influence of vegetation on sediment retention was highlighted (Dillaha et al. 1989; Haan et al. 1994; Lowrance et al. 1995; Isselin-Nondedeu and Bédécarrats 2007; Dabney et al. 2009; Burylo et al. 2012a). The relationship between vegetation and sediment retention can be understood only if the vegetation effect on hydraulic roughness, which is the frictional resistance due to the contact of runoff with the vegetation, is characterised, as it is the main process with gravity furthering sediment retention. This effect has been previously investigated (Temple et al. 1987; Haan et al. 1994; Järvelä 2002; Akram et al. 2014; Cantalice et al. 2015; Cao et al. 2015). The presence of herbaceous vegetation has positive impacts on hydraulic roughness, as it reduces flow velocity and increases backwater depth (Hussein et al. 2007; Akram et al. 2014; Cantalice et al. 2015), thereby increasing sediment retention due to its linear relationship with backwater depth (Dabney et al. 1995; Meyer et al. 1995; Hussein et al. 2007). Plant effects on hydraulic roughness are highly variable among species and are difficult to explain without characterisation of all aboveground morphological traits (Dabney et al. 1995; Cantalice et al. 2015; Cao et al. 2015). The relationship between aboveground plant morphology and hydraulic roughness should be specified to globally understand runoff and soil erosion processes.

One of the challenges to improving the understanding in plant and vegetation (e.g. herbaceous hedges) effects on hydraulic roughness and soil erosion is the development of a functional trait-based approach (Faucon et al. 2017). This approach, which allows for characterising trait effects on ecosystem processes and services (Lavorel and Garnier 2002), has been developed with the establishment of the relationship between the soil detachment ratio and root length density for underground biomass (De Baets and Poesen 2010; Vannoppen et al. 2015; Mekonnen et al. 2016). Concerning aboveground characteristics, trait-based approaches highlighted the relationships between stem density, diameter and stiffness, and between leaf area and density with sediment retention (Bochet et al. 2000; Burylo et al. 2012a; Zhu et al. 2015; Mekonnen et al. 2016). Because the hydraulic roughness is one of the main process influencing sediment retention, plant functional traits known to influence sediment retention could influence the hydraulic roughness. Those traits, such as the stem and tiller density (Hayes et al. 1978; Temple 1982; Isselin-Nondedeu and Bédécarrats 2007; Morgan and Duzant 2008), stem diameter (Meyer et al. 1995; Bochet et al. 2000; Morgan and Duzant 2008), stem stiffness (Meyer et al. 1995; Dabney et al. 2009), specific leaf area (Graff et al. 2005), leaf area (Burylo et al. 2012a) and leaf density (Lambrechts et al. 2014), should be considered to specifically characterise the effect of aboveground traits on hydraulic roughness. In addition to characterising vegetation effects on hydrological processes and, notably, hydraulic roughness, the weight of traits in the vegetation should be considered (Garnier and Navas 2012) to improve the overall understanding of soil erosion.

Plant functional trait effects on hydraulic roughness should vary according to water discharge and different hydraulic processes (Cao et al. 2015). Vieira and Dabney (2012) showed that flow resistance of vegetation changed with flow depth. Temple et al. (1987) and Van Dijk et al. (1996) found that for low flows, the mean flow velocity was dependent on the vegetation density. However, for higher flows, when the flow depth was higher than the deflecting vegetation height, the leaf structures had less impact and the flow resistance was primarily dependent on the stem density and length and on the stem diameter and stiffness (Temple et al. 1987; Meyer et al. 1995). It is thus expected that high discharges would challenge the mechanical resistance through the stiffness, the density and the diameter of the stems, while low discharges would be impacted by the overall vegetation density. The challenge is to highlight plant functional trait effects on hydraulic roughness at several discharges that are representative of those present in catchments of north-west Europe.

This study of trait-based plant ecohydrology examined the relationship between aboveground plant functional traits with the hydraulic roughness at different discharges in fourteen perennial plant species presenting contrasting aboveground functional traits. The objectives are (1) to highlight the major functional traits influencing hydraulic roughness and (2) to examine the effect of discharges on the relationship between plant functional traits and hydraulic roughness to improve the understanding of soil erosion and select candidate species to create reconstructed herbaceous ecosystems to mitigate soil erosion in north-west Europe.

4.2. Materials and methods

4.2.1. Plant materials

Fourteen plant species that display contrasting aboveground morphological traits were chosen from 76 candidate species, resulting from six filters of selected functional types involved in mitigation of soil erosion in north-west Europe applied to the 3,500 spermatophyte species from north-west Europe (Lambinon et al. 2012). These selective filters were as follows: (1) Raunkiaer's life-form categories of "herbaceous chamaephytes", "hemicryptophytes" and "geophytes", i.e. perennial herbaceous vegetation that provide an effective soil cover during all seasons; (2) the presence of fresh (i.e. herbaceous chamaephytes and caespitose hemicryptophytes) or dry (i.e. non-caespitose hemicryptophytes and geophytes) biomass in winter when soil erosion is observed in north-west Europe (Boardman and Poesen 2006); (3) the presence of rhizomes or stolon to ensure lateral spreading capacity and burial tolerance due to sediment deposition; (4) vegetative height ≥ 20 cm, as it is the water maximal level in the catchment in north-west Europe; (5) a broad ecological niche to select species able to grow in several silty agricultural soils; and (6) non-weed species to prohibit their expansion in agricultural territories of north-west Europe.

Thirteen of the tested species were from the list of candidates (*Carex sylvatica, Carex flacca, Carex acutiformis, Carex pendula, Artemisia vulgaris, Origanum vulgare, Lolium perene, Senecio jacobaea, Tanacetum vulgare, Festuca arundinacea, Dactylis glomerata, Melica nutans, Phalaris arundinacea)* (Table 4). An exotic species, *Miscanthus sinensis,* was also tested along the thirteen indigenous species as it is considered a model plant in studies of plant hydraulic properties and erosion mitigation (Dabney et al. 2009).These species, varying in leaf and stem traits (e.g. density, area and specific area – density, diameter, specific density and dry matter content), were chosen to establish a range of traits to highlight the effect of aboveground plant traits on hydraulic roughness. The species were collected *in natura*, selecting only established individuals, and planted in 60 x 30 x 15 cm plots in early April 2016, creating 14 monospecific herbaceous hedges. These vegetation plots consisted of a wooden frame with a 1.5 cm grid fence at the bottom and were buried for three months prior to the experiments to allow the full development of the plants and roots. The plot design allowed for both plant growth and plot extraction for the experiments in the runoff simulator.

Table 4. List of the species used for the study and basic information.

Category	Species name	Family	Life form	Vegetative height (m)
Graminoid	*Dactylis glomerata L.*	Poaceae	Hemicryptophyte	0.96 (± 0.11)
	Festuca arundinacea Schreb.	Poaceae	Hemicryptophyte	0.54 (± 0.14)
	Lolium perenne L.	Poaceae	Hemicryptophyte	0.34 (± 0.02)
	Melica nutans L.	Poaceae	Hemicryptophyte	0.28 (± 0.02)
	Miscanthus sinensis	Poaceae	Hemicryptophyte; Geophyte	1.03 (± 0.26)
	Phalaris arundinacea L.	Poaceae	Hemicryptophyte	0.49 (± 0.11)
Herb	*Artemisia vulgaris L.*	Asteraceae	Hemicryptophyte	0.96 (± 0.17)
	Origanum vulgare L.	Lamiaceae	Chamaephyte; Hemicryptophyte	0.48 (± 0.06)
	Senecio jacobaea L.	Asteraceae	Hemicryptophyte	0.98 (± 0.04)
	Tanacetum vulgare L.	Asteraceae	Hemicryptophyte	0.64 (± 0.07)
Sedge	*Carex acutiformis Ehrh.*	Cyperaceae	Hemicryptophyte	0.17 (± 0.03)
	Carex flacca Schreb.	Cyperaceae	Hemicryptophyte	0.31 (± 0.04)
	Carex pendula Huds.	Cyperaceae	Caespitose hemicryptophyte	0.23 (± 0.15)
	Carex sylvatica Huds.	Cyperaceae	Caespitose hemicryptophyte	0.12 (± 0.03)

The stem height values represent the mean values (± standard deviation) measured on the experimental plots.

4.2.2. Plant morphological trait measurements

Eight aboveground plant morphological traits (leaf – area, density and specific area; stem – density, diameter, specific density, area and dry matter content), potentially involved in increasing hydraulic roughness, were measured (Table 5) at three levels along the stem – between 0 and 5 cm, 0 and 10 cm, and 0 and 20 cm – related to the variation of the water flow depth. Sampling collection and process methods followed the guidelines from Pérez-Harguindeguy et al. (2013). The leaves and stems were wrapped in moist paper and sealed in bags to limit water loss until the measures were complete, and they were then dried at 70°C for 72 h.

Table 5. List of the measured traits, their abbreviations and formulas used.

Morphological trait	Abbreviation	Unit	Formula[a]	Abbreviation after density-weighting
Stem density	SD	stems.dm^{-2}	-	-
Leaf density	LD	leaves.dm^{-2}	-	-
Leaf area	LA	mm^{2}	-	DLA
Specific leaf area	SLA	mm^{2}.mg^{-1}	$SLA = LA\ (Leaf\ mass_{dry})^{-1}$	DSLA
Stem diameter	SDm	mm	-	DSDm
Specific stem density	SSD	mg.mm^{-3}	$SSD = Mass_{oven\ dry}\ (Stem\ volume)^{-1}$	DSSD
Stem dry matter content	SDMC	-	$SDMC = Mass_{oven\ dry}\ (Mass_{fresh})^{-1}$	DSDMC
Projected stem area	SA	mm^{2}	$SA = L\ SDm$	DSA

[a] Volume formulas used were (1) for cylindrical stems: $V = \pi\ L\ [(SDm)\ (0.5)]^{2}$ and (2) for triangular stems (*Carex* sp.): $V = [\sqrt{(3)/4}]\ SDm^{2}\ L$ with L = height of the stem portion on which the concerned trait is measured

Trait measurements were performed within two 10 x 10 cm quadrats in each plot, to ensure representative sampling. Stem density was measured within each quadrat, defining pseudoculms in sedge species (Cyperaceae) and tillers in grass species as stems. Fresh and dry leaves were counted to determine the leaf density at each level along the stems in the quadrats. Specific leaf area (SLA) and leaf area were calculated from three mature leaves per quadrat. The leaves were scanned while fresh using a 600 dpi resolution, and the images were then analysed using the software Gimp 2.8 to determine the leaf area. The SLA was calculated by dividing the leaf area by the oven-dry mass of the leaf. Stem diameter, stem specific density and stem dry matter content were measured on three stems per quadrat. Stem diameter (mm) was measured three times along each vertical level of the fresh stem using a calliper. From the measurements of stem diameter, the projected stem area was calculated using the rectangle area formula and represented the contact area of a stem toward the flow direction. The stem specific density (mg.mm^{-3}) was calculated by dividing the oven-dry mass of the first 20 cm of the stem by the volume of the stem, measured when still fresh. The volume of the stems was calculated using the formula for the volume of a cylinder, except for the sledge species, which have triangular stems, and for which we used the formula for the volume of a triangular prism. The stem specific density of each height level along the stem was estimated using the volume of each level by assuming the density was homogeneous within the stem section. The stem specific density, representing the structural strength of a stem, was used as the estimation of the plant resistance to the water flow (Cornelissen et al. 2003; Burylo et al. 2012a; Pérez-Harguindeguy et al. 2013). The stem dry matter content was calculated from the ratio of the oven dry-mass of the first 20 cm of the stem and the fresh mass of the stem. The mean values of the measured traits are listed in Supplementary materials 1 and 2.

To characterise the effect of the herbaceous hedge on hydraulic roughness, the density-weighted mean of the trait values was calculated for each trait as the mean value of the trait multiplied by the proportion of the trait, here by the stem density for stem traits and by leaf density for leaf traits. This method does not include plant cover, given that all monospecific vegetation plot presented 100% cover and more precisely characterise the abundance of traits from stem and leaf densities. These density-weighted traits were determined for each vertical level along the stem (i.e. 0 – 5 cm, 0 – 10 cm and 0 – 20 cm).

4.2.3. Hydraulic measurements

We used the same runoff simulator as Richet et al. (2017) to quantify the effect of plant morphological traits on hydraulic roughness (Figure 15). The simulator allowed the recreation of a flow at chosen discharges and the measurement of hydrological parameters resulting from the presence of plants. The upper and lower parts of the simulator are equipped with flowmeters made of Venturi channels with a flow range of 0.06 $L.s^{-1}$ to 6 $L.s^{-1}$, comprising ultrasound probes that measure the water level in the channel at ± 1.26 mm. This system was manufactured by ISMA, France (Richet et al. 2017). The water was circulating within the system, with the aid of two pumps and a reservoir, in a closed circuit. The central part of the simulator is a channel setup with two galvanised iron sheets. The channel was 60 cm wide and 5.40 m long along a 5% slope. The entire channel was waterproofed using a plastic tarpaulin to avoid any water loss during the experiments. The tarpaulin was placed in order to obtain a smooth channel bottom and limit bottom roughness as much as possible. The roughness of the tarpaulin was determined by experiment using a control plot without any plants and represented a small percentage of the roughness created by the plants (Supplementary material 3). The vegetation was placed 4 m away from the head of the channel, in a 17 cm deep rectangular hole to level the ground with the flow and the slope. The tarpaulin used in the upper part of the channel was placed continually underneath the plot and through the lower part of the channel to avoid water loss by infiltration. The boundary effects were minimal as the plants were left in the wooden frame where they grew, and a wooden plank was placed along each side the entire channel. The small gap areas along the base of the planks and the bottom of the channel were sealed using clay. Along the channel, 7 spacers were set up to measure the topography of the channel bed and the water heights in the backwater and downstream of the plot. Five were located upstream of the plants and two were located downstream. At 1.46 m from the channel head, the spacers were spaced at 0.75 m.

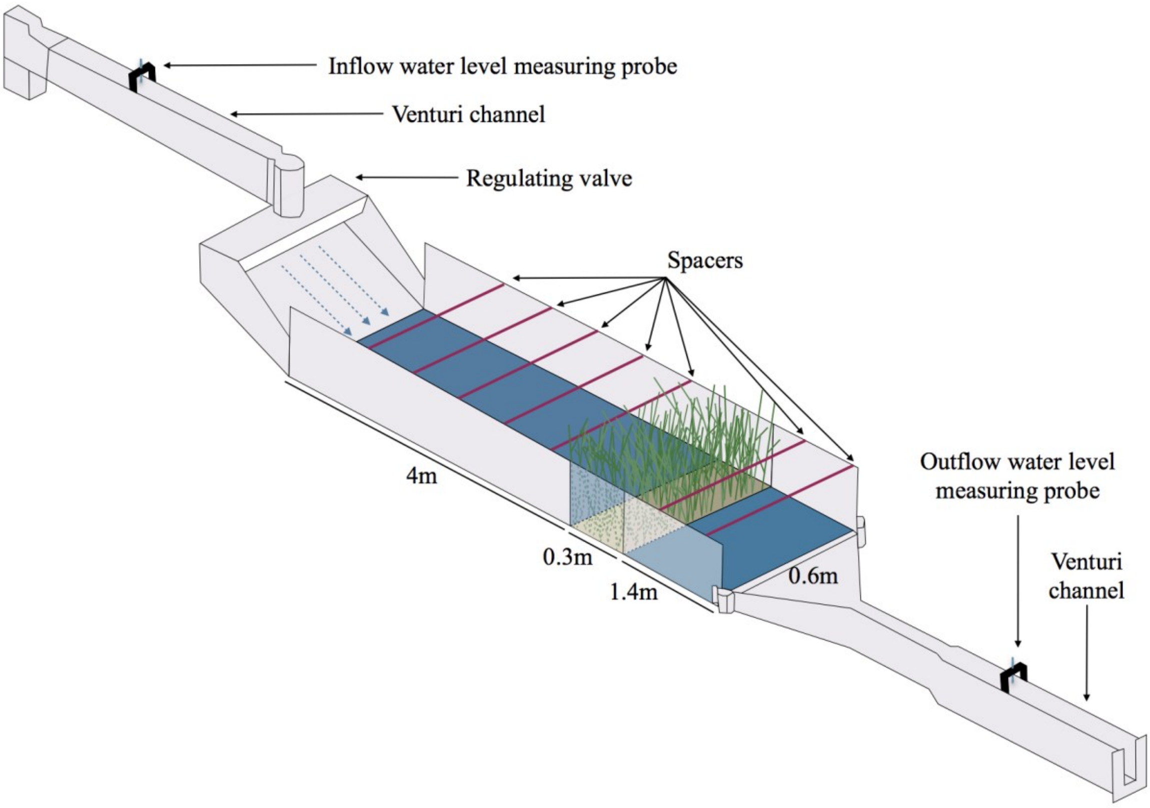


Figure 15. Runoff simulator used during the study.

The four discharges used in this study were 2, 4, 8 and 11 $L.s^{-1}.m^{-1}$ at ± 7%. The tested discharges are observed approximately every 0.5, 1, 2 and 5 years, respectively, in 5 ha catchments in the European loess belt with a 5 m-wide thalweg, as precised by (Richet et al. 2017). Both upstream and downstream discharges were continuously monitored. Water level were measured when the upstream and downstream discharges were equivalent. No infiltration occurred as the soil in the plots was saturated in water. The backwater and downstream flow levels were measured using the spacers as elevation-known baselines. The levels were determined by measuring the distance between the top of the water flow and the spacer every 10 cm from the edges of the channel, corresponding to seven vertical profiles.

To express the hydraulic resistance related to the plant presence, we used the unit stream power (*USP*), a sediment transport capacity index (Yang 1972; Govers 1992). USP is defined as the "energy dissipation per unit of time and per unit of weight of the flow" (Govers 1992), depending on its velocity and the slope:

$$USP = V\,S \qquad (1)$$

where *USP* is expressed in $m.s^{-1}$, V is the mean velocity ($m.s^{-1}$), and S is the channel slope ($m.m^{-1}$) (Morgan et al. 1998; Cao et al. 2015; Hessel et al. 2016). The lower the *USP* is, the greater the hydraulic roughness will be. The mean velocity was calculated using the water levels measured at the closest spacer upstream of the plot. Govers (1990) determined a *USP* critical value of 0.004 $m.s^{-1}$ that indicates the threshold from which soil is most likely to erode in the loamy soils found in the European loess belt. Govers (1990) established this critical value for bare loess soils with a D_{50} from 58 µm to 218 µm, at slopes ranging from 1° to 8° and for discharges varying from 0.2 to 10 $L.s^{-1}.m^{-1}$. The *USP*, Manning coefficients and backwater depths are presented in Supplementary material 3.

4.2.4. Data analysis

Principal component analysis (PCA) was conducted to examine the link between each trait. Data used for the PCA included the measured traits in the two quadrats within the plots. Generalised linear models (GLM) for the inverse-link gamma family were then processed to examine the effect of plant morphological traits on the *USP* at each discharge.

Another analysis using GLMs were then used to analyse the relationship between the *USP* and the significant traits and density-weighted traits identified in the previous step between 0 and 10 cm. These models were run separately for each discharge to highlight differences of trait effects among the discharge levels. To avoid autocorrelation within the models, traits and density-weighted traits were processed in separate models. Due to the small sample size *n* and ratio $n/K < 40$ (where *K* the number of parameters used in the models), second order Akaike's Information Criterion (AICc) and ΔAICc were used to assess the model performance, as recommended in Burnham and Anderson (2002). ΔAICc is the difference between the AICc of a model *i* and the model with the lowest AICc (also characterised as the best model fit). Burnham and Anderson (2002) recognise the models with a ΔAICc < 2 as models with substantial support, which are identified as the best model fits in this study. Models with ΔAICc varying between 2 and 7, indicating less support, were also analysed as recommended by Burnham et al. (2011). Akaike weights (wAICc) were used in this study to assess the relative likelihood of the models, as this indicates the probability of a model *i* being the best among the set of tested models (Burnham and Anderson 2002; Brown et al. 2011). All the data in this study were analysed using the statistical software R (version 3.3.2).

4.3. Results

4.3.1. Variations of plant morphological traits

Covariation among the seven traits of the 14 species studied were analysed using a PCA (Figure 16), which showed that the first two principal components explained 71.9% of the variance. The first principal component (PC1) accounted for 47% of the total variance and was associated with the projected stem area, the stem diameter and the stem density. The variance of PC1 was explained by the leaf area, the stem specific density and the specific leaf area. Two groups of variables were observed along the PC1 axis: the projected stem area and the stem diameter on the positive end and the stem density on the negative end. The second principal component (PC2) accounted for 24.9% of the total variance and was explained by the stem dry matter content, which was found on the negative end of the axis. The variance of PC2 was explained by the leaf density and the stem height.

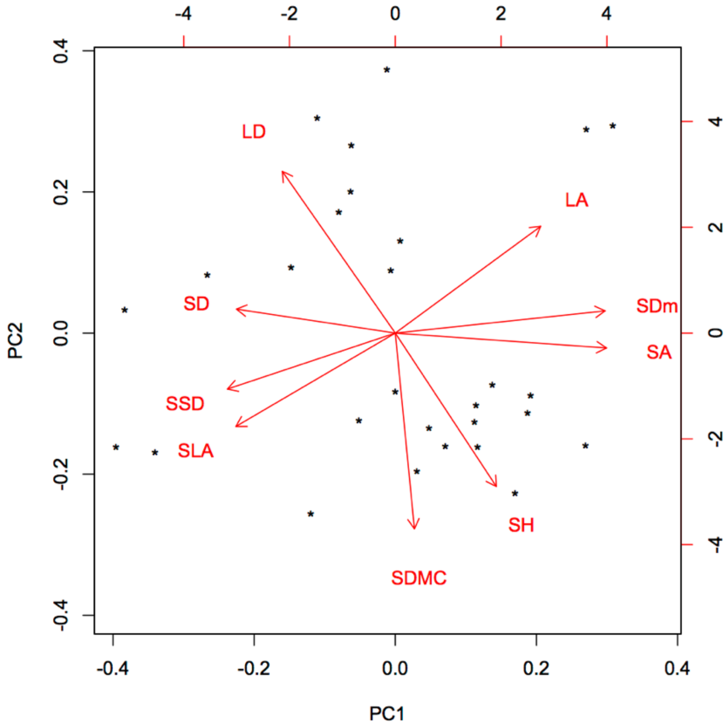


Figure 16. Principal component analysis of nine morphological traits measured on 14 plant species within two quadrats. PC1 explained 47% of the variance and PC2 explained 24.9%. LA = leaf area, LD = leaf density, SA = projected stem area, SD = stem density, SDm = stem diameter,

SDMC = stem dry matter content, SLA = specific leaf area, SSD = stem specific density. The vegetative stem height (SH) was added to the other traits for this analysis.

4.3.2. Effect of morphological traits on the Unit Stream Power

The effects of traits on hydraulic roughness were analysed using GLMs to show the traits affecting the *USP* at each discharge (Table 6). The leaf densities (0-5 cm and 0-10 cm) were correlated to the *USP* for the four discharge levels. The leaf area had a significant relationship with the *USP* at discharges Q1 and Q2, while the leaf density (0-20 cm) was significant with the *USP* at discharges Q3 and Q4. The weighted leaf area (0-5 cm, 0-10 cm and 0-20 cm), the weighted projected stem area (0-5 cm, 0-10 cm and 0-20 cm), the weighted stem diameter (0-5 cm, 0-10 cm and 0-20 cm) and the weighted SLA (0-5 cm) were correlated to the *USP* at discharges Q1, Q2, Q3 and Q4. The weighted SLA (0-10 cm) influenced the *USP* at discharges Q2, Q3 and Q4.

Table 6. Morphological trait effects on USP for each discharge used. Generalised linear models (GLM) of each trait and density-weighted trait at each stem level in relation to the USP for each discharge. LA = leaf area, LD = leaf density, SA = projected stem area, SD = stem density, SDm = stem diameter, SDMC = stem dry matter content, SLA = specific leaf area, SSD = stem specific density. The density-weighted traits were named by adding “D” at the beginning of their existing abbreviations.

Traits	Level along the stem	Q1 = 2 L.s^{-1}.m^{-1}		Q2 = 4 L.s^{-1}.m^{-1}		Q3 = 8 L.s^{-1}.m^{-1}		Q4 = 11 L.s^{-1}.m^{-1}	
		AIC	ß	AIC	ß	AIC	ß	AIC	ß
LA		-158.15	**0.04 ***	-147.27	**0.03 ***	-131.38	0.02 ns	-125.83	0.02 ns
LD	0 - 5 cm	-159.11	**1.33 ***	-150.06	**1.07 ****	-135.45	**0.78 ****	-131.14	**0.76 ****
	0 - 10 cm	-157.68	**0.81 ***	-148.34	**0.65 ***	-134.21	**0.49 ***	-129.23	**0.46 ****
	0 - 20 cm	-154.49	0.44 ns	-145.21	0.37 ns	-131.54	**0.29 ***	-126.12	**0.27 ***
SA	0 - 5 cm	-152.71	0.46 ns	-141.33	0.22 ns	-126.83	0.11 ns	-120.93	0.1 ns
	0 - 10 cm	-152.55	0.22 ns	-141.25	0.11 ns	-126.78	0.05 ns	-120.87	0.05 ns
	0 - 20 cm	-151.70	0.08 ns	-140.75	0.02 ns	-126.51	0.0048 ns	-120.58	0.0037 ns
SD		-151.71	0.73 ns	-142.22	0.84 ns	-128.89	0.77 ns	-122.19	0.57 ns
SDMC		-153.37	-707.3 ns	-143.40	-571.4 ns	-130.15	-475.66 ns	-124.26	-429.54 ns
SDm	0 - 5 cm	-152.70	22.9 ns	-141.33	11.02 ns	-126.83	5.54 ns	-120.93	5.18 ns
	0 - 10 cm	-152.58	22.47 ns	-141.27	10.76 ns	-126.79	5.32 ns	-120.89	4.96 ns
	0 - 20 cm	-152.41	21.78 ns	-141.15	9.93 ns	-126.72	4.72 ns	-120.80	4.33 ns
SLA		-154.96	-7.87 ns	-142.59	-4.47 ns	-127.46	-2.39 ns	-121.92	-2.46 ns
SSD	0 - 5 cm	-153.46	-128.71 ns	-142.06	-75.4 ns	-127.63	-49.26 ns	-121.86	-46.93 ns
	0 - 10 cm	-153.64	-277 ns	-141.95	-151.2 ns	-127.38	-91.26 ns	-121.75	-93.63 ns
	0 - 20 cm	-153.33	-569.8 ns	-141.35	-251.1 ns	-126.88	-134.38 ns	-121.05	-134.77 ns
DLA	0 - 5 cm	-163.29	**0.0004 ****	-154.63	**0.0003 ****	-138.44	**0.0002 ****	-136.08	**0.0002 ****
	0 - 10 cm	-163.26	**0.0003 ****	-153.79	**0.0002 ****	-137.69	**0.0001 ****	-135.63	**0.0001 ****
	0 - 20 cm	-163.44	**0.0002 ****	-153.65	**0.0001 ****	-137.78	**0.0001 ****	-136.37	**0.0001 ****
DSA	0 - 5 cm	-161.43	**0.02 ****	-154.14	**0.02 ****	-141.02	**0.02 ****	-133.45	**0.01 ****
	0 - 10 cm	-160.97	**0.01 ****	-153.49	**0.01 ****	-140.30	**0.0081 ****	-132.81	**0.0071 ****
	0 - 20 cm	-158.44	**0.0055 ***	-149.75	**0.0046 ***	-136.37	**0.0036 ****	-129.07	**0.0031 ***
DSDMC		-151.38	1.72 ns	-141.76	2.31 ns	-128.25	2.14 ns	-121.66	1.51 ns
DSDm	0 - 5 cm	-161.43	**1.25 ****	-154.14	**1.05 ****	-141.02	**0.82 ****	-133.45	**0.71 ****
	0 - 10 cm	-161.06	**1.24 ****	-153.64	**1.05 ****	-140.46	**0.82 ****	-132.96	**0.71 ****
	0 - 20 cm	-160.46	**1.21 ***	-152.56	**1.01 ****	-139.27	**0.79 ****	-131.86	**0.68 ****
DSLA	0 - 5 cm	-157.33	**0.06 ***	-148.47	**0.05 ***	-134.37	**0.04 ***	-129.65	**0.04 ****
	0 - 10 cm	-154.34	0.03 ns	-145.19	**0.03 ***	-131.64	**0.02 ***	-125.92	**0.02 ***
	0 - 20 cm	-151.38	0.0058 ns	-141.71	0.0076 ns	-128.17	0.007 ns	-122.10	0.0061 ns
DSSD	0 - 5 cm	-151.10	0.12 ns	-141.05	0.22 ns	-127.32	0.23 ns	-121.02	0.15 ns
	0 - 10 cm	-151.07	0.19 ns	-141.03	0.41 ns	-127.32	0.45 ns	-120.99	0.28 ns
	0 - 20 cm	-151.04	0.23 ns	-141.00	0.8 ns	-127.33	0.91 ns	-121.00	0.58 ns

N = 14; AIC = Aikake's Information Criterion; ß = regression coefficient; *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant. The significant correlations are indicated in bold.

From the results in Table 6, GLMs were used to highlight traits and density-weighted traits (0-10 cm) that have a greater impact on the *USP* within the traits previously identified as significantly impacting the *USP* (Figure 17, Table 7, Table 8). The GLMs for single traits (Table 7) highlighted that the combination of leaf area and leaf density was the best model fit for all discharges (wAICc > 0.50), although the leaf density was also a good fit for the data at discharges Q3 and Q4 (wAICc = 0.39 and wAICc = 0.34, respectively). The results of the density-weighted trait GLMs (Table 8) showed that models USP ~ DLA + DSA and USP ~ DLA + DSDm were the best fit for all discharges, with cumulative wAICc ranging from 0.75 at discharge Q1 to 0.84 at Q4, showing a growing significance along with the discharge gradient. However, the ranking of importance changed with the discharges, as USP ~ WLA + WSA was greater for discharges Q1 and Q4, USP ~ DLA + DSDm was greater for Q3 and both combinations were equivalent for Q2.

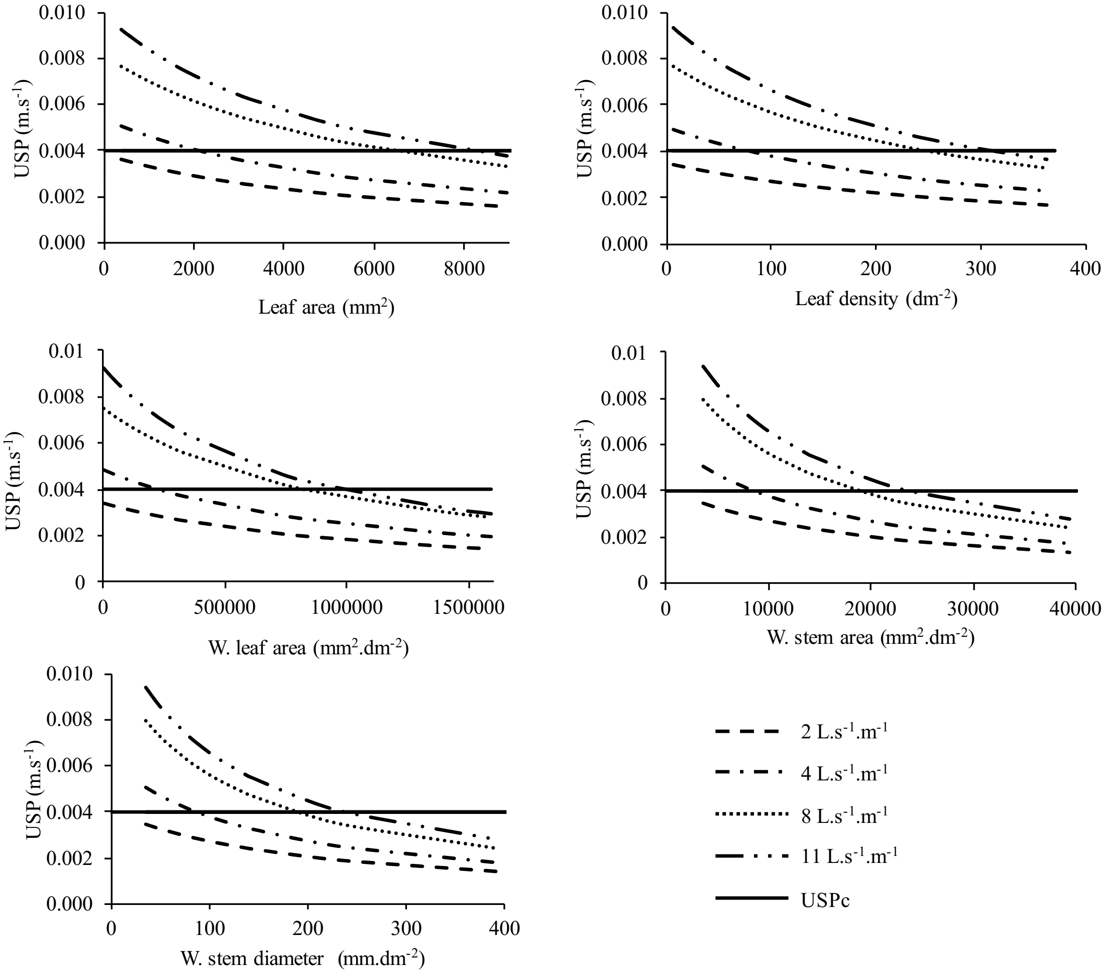


Figure 17. Relationship between USP and traits and density-weighted traits identified as the best fit to hydraulic roughness at 0 – 10 cm. USPc represents the threshold of 0.004 m.s^{-1} from which soil is likely to erode in loamy soils found in the European loess belt (Govers 1990).

Table 7. Selected GLMs fitted to USP and two traits as estimation variables for each discharge used. The models are sorted from the smallest ΔAICc to the highest ΔAICc at each discharge used.

Discharge	Models	AICc	ΔAICc	wAICc
$Q1 = 2\ L.s^{-1}.m^{-1}$	USP ~ LA + LD	-158.68	0.0	0.707
	USP ~ LA	-155.75	2.9	0.164
	USP ~ LD	-155.28	3.4	0.129
$Q2 = 4\ L.s^{-1}.m^{-1}$	USP ~ LA + LD	-148.93	0.0	0.737
	USP ~ LD	-145.94	3.0	0.166
	USP ~ LA	-144.87	4.1	0.097
$Q3 = 8\ L.s^{-1}.m^{-1}$	USP ~ LA + LD	-132.34	0.0	0.512
	USP ~ LD	-131.81	0.5	0.393
	USP ~ LA	-128.98	3.4	0.096
$Q4 = 11\ L.s^{-1}.m^{-1}$	USP ~ LA + LD	-127.94	0.0	0.595
	USP ~ LD	-126.83	1.1	0.342
	USP ~ LA	-123.43	4.5	0.063

Full model was: USP ~ LA + LD; LD from (0-10 cm). AICc = second order Aikake's Information Criterion; see text for more details on ΔAICc and wAICc. LA = leaf area and LD = leaf density

Table 8. Selected GLMs fitted to USP and four density-weighted traits as estimation variables for each discharge used. The models are sorted from the smallest ΔAICc to the highest ΔAICc for each discharge used.

Discharge	Models	AICc	ΔAICc	wAICc
Q1 = 2 $L.s^{-1}.m^{-1}$	USP ~ DLA + DSA	-165.33	0.00	0.377
	USP ~ DLA + DSDm	-165.29	0.04	0.370
	USP ~ DLA + DSLA + DSDm	-161.93	3.40	0.069
	USP ~ DLA + DSA + DSLA	-161.92	3.41	0.069
	USP ~ DLA	-160.86	4.47	0.040
	USP ~ DLA + DSDm + DSA	-160.48	4.85	0.033
	USP ~ DSDm	-158.66	6.67	0.013
	USP ~ DSA	-158.57	6.76	0.013
Q2 = 4 $L.s^{-1}.m^{-1}$	USP ~ DLA + DSA	-160.22	0.00	0.412
	USP ~ DLA + DSDm	-160.22	0.00	0.412
	USP ~ DLA + DSLA + DSDm	-156.45	3.77	0.063
	USP ~ DLA + DSA + DSLA	-156.38	3.84	0.060
	USP ~ DLA + DSDm + DSA	-155.16	5.05	0.033
Q3 = 8 $L.s^{-1}.m^{-1}$	USP ~ DLA + DSDm	-143.44	0.00	0.405
	USP ~ DLA + DSA	-143.44	0.01	0.404
	USP ~ DLA + DSLA + DSDm	-138.78	4.67	0.039
	USP ~ DLA + DSA + DSLA	-138.73	4.71	0.038
	USP ~ DLA + DSDm + DSA	-138.39	5.06	0.032
	USP ~ DSDm	-138.06	5.39	0.027
	USP ~ DSA	-137.9	5.55	0.025
Q4 = 11 $L.s^{-1}.m^{-1}$	USP ~ DLA + DSA	-140.87	0.00	0.423
	USP ~ DLA + DSDm	-140.86	0.02	0.419
	USP ~ DLA + DSLA + DSDm	-136.7	4.17	0.053
	USP ~ DLA + DSA + DSLA	-136.68	4.20	0.052
	USP ~ DLA + DSDm + DSA	-135.85	5.03	0.034

Full model was: USP ~ WLA + WSA + WSLA + WSDm. All variables are for traits (0-10 cm). AICc = second order Aikake's Information Criterion; see text for more details on ΔAICc and wAICc. WLA = weighted leaf area, WSA = weighted projected stem area, WSDm = weighted stem diameter, WSLA = weighted specific leaf area.

4.4. Discussion

Contrary to processes of soil detachment by water flow (De Baets and Poesen 2010; Vannoppen et al. 2015) and sediment retention (Burylo et al. 2012a), the effect of morphological plant traits on hydraulic roughness presents a lack of research to understand the role of plant and vegetation on soil erosion. This study examined the effects of plant morphological traits on hydraulic roughness for four discharges.

4.4.1. Effect of morphological traits and density-weighted traits on hydraulic roughness

Stem and leaf traits influenced hydraulic roughness, given that they constitute a hydraulic brake on water flows. However, some stem and leaf traits may have a greater effect on hydraulic roughness. This study has highlighted that, among the considered aboveground traits involved in soil erosion (i.e. leaf area, SLA, leaf density, stem density, stem diameter, stem specific density, projected stem area and stem dry matter content), only the leaf area and the leaf density presented a significant effect on hydraulic roughness. The leaf traits have a stronger impact on hydraulic roughness than stem traits, regarding non-weighted traits. The GLMs showed that the combination of leaf density and leaf area better explained the effect on hydraulic roughness than these traits alone for any discharge used. Plant individuals with better trade-off between leaf density and leaf area, meaning high leaf density and long leaves, such as some graminoid species, would have a great impact on mitigating the unit stream power and thus increase hydraulic roughness. These results are in agreement with other studies highlighting the efficiency of several graminoid species in soil erosion mitigation (Morgan 2004; Isselin-Nondedeu and Bédécarrats 2007). The absence of the stem density effect on hydraulic roughness is not in agreement with the literature where the stem density is considered a main trait impacting flow velocity and soil erosion (Temple et al. 1987; Meyer et al. 1995; Isselin-Nondedeu and Bédécarrats 2007; Morgan and Duzant 2008; Mekonnen et al. 2016). This contradiction could be explained by the lack of a standard characterisation method of all stem and leaf traits involved in hydraulic roughness and soil erosion (e.g. defining the tillers and pseudoculms as stems when characterising the stem density). The stem density is one of the main traits included in hydraulic and soil erosion models such as VFSMOD (Muñoz Carpena and Parsons 2014) and in studies focusing on the relationship between vegetation and hydraulic roughness or sediment retention (Temple 1982; Van Dijk et al. 1996; Morgan 2004; Xiao et al. 2011), which could be improved by considering the effect of other stem traits (e.g. stem diameter). In the trait-based approach, the importance of stem density in the plant-hydraulic roughness relationship lays in its use in the calculation of weighted stem trait values in the vegetation. Indeed, this approach highlighted that mainly density-weighted traits influenced hydraulic roughness. Specifically, all the GLMs included weighted leaf area, indicating its great importance in the increase of hydraulic roughness. Projected stem area or stem diameter showed no significance on the hydraulic roughness at the trait level but, by considering weighted stem traits, weighted projected stem area and weighted stem diameter showed highly significant effects on the unit stream power. The GLMs showed that the best fit model was DSA + DLA (weighted projected stem area + weighted leaf area) as these traits represent the interception area of the leaves and stems with the water flow in the vegetation, i.e. a hydraulic brake. As the stem diameter, projected stem area and leaf area were negatively associated with the stem density, trade-offs among these stem and leaf traits can be considered to improve herbaceous hedge effects on hydraulic roughness. The effect of weighted SLA, when associated with weighted leaf area and weighted stem diameter or weighted leaf area and weighted projected stem area, was also observed ($3 < \Delta AICc < 5$). Overall, vegetation presenting the best trade-off between stem density and weighted stem diameter, as well as between leaf density and leaf area, will have a greater efficiency to increase hydraulic roughness. Herbaceous hedges that present these weighted leaf and stem traits would be partly composed of graminoid species, given that these present large leaf density, leaf area, stem diameter and a greater hydraulic roughness than non-graminoid species (Isselin-Nondedeu and Bédécarrats 2007). Stem and leaf densities should be considered to calculate weighted-traits in herbaceous hedges and quantify the effect on soil erosion. Characterisation of trait weights in herbaceous hedges vegetation allowed to highlight the main morphological aboveground traits and their combinations involved in hydraulic roughness, as well as the importance of stem density as a plant marker to examine the effect of vegetation on runoff. As a result, this trait-based approach can be effectively applied at the vegetation level to understand and model runoff and soil erosion.

4.4.2. Effects of morphological traits on hydraulic roughness depending on runoff processes

Flow rate variations can trigger different soil-plant-water processes (Temple et al. 1987; Dabney et al. 2004; Vieira and Dabney 2012). The results here are consistent with the hypothesis that the influence of aboveground traits on hydraulic roughness can change with the discharge. The effect of leaf density (0-20 cm) and leaf area on hydraulic roughness varied with the discharge. The results showed the importance of leaf density in increasing hydraulic roughness at higher discharges (ΔAIC < 2). However, for lower discharges, a combination of leaf area and leaf density should be considered rather than the traits alone. The results for the leaf area are in accordance with the one found by Temple et al. (1987) showing a decreasing impact of the leaf structure with an increasing discharge. At a small discharge (2 $L.s^{-1}.m^{-1}$), weighted SLA (0-10 cm) did not present an effect on the hydraulic roughness, but a positive influence was observed at 4 $L.s^{-1}.m^{-1}$. Differences in the influence of leaf density and weighted SLA among the discharges may be interpreted as the water depth being too low to enter into contact with all the leaves between 0 and 20 cm of each individual and with large SLA until 5 cm of the vegetation at small discharges. Herbaceous hedges, playing a key role in hydraulic roughness, presents the best trade-off between stem density and diameter, as well as leaf density and area at low discharges, and with increasing water discharge, larger basal leaf density and basal SLA. This study indicates that some trait and density-weighted trait effects on hydraulic roughness are linked to the flow water level. The characterisation of these effects according to flow depth constitutes an advance to model water flows and soil erosion in ecosystems and landscapes.

4.4.3. Consequences on sediment retention

As hydraulic roughness is linked to sediment retention and transport capacities (Munoz-Carpena et al. 1999; Isselin-Nondedeu and Bédécarrats 2007; Dabney et al. 2009; Lambrechts et al. 2014), plant morphological traits, which have positive effects on hydraulic roughness, can be discussed with studies highlighting plant trait effects on sediment retention. Indeed, results showed the positive effect of the leaf area on hydraulic roughness, whereas there was no effect of stem specific density at small discharges, such as 2 $L.s^{-1}.m^{-1}$, which is consistent with Burylo et al. (2012) on the sediment retention capacity for more intense erosion processes. Results display the greater impact of density-weighted traits, which were previously not considered in studies on plant trait effects on sediment retention. The density-weighted trait approach is therefore important in understanding the plant-soil interaction involved in soil erosion.

Application of this trait-based approach in ecohydrology involves using the results to manage the reduction of soil erosion. Use of the unit stream power allows to characterise the plant efficiency with regard to sediment retention, with a critical USP (USPc) value of 0.004 $m.s^{-1}$ determined by Govers (1990), which indicates the threshold from which soil is most likely to erode in loamy soils found in the European loess belt. From identified traits and density-weighted traits presenting an effect on hydraulic roughness and their values ($USP < 0.004$ $m.s^{-1}$) plant species selection could be performed to create new herbaceous ecosystems that will be efficient to reduce runoff and further sediment retention on degraded areas (e.g. bare soils in degraded agroecosystems, urban and mining habitats) (Figure 17).

4.5. Conclusions

This trait-based ecohydrology study allows the identification of important plant traits that influence the hydraulic roughness. The results indicate the stronger effect of density-weighted traits, showing that communities with the best trade-offs between stem density, diameter and leaf area are the key to mitigate soil erosion. This new knowledge in the relationship between plant functional traits with hydraulic roughness and soil erosion constitutes a new advancement for modelling vegetation effects on soil erosion and creating new herbaceous ecosystems in degraded areas (e.g. bare soils of agroecosystems, mining and urban habitats). These newly reconstructed herbaceous ecosystems will play an important role in soil erosion mitigation. Future work should (1) include these relationships between aboveground traits and hydraulic roughness in existing models to estimate the transport and sediment retention capacities of flows and design herbaceous hedges to mitigate soil erosion and (2) examine the effect of functional diversity on runoff and soil erosion, as it could influence hydraulic roughness by ecologically complementing aboveground biomass and, more precisely, by limiting vegetation lodging.

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REFERENCES

Akram S, Yu B, Ghadiri H, et al (2014) The links between water profile, net deposition and erosion in the design and performance of stiff grass hedges. J Hydrol 510:472–479. doi: 10.1016/j.jhydrol.2014.01.001

Berendse F, van Ruijven J, Jongejans E, Keesstra S (2015) Loss of plant species diversity reduces soil erosion resistance. Ecosystems 18:881–888. doi: 10.1007/s10021-015-9869-6

Blanco-Canqui H, Gantzer CJ, Anderson SH (2006) Performance of grass barriers and filter strips under interrill and concentrated flow. J Environ Qual 35:1969. doi: 10.2134/jeq2006.0073

Boardman J, Poesen J (eds) (2006) Soil Erosion in Europe. John Wiley & Sons, Ltd

Bochet E, Poesen J, Rubio JL (2000) Mound development as an interaction of individual plants with soil, water erosion and sedimentation processes on slopes. Earth Surf Process Landf 25:847–867

Brown KA, Flynn DFB, Abram NK, et al (2011) Assessing natural resource use by forest-reliant communities in Madagascar using functional diversity and functional redundancy metrics. PLoS ONE 6:e24107. doi: 10.1371/journal.pone.0024107

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer, New York

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav Ecol Sociobiol 65:23–35. doi: 10.1007/s00265-010-1029-6

Burylo M, Rey F, Bochet E, Dutoit T (2012) Plant functional traits and species ability for sediment retention during concentrated flow erosion. Plant Soil 353:135–144. doi: 10.1007/s11104-011-1017-2

Cantalice JRB, Melo RO, Silva YJAB, et al (2015) Hydraulic roughness due to submerged, emergent and flexible natural vegetation in a semiarid alluvial channel. J Arid Environ 114:1–7. doi: 10.1016/j.jaridenv.2014.10.012

Cao L, Zhang Y, Lu H, et al (2015) Grass hedge effects on controlling soil loss from concentrated flow: A case study in the red soil region of China. Soil Tillage Res 148:97–105. doi: 10.1016/j.still.2014.12.009

Cornelissen JHC, Lavorel S, Garnier E, et al (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust J Bot 51:335–380

Dabney SM, McGregor KC, Wilson GV, Cullum RF (2009) How management of grass hedges affects their erosion reduction potential. Soil Sci Soc Am J 73:241. doi: 10.2136/sssaj2007.0434

Dabney SM, Meyer LD, Harmon WC, et al (1995) Depositional patterns of sediment trapped by grass hedges. Trans ASAE 38:1719–1729

Dabney SM, Shields Jr FD, Temple DM, Langendoen EJ (2004) Erosion processes in gullies modified by establishing grass hedges. Trans ASAE 47:1561

De Baets S, Poesen J (2010) Empirical models for predicting the erosion-reducing effects of plant roots during concentrated flow erosion. Geomorphology 118:425–432. doi: 10.1016/j.geomorph.2010.02.011

De Baets S, Poesen J, Gyssels G, Knapen A (2006) Effects of grass roots on the erodibility of topsoils during concentrated flow. Geomorphology 76:54–67. doi: 10.1016/j.geomorph.2005.10.002

Dillaha TA, Reneau RB, Mostaghimi S, Lee D (1989) Vegetative filter strips for agricultural nonpoint source pollution control. Trans ASAE 32:513–0519

Dosskey MG, Vidon P, Gurwick NP, et al (2010) The role of riparian vegetation in protecting and improving chemical water quality in streams. J Am Water Resour Assoc 1–18. doi: 10.1111/j.1752-1688.2010.00419.x

Faucon M-P, Houben D, Lambers H (2017) Plant functional traits: soil and ecosystem services. Trends Plant Sci 22:385–394. doi: 10.1016/j.tplants.2017.01.005

Garnier E, Navas M-L (2012) A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. Agron Sustain Dev 32:365–399

Gobin A, Govers G, Jones R, et al (2003) Assessment and reporting on soil erosion: Background and workshop report. European Environment Agency, Copenhagen

Govers G (1992) Relationship between discharge, velocity and flow area for rills eroding loose, non-layered materials. Earth Surf Process Landf 17:515–528

Govers G (1990) Empirical relationships for the transport capacity of overland flow. Int Assoc Hydrol Sci 189:45–63

Graff CD, Sadeghi AM, Lowrance RR, Williams RG (2005) Quantifying the sensitivity of the riparian ecosystem management model (REMM) to changes in climate and buffer characteristics common to conservation practices. Trans ASAE 48:1377–1387

Gyssels G, Poesen J, Bochet E, Li Y (2005) Impact of plant roots on the resistance of soils to erosion by water: A review. Prog Phys Geogr 29:189–217. doi: 10.1191/0309133305pp443ra

H**aan CT, Barfield BJ, Hayes JC (1994)** Design Hydrology and Sedimentology for Small Catchments. Academic Press

Hayes JC, Barfield BJ, Barnhisel RI (1978) Evaluation of grass characteristics related to sediment filtration. ASAE 78–2513:21

Hessel R, Jetten VG, Liu B, Qiu Y (2016) Evaluating Effects of Soil and Water Management and Land Use Change on the Loess Plateau of China Using LISEM. In: Morgan RPC, Nearing M (eds) Handbook of Erosion Modelling. John Wiley and Sons, pp 223–248

Hussein J, Yu B, Ghadiri H, Rose C (2007) Prediction of surface flow hydrology and sediment retention upslope of a vetiver buffer strip. J Hydrol 338:261–272

Isselin-Nondedeu F, Bédécarrats A (2007) Influence of alpine plants growing on steep slopes on sediment trapping and transport by runoff. Catena 71:330–339. doi: 10.1016/j.catena.2007.02.001

Järvelä J (2002) Flow resistance of flexible and stiff vegetation: A flume study with natural plants. J Hydrol 269:44–54

Knapen A, Poesen J, Govers G, et al (2007) Resistance of soils to concentrated flow erosion: A review. Earth-Sci Rev 80:75–109. doi: 10.1016/j.earscirev.2006.08.001

Lambinon J, Delvosalle L, Duvigneaud J (2012) Nouvelle flore de la Belgique, du G.-D. de Luxembourg, du nord de la France et des régions voisines, 6th edn.

Lambrechts T, François S, Lutts S, et al (2014) Impact of plant growth and morphology and of sediment concentration on sediment retention efficiency of vegetative filter strips: Flume experiments and VFSMOD modeling. J Hydrol 511:800–810. doi: 10.1016/j.jhydrol.2014.02.030

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Funct Ecol 16:545–556

Le Bissonnais Y, Cerdan O, Lecomte V, et al (2005) Variability of soil surface characteristics influencing runoff and interrill erosion. CATENA 62:111–124. doi: 10.1016/j.catena.2005.05.001

Lowrance RR, Altier LS, Newbold JD, et al (1995) Water quality functions of riparian forest buffer systems in the Chesapeake Bay watershed. U.S. Environmental Protection Agency, Chesapeake Bay Program

Ludwig JA, Wilcox BP, Breshears DD, et al (2005) Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. Ecology 86:288–297. doi: 10.1890/03-0569

Mekonnen M, Keesstra SD, Ritsema CJ, et al (2016) Sediment trapping with indigenous grass species showing differences in plant traits in northwest Ethiopia. Catena 147:755–763. doi: 10.1016/j.catena.2016.08.036

Meyer LD, Dabney SM, Harmon WC (1995) Sediment-trapping effectiveness of stiff-grass hedges. Am Soc Agric Eng 38:809–815

Morgan RPC (2004) Vegetative-Based Technologies for Erosion Control. In: Stokes A, Spanos I, Norris JE, Cammeraat E (eds) Eco- and Ground Bio-Engineering: The Use of Vegetation to Improve Slope Stability. Springer, Dordrecht, The Netherlands, pp 265–272

Morgan RPC, Duzant JH (2008) Modified MMF (Morgan–Morgan–Finney) model for evaluating effects of crops and vegetation cover on soil erosion. Earth Surf Process Landf 33:90–106. doi: 10.1002/esp.1530

Morgan RPC, Quinton JN, Smith RE, et al (1998) The EUROSEM model. In: Boardman J, Favis-Mortlock D (eds) Modelling Soil Erosion by Water. Springer Science and Business Media, pp 389–398

Muñoz Carpena R, Parsons JE (2014) VFSMOD - Vegetative filter strips modelling system. University of Florida

Munoz-Carpena R, Parsons JE, Gilliam JW (1999) Modeling hydrology and sediment transport in vegetative filter strips. J Hydrol 214:111–129

Ouin A, Burel F (2002) Influence of herbaceous elements on butterfly diversity in hedgerow agricultural landscapes. Agric Ecosyst Environ 93:45–53

Pérez-Harguindeguy N, Díaz S, Garnier E, et al (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167–234. doi: 10.1071/BT12225

Richet J-B, Ouvry J-F, Saunier M (2017) The role of vegetative barriers such as fascines and dense shrub hedges in catchment management to reduce runoff and erosion effects: Experimental evidence of efficiency, and conditions of use. Ecol Eng 103:455–469. doi: 10.1016/j.ecoleng.2016.08.008

Ruiz-Colmenero M, Bienes R, Eldridge DJ, Marques MJ (2013) Vegetation cover reduces erosion and enhances soil organic carbon in a vineyard in the central Spain. Catena 104:153–160. doi: 10.1016/j.catena.2012.11.007

Smith J, Potts S, Eggleton P (2008) The value of sown grass margins for enhancing soil macrofaunal biodiversity in arable systems. Agric Ecosyst Environ 127:119–125. doi: 10.1016/j.agee.2008.03.008

Stokes A, Douglas GB, Fourcaud T, et al (2014) Ecological mitigation of hillslope instability: ten key issues facing researchers and practitioners. Plant Soil 377:1–23. doi: 10.1007/s11104-014-2044-6

Temple DM (1982) Flow Retardance of Submerged Grass Channel Linings. Trans ASAE 25:1300–1303. doi: 10.13031/2013.33717

Temple DM, Robinson KM, Ahring RM, Davis AG (1987) Stability Design of Grass-Lined Open Channels. U.S. Department of Agriculture, Washington, D.C.

Van Dijk PM, Kwaad FJPM, Klapwijk M (1996) Retention of water and sediment by grass strips. Hydrol Process 10:1069–1080. doi: 10.1002/(SICI)1099-1085(199608)10:8<1069::AID-HYP412>3.0.CO;2-4

Vannoppen W, Vanmaercke M, De Baets S, Poesen J (2015) A review of the mechanical effects of plant roots on concentrated flow erosion rates. Earth-Sci Rev 150:666–678. doi: 10.1016/j.earscirev.2015.08.011

Vieira DAN, Dabney SM (2012) Two-dimensional flow patterns near contour grass hedges. Hydrol Process 26:2225–2234. doi: 10.1002/hyp.8262

Xiao B, Wang Q, Wang H, et al (2011) The effects of narrow grass hedges on soil and water loss on sloping lands with alfalfa (Medicago sativa L.) in Northern China. Geoderma 167–168:91–102. doi: 10.1016/j.geoderma.2011.09.010

Yang CT (1972) Unit stream power and sediment transport. ASCE J Hydraul Div 98:1805–1826

Yuan Y, Bingner RL, Locke MA (2009) A Review of effectiveness of vegetative buffers on sediment trapping in agricultural areas. Ecohydrology 2:321–336. doi: 10.1002/eco.82

Zhu H, Fu B, Wang S, et al (2015) Reducing soil erosion by improving community functional diversity in semi-arid grasslands. J Appl Ecol 52:1063–1072. doi: 10.1111/1365-2664.12442

Supplementary material 1. Mean of the measured stem traits for the species tested.

Species	Stem Density (dm^{-2})	Stem Area (mm^{2})			Specific Stem Density (mg.mm^{-3})			Stem Dry Matter Content	Stem Diameter (mm)		
		0 - 5 cm	0 - 10 cm	0 - 20 cm	0 - 5 cm	0 - 10 cm	0 - 20 cm		0 - 5 cm	0 - 10 cm	0 - 20 cm
Carex acutiformis	35 (± 0)	213 (± 31.4)	398.8 (± 49.4)	623.3 (± 180.1)	1.03 (± 0.26)	0.59 (± 0.17)	0.42 (± 0.13)	0.22 (± 0.01)	4.26 (± 0.63)	3.99 (± 0.57)	3.74 (± 0.67)
Lolium perene	131 (± 23)	80.4 (± 33.5)	159.7 (± 61.6)	315.2 (± 111.5)	2.15 (± 0.57)	1.06 (± 0.23)	0.52 (± 0.08)	0.27 (± 0.03)	1.61 (± 0.67)	1.6 (± 0.59)	1.58 (± 0.55)
Artemisia vulgaris	11 (± 4)	277.8 (± 48.2)	551 (± 94.4)	1095.1 (± 183.8)	1.37 (± 0.26)	0.7 (± 0.12)	0.35 (± 0.07)	0.3 (± 0.04)	5.56 (± 0.96)	5.51 (± 0.91)	5.48 (± 0.87)
Melica nutans	90 (± 8)	47.3 (± 6.2)	86.8 (± 12.2)	162.2 (± 22.7)	1.63 (± 0.42)	0.97 (± 0.24)	0.55 (± 0.12)	0.33 (± 0.04)	0.95 (± 0.12)	0.87 (± 0.15)	0.81 (± 0.16)
Carex flacca	27 (± 1)	159 (± 20.6)	311.3 (± 41.2)	617.1 (± 81.3)	1.22 (± 0.35)	0.64 (± 0.18)	0.32 (± 0.09)	0.21 (± 0.01)	3.18 (± 0.41)	3.11 (± 0.4)	3.09 (± 0.39)
Dactylis glomerata	24 (± 8)	173.3 (± 32.6)	342 (± 50.9)	677.5 (± 91)	1.52 (± 0.47)	0.77 (± 0.22)	0.39 (± 0.1)	0.32 (± 0.07)	3.47 (± 0.65)	3.42 (± 0.52)	3.39 (± 0.47)
Festuca arundinacea	110 (± 1)	116.1 (± 31.7)	222.7 (± 61.7)	455.3 (± 122.8)	1.35 (± 0.5)	0.73 (± 0.26)	0.35 (± 0.1)	0.27 (± 0.03)	2.32 (± 0.63)	2.23 (± 0.6)	2.28 (± 0.61)
Phalaris arundinacea	13 (± 3)	206.6 (± 21.4)	388.4 (± 29.9)	731.4 (± 44.2)	1.02 (± 0.18)	0.57 (± 0.07)	0.32 (± 0.03)	0.4 (± 0.01)	4.13 (± 0.43)	3.88 (± 0.42)	3.66 (± 0.47)
Carex sylvatica	34 (± 2)	169.5 (± 21.4)	304.8 (± 39.2)	335.9 (± 116.7)	0.61 (± 0.12)	0.35 (± 0.05)	0.31 (± 0.02)	0.18 (± 0.01)	3.39 (± 0.43)	3.18 (± 0.4)	2.66 (± 1.07)
Tanacetum vulgare	11 (± 4)	264.1 (± 25.5)	523.1 (± 53.8)	1033.9 (± 103.3)	1.56 (± 0.29)	0.8 (± 0.16)	0.41 (± 0.08)	0.37 (± 0.02)	5.28 (± 0.51)	5.23 (± 0.52)	5.17 (± 0.5)
Carex pendula	17 (± 9)	423.2 (± 54.1)	827.9 (± 106.3)	1340.3 (± 161.1)	0.89 (± 0.32)	0.46 (± 0.16)	0.29 (± 0.07)	0.22 (± 0.01)	8.46 (± 1.08)	8.28 (± 1.05)	7.87 (± 1.12)
Origanum vulgare	17 (± 7)	105.9 (± 27.4)	212.1 (± 44)	415.6 (± 81.4)	1.61 (± 0.91)	0.77 (± 0.4)	0.4 (± 0.2)	0.39 (± 0.2)	2.12 (± 0.55)	2.12 (± 0.44)	2.08 (± 0.41)
Senecio jacobaea	8 (± 1)	316.4 (± 108.2)	611.9 (± 214.2)	1199.8 (± 435.1)	0.9 (± 0.14)	0.48 (± 0.07)	0.25 (± 0.04)	0.33 (± 0.05)	6.33 (± 1.93)	6.12 (± 1.75)	6 (± 1.73)
Miscanthus sinensis	85 (± 6)	230.3 (± 77.3)	464.6 (± 161.7)	942.4 (± 327)	1.48 (± 0.18)	0.74 (± 0.11)	0.36 (± 0.05)	0.39 (± 0.04)	4.61 (± 1.55)	4.65 (± 1.55)	4.71 (± 1.54)

The data represent the mean values of the traits (± standard deviation).

Supplementary material 2. Mean of the measured leaf traits for the species tested.

Species	Leaf density (dm^{-2})			Specific leaf area ($mm.mg^{-1}$)	Leaf area (mm^2)
	0 - 5 cm	0 - 10 cm	0 - 20 cm		
Carex acutiformis	171 (± 11)	287 (± 119)	463 (± 270)	18.39 (± 1.32)	5549.36 (± 1025.32)
Lolium perene	87 (± 15)	230 (± 12)	455 (± 7)	29.31 (± 6.01)	991.66 (± 239.8)
Artemisia vulgaris	9 (± 2)	14 (± 6)	49 (± 10)	24.35 (± 4.69)	3196.87 (± 865.78)
Melica nutans	10 (± 8)	54 (± 29)	203 (± 70)	41.02 (± 5.17)	496.84 (± 63.32)
Carex flacca	68 (± 1)	96 (± 3)	141 (± 10)	16.54 (± 0.55)	1551.52 (± 335.97)
Dactylis glomerata	91 (± 2)	110 (± 6)	148 (± 36)	25.05 (± 3.12)	2983.32 (± 507.33)
Festuca arundinacea	148 (± 62)	253 (± 55)	382 (± 81)	17.9 (± 3.43)	2818.71 (± 1332.19)
Phalaris arundinacea	23 (± 11)	47 (± 4)	67 (± 6)	21.85 (± 0.94)	2690.76 (± 422.81)
Carex sylvatica	285 (± 71)	362 (± 88)	407 (± 88)	18.03 (± 1.34)	2416.78 (± 536.73)
Tanacetum vulgare	21 (± 8)	32 (± 10)	47 (± 16)	18.06 (± 1.57)	4774.24 (± 1533.63)
Carex pendula	122 (± 50)	156 (± 54)	210 (± 73)	15.94 (± 2.06)	8925.34 (± 2271.98)
Origanum vulgare	4 (± 5)	6 (± 6)	95 (± 49)	23.75 (± 3.36)	394.97 (± 93.43)
Senecio jacobaea	26 (± 15)	43 (± 9)	83 (± 18)	17.77 (± 2.53)	1954.64 (± 650.37)
Miscanthus sinensis	51 (± 1)	63 (± 2)	122 (± 4)	15.81 (± 0.88)	4664.62 (± 1146.56)

The data represent the mean values of the traits (± standard deviation).

Supplementary material 3. USP, Manning coefficient and water depth data.

Species	Q1 = 2 $L.s^{-1}.m^{-1}$			Q2 = 4 $L.s^{-1}.m^{-1}$			Q3 = 8 $L.s^{-1}.m^{-1}$			Q4 = 11 $L.s^{-1}.m^{-1}$		
	USP	Manning coefficient n	Water depths	USP	Manning coefficient n	Water depths	USP	Manning coefficient n	Water depths	USP	Manning coefficient n	Water depths
Carex acutiformis	0.00187	0.84	0.05	0.00262	0.72	0.07	0.00397	0.54	0.10	0.00376	0.62	0.13
Lolium perenne	0.00278	0.47	0.03	0.00379	0.38	0.05	0.00552	0.33	0.07	0.00667	0.28	0.08
Artemisia vulgaris	0.00326	0.28	0.03	0.00475	0.24	0.04	0.00668	0.23	0.06	0.00805	0.20	0.07
Melica nutans	0.00413	0.32	0.02	0.00499	0.31	0.04	0.00689	0.25	0.06	0.00901	0.20	0.06
Carex flacca	0.00311	0.57	0.03	0.00443	0.44	0.04	0.00629	0.33	0.06	0.00762	0.29	0.07
Dactylis glomerata	0.00247	0.63	0.04	0.00311	0.58	0.06	0.00439	0.47	0.09	0.00494	0.45	0.11
Festuca arundinacea	0.00140	1.21	0.07	0.00215	0.89	0.09	0.00316	0.70	0.12	0.00380	0.61	0.14
Phalaris arundinacea	0.00233	0.64	0.04	0.00360	0.46	0.05	0.00554	0.34	0.07	0.00662	0.29	0.08
Carex sylvatica	0.00225	0.76	0.04	0.00288	0.67	0.07	0.00429	0.51	0.09	0.00483	0.48	0.11
Tanacetum vulgare	0.00382	0.22	0.02	0.00542	0.19	0.03	0.00946	0.12	0.04	0.01140	0.11	0.05
Carex pendula	0.00151	1.38	0.06	0.00195	1.21	0.10	0.00279	0.94	0.14	0.00324	0.86	0.17
Origanum vulgare	0.00421	0.44	0.02	0.00599	0.31	0.03	0.00992	0.19	0.04	0.01100	0.18	0.05
Senecio jacobaea	0.00303	0.32	0.03	0.00500	0.22	0.04	0.00806	0.16	0.05	0.00978	0.14	0.06
Miscanthus sinensis	0.00164	1.23	0.06	0.00201	1.14	0.09	0.00282	0.92	0.14	0.00328	0.84	0.17

USP: Unit Stream Power ($m.s^{-1}$); Manning coefficient n: roughness coefficient from Manning's formula; Water depths: level of the water at the spacer in front of the vegetation (m)

CHAPTER 2

5. NON-COMPLEMENTARITY EFFECTS OF PLANT SPECIES DIVERSITY ON RUNOFF AND SEDIMENT RETENTION IN HERBACEOUS VEGETATION

Léa Kervroëdan, Romain Armand, Mathieu Saunier and Michel-Pierre Faucon

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Abstract

Plant species diversity impacts ecosystem processes integrating soil-plant interactions, although the effects on processes associated with runoff and soil erosion are not fully understood. Herbaceous vegetation control concentrated runoff and soil erosion in north-west Europe through the increase of hydraulic roughness, which leads to sediment retention by decreasing flow velocity and is influenced by aboveground biomass and traits (i.e. stem diameter and density, and leaf area and density). Hypothesis was that traits' complementarity would lead to a more optimal space-use, furthering aboveground biomass productivity and thus, better hydraulic roughness and sediment retention. Runoff experimentations were performed, using a sediment input, on three mono-specific and one multi-specific communities composed of indigenous species from north-west Europe with contrasting traits furthering hydraulic roughness and sediment retention. The results emphasised non-complementarity effects on the hydraulic roughness and sediment retention through the dominant effect of the leaf density and density-weighted leaf area. This absence of complementarity effects on hydraulic roughness and sediment retention would be explained by the non-increase of aboveground biomass productivity with species diversity. This absence of complementarity effects on hydraulic roughness and sediment retention constitutes a new advance in the characterisation of diversity effects on runoff and soil erosion processes under temperate climates.

Key-words

Complementarity effect; Leaf and stem functional traits; Plant-soil-runoff interactions; Sediment transport; Sediment trapping and deposition; Soil erosion control

5.1. Introduction

Ecosystem processes are affected by plant species diversity (Naeem, Thompson, Lawler, Lawton, & Woodfin, 1994; Tilman, 2001). The loss of diversity can lead to a reduction of ecosystem functioning by the decline of the biomass productivity and perturbation of the carbon, nutrients and water cycling as well as of the stability of ecosystem functions (Cardinale et al. 2012). The mechanisms driving the effects of plant species diversity can follow two non-exclusive hypotheses (Loreau 2000; Garnier et al. 2016). The selection hypothesis stipulates that one or more dominant species in the community would increase the overall productivity and efficiency of the community. On the other hand, the complementarity hypothesis specifies that diversity effects on ecosystem processes result from the niche differentiation between the species in the community leading to a more complete space and resources uses (Loreau and Hector 2001; Fargione et al. 2007). Influenced by neighbouring, the interspecific differences in functional traits (i.e. “morpho-physio-phenological traits which indirectly impact fitness via their effects on growth, reproduction and survival” (Violle et al. 2007)) among diverse plant communities have been found to impact positively ecosystem processes (e.g. productivity, soil erosion, water cycling) (Naeem et al. 1994; Caldeira et al. 2001; Spehn et al. 2005; Zhu et al. 2015). These positive effects of trait divergence – or functional diversity (i.e. “the value, range, and relative abundance of plant functional traits in a given ecosystem” (Tilman 2001b; Díaz et al. 2007a)) – are driven by trait complementarity (e.g. plant height and stature on light capture and space use for aboveground biomass productivity), which lead a better space occupation inducing greater effects of the community structure and distribution towards ecosystem processes (Naeem et al. 1994; Spehn et al. 2000; Anten 2004; Zhu et al. 2015; Cadotte 2017). The effects of plant species diversity on numerous ecosystem processes have been studied and emphasised (e.g. net productivity, biogeochemical cycling); however, the relationships with other ecosystem processes, such as soil erosion, still need to be understood.

The relationships between plant species diversity and soil erosion processes have been studied, mostly focussing on the effects of non-herbaceous plant roots on soil stabilisation and vegetation patch pattern impact on erosion rates (Gyssels et al. 2005; Bautista et al. 2007; Pohl et al. 2009; Martin et al. 2010; Berendse et al. 2015; Hou et al. 2016). Under temperate climates, concentrated runoff and soil erosion are mainly controlled by the hydraulic roughness of herbaceous vegetation patches (i.e. frictional resistance of the vegetation in contact with the flow) which induces sediment retention by slowing the flow velocity. The effects of functional traits on hydraulic roughness and sediment retention have been studied over the past decades, showing the effects of aboveground biomass, stem projected area (i.e. stem area towards the flow direction), density and diameter as well as leaf area and density (Burylo et al. 2012a; Zhu et al. 2015; Mekonnen et al. 2016; Kervroëdan et al. 2018). However, some of these traits are negatively correlated (e.g. leaf area and density), implying that trait diversity could bring a better impact on hydraulic roughness and sediment retention by exerting a complementary effect of the traits (Kervroëdan et al. 2018). Studies focussing on the effects of functional diversity on sediment retention and erosion rates showed contradictory effects on the functional diversity (Erktan et al. 2013; Zhu et al. 2015). These debated results stress the need to deepen the knowledge on the effects of traits' aggregation in herbaceous vegetation on concentrated runoff and soil erosion to increase hydraulic roughness and sediment retention in north-west European agricultural landscapes.

This trait-based ecohydrological study aimed to examine the complementarity effect of plant species presenting contrasting traits involved in hydraulic roughness and sediment retention by comparing monospecific and multi-specific communities. The aggregation of contrasting traits, involved in the increase of hydraulic roughness, would induce a complementarity effect of the traits in the aboveground space use and a better sediment retention. This competitive balance among the species in the multi-specific communities would generate a more efficient use of the aboveground space, lead to an increase of biomass productivity and trait values in the community and thus, higher hydraulic roughness and sediment retention. Through the complementarity in space use and the higher hydraulic roughness, the retained sediments would also present a wider variety of sizes in the multi-specific plant communities.

5.2. Materials and methods

5.2.1. Experimental site

The plots were implanted at the bottom edge of a loamy field cultivated with winter wheat located in the municipality of Drosay, Normandy, France (Figure 18.A). The soil, defined as luvisol, was characterised by 12.5% (± 0.66%) clay, 64.3% (± 0.84%) silt, 23.2% (± 0.64%) sand with a pH of 5.3 (±0.1), 2.1% (±0.19%) of organic matter content and a crusting index of 1.8 (± 0.08) (Rémy and Marin-Laflèche 1974).

In October 2016, one year *prior* experiments, the plants were planted in 1m^2 plots with a density of 53 seedlings.m^{-2} (Figure 19). The multi-specific plots were planted with the same proportion of each species and the seedlings were placed so seedlings of the same species would not be next to each other. A control plot, with no vegetation, was also tested with three replicates. Each plot was randomly distributed along a 50m strip and 2m were left between each plot to allow movement and limit plant spreading in the next plot (Figure 18.B).

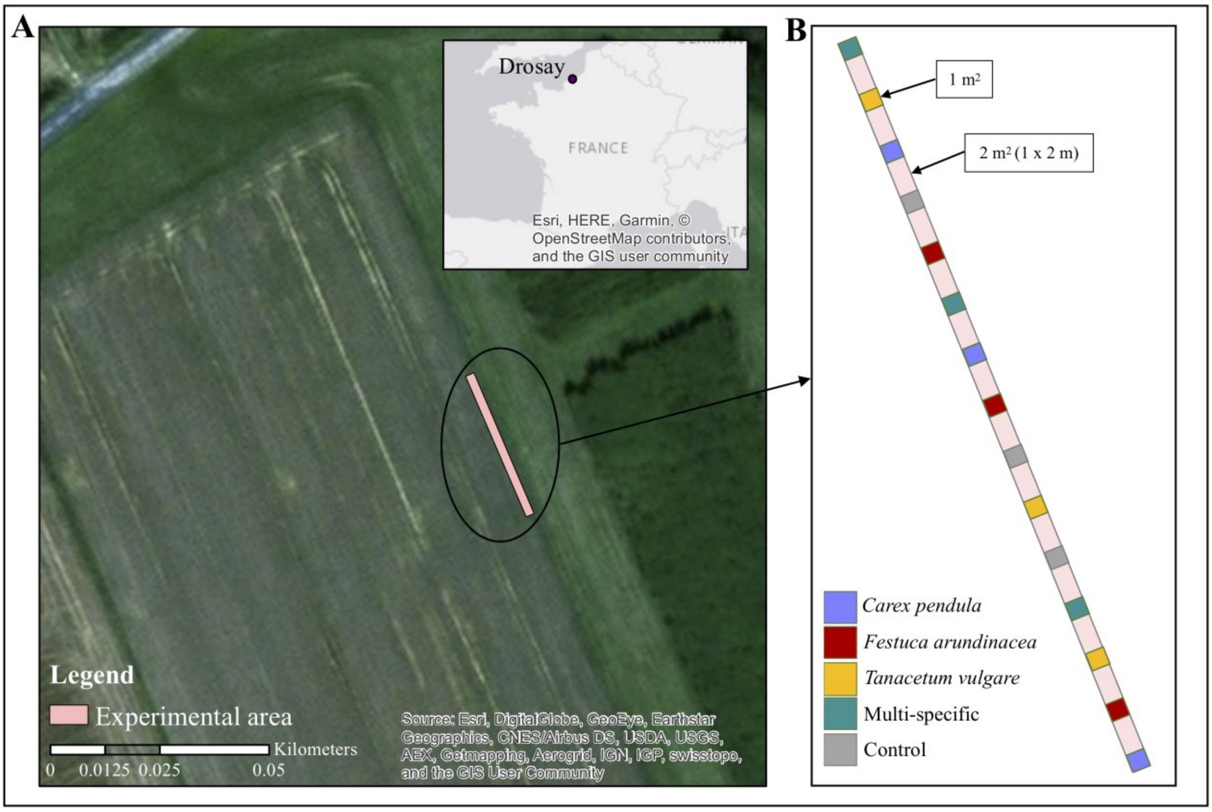

Figure 18. Experimental site. A – Localisation of the experimental site in Drosay, France and B – Placement of the plots within the experimental area.

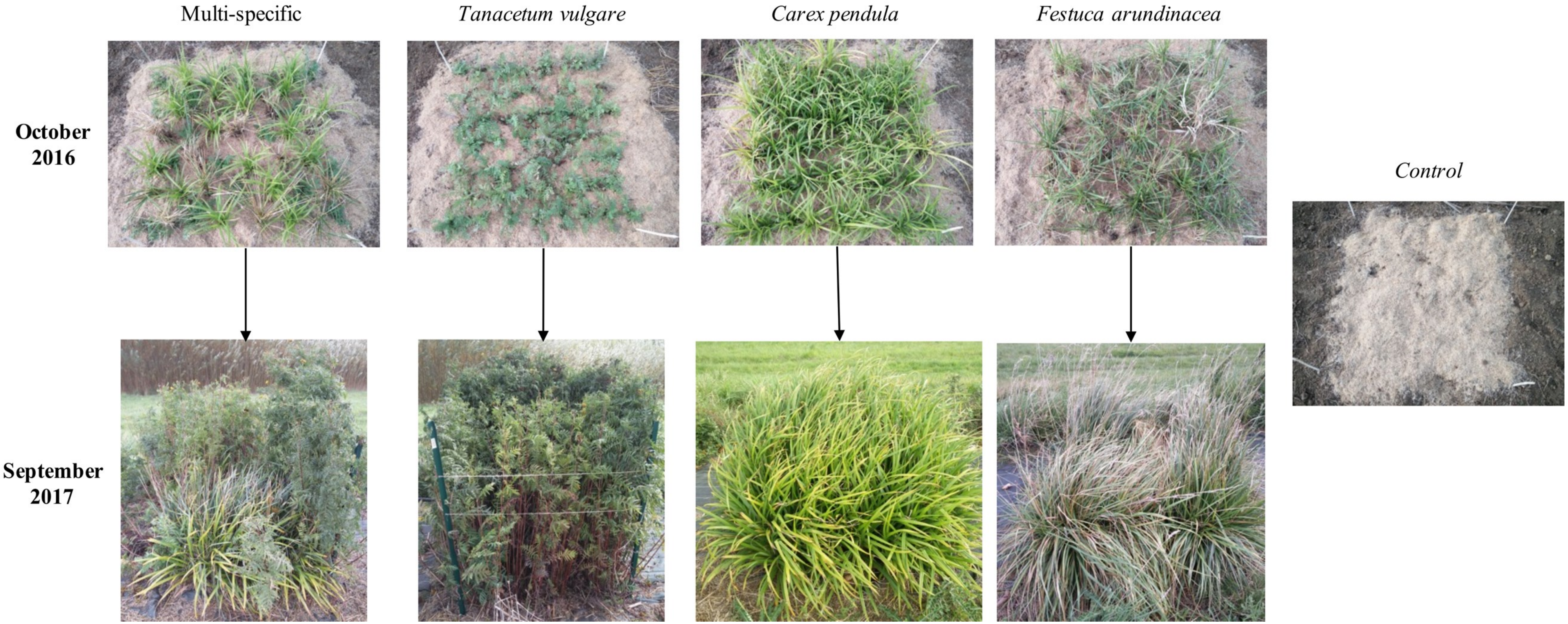

Figure 19. Experimental plots with three monospecific and one multi-specific communities. The photos from October 2016 were taken just after the plantation and the ones from September 2017 were taken a month prior experiment.

5.2.2. Plant material

Three herbaceous species presenting contrasting aboveground morphological traits furthering hydraulic roughness were selected from a list of 76 potential candidate species of indigenous plants from north-west Europe. This list was obtained by applying six filters to the 3500 spermatophyte species of north-west Europe (Lambinon et al. 2012) based on the identified functional types influencing runoff and soil erosion in this phytogeographical territory (Kervroëdan et al. 2018): (1) the Raunkiaer's life-form categories "herbaceous chamaephytes", "hemicryptophytes" and "geophytes" which select perennial herbaceous species with an effective soil cover all year; (2) the presence of biomass during winter, when soil erosion is observed at its highest in north-west Europe (Boardman and Poesen 2006), either dry (i.e. non-caespitose hemicryptophytes and geophytes) or fresh (i.e. herbaceous chamaephytes and caespitose hemicryptophytes); (3) the presence of stolon or rhizomes which ensure a lateral spreading growth pattern forming a homogenous cover and burying tolerance towards sediment deposition; (4) a vegetative height ≥ 20 cm to avoid any submergence of the vegetation by the water flow and ensure the efficiency towards concentrated flows (Dillaha et al. 1989), as the water maximal level is 20 cm in north-west European catchments; (5) a broad ecological niche which guarantees plant development within a wide range of soil conditions and (6) the non-invasiveness of the plants to select non-weed species and avoid the plant spreading into agricultural fields.

To restrict the competition for light, the species were chosen considering their vegetative height range with a minimal height comprised between 40 and 70cm. The species *Carex pendula, Tanacetum vulgare and Festuca arundinacea* were tested under three monospecific and one multi-specific communities with three replicates (Table 9). The multi-specific communities were composed of the three species.

Table 9. List of the species used for the study and information about their life form and traits. The traits and density-weighted (DW) traits data are mean values (± standard deviation) of the measures done on the monospecific communities.

		Carex pendula	*Festuca arundinacea*	*Tanacetum vulgare*
Category		Sedge	Graminoid	Herb
Family		Cyperaceae	Poaceae	Asteraceae
Life form		Caespitose hemicryptophyte	Hemicryptophyte	Hemicryptophyte
Leaf density (.m^{-2})	0 - 5 cm	64.3 (± 13.5)	107.7 (± 8)	35.7 (± 9.1)
	0 - 10 cm	99.7 (± 30.1)	175.7 (± 22)	39.7 (± 10.3)
	0 - 20 cm	142.3 (± 44.7)	293 (± 18.4)	46.7 (± 12.5)
Leaf area (mm^2)		8347.6 (± 827.9)	4023.1 (± 345.2)	5754 (± 966.2)
DW Leaf area (mm^2.m^{-2})	0 - 5 cm	533774.2 (± 97509.9)	434827.5 (± 69051.4)	211063.6 (± 90971.8)
	0 - 10 cm	820025.9 (± 185637.9)	702247 (± 45231.6)	234827.9 (± 101477.6)
	0 - 20 cm	1164373.8 (± 254585.1)	1181414.5 (± 159217)	276124.8 (± 118336.5)
DW specific leaf area (mm^2.mg^{-1}.m^{-2})	0 - 5 cm	660.7 (± 162.2)	1599.2 (± 257.3)	844.9 (± 392.9)
	0 - 10 cm	1026 (± 349.9)	2589.9 (± 316.9)	944.3 (± 445.9)
DW projected stem area (mm^2.m^{-2})	0 - 5 cm	7027.6 (± 1729.6)	14227.4 (± 2716.7)	4654.6 (± 1767.6)
	0 - 10 cm	13661.4 (± 3296.1)	27752.6 (± 5373)	9027.6 (± 3341.8)
	0 - 20 cm	26122.1 (± 6255.1)	49430.4 (± 10903.8)	17707.1 (± 6402.3)
DW stem diameter (mm.m^{-2})	0 - 5 cm	140.6 (± 34.6)	284.5 (± 54.3)	93.1 (± 35.4)
	0 - 10 cm	136.6 (± 33)	277.5 (± 53.7)	90.3 (± 33.4)
	0 - 20 cm	130.6 (± 31.3)	259.1 (± 53.2)	88.5 (± 32)

5.2.3. Hydraulic measurements

A runoff simulator (Figure 20) generating a flow at set discharges in controlled conditions was used to perform the experiments in October and November 2017 (Richet et al. 2017; Kervroëdan et al. 2018). The simulator was composed of three parts, two Venturi channels with ultrasound probes measuring the water level in the channels (± 1.26 mm) on both ends of a channel where measurements were performed. The central channel was a 5.2 m by 0.90 m stainless steel channel with a 1.2 m bottomless part where the vegetation was located. The channel slope was measured for each plot using an automatic rotating laser (Geo Fennel EL 515plus) and was adjusted to 4.90% (± 0.13%), using wooden planks to ensure stability during experiments. The backwater levels in front of the plots were measured using six spacers placed upstream the plants. The closest spacer from the plants was 13 cm away, the next two were spaced by 25 cm, the forth spacer was 50 cm away from the third and the last two were spaced by 75 cm. Each spacer was levelled and their elevations were measured and used as elevation-known baselines for the water level measurements.

The discharge used for the experiments was 3.6 $L.s^{-1}.m^{-1}$ (± 0.06 $L.s^{-1}.m^{-1}$), continuously monitored using both upstream and downstream flowmeters. The water level measurements in the backwater area were carried out when upstream and downstream discharges were equivalent, by measuring the perpendicular distance between the bottom of the spacers and the top of the water flow. Ten water level measures were made per spacer, one every 10 cm along the spacer from one channel edge to the other. All the water level determinations were undertaken using clear water flows.

The unit stream power (USP, $m.s^{-1}$) was used to characterise the hydraulic roughness (Yang 1972; Govers 1992). Often used as a sediment transport capacity index, it defines the energy dissipation of the flow, per unit of time and per unit of weight, and depends on the mean flow velocity (V, $m.s^{-1}$) and the slope (S, $m.m^{-1}$) (Govers 1992):

$$USP = VS \tag{1}$$

The USP is negatively related to the hydraulic roughness: the lower it is, the higher the hydraulic roughness will be.

Figure 20. Runoff simulator used for the experiments.

5.2.4. Sediment retention

In June 2017, soil in the experimental site was taken off within the top 15cm, sifted at 2 mm and stored until October 2017. *Prior* the experiments, the sediments were dried at 40°C for 72h and stored in sealed containers. After conducting the water level measurements, sediments were integrated into the flow in order to characterise the plant diversity effect on sediment retention capacity. The sediment concentration was at 11 $g.L^{-1}$ (± 0.36 $g.L^{-1}$) at a discharge of 3.6 $L.s^{-1}.m^{-1}$ (± 0.09 $L.s^{-1}.m^{-1}$). The experiment lasted 3 min of sediment input and was followed by 30 sec of clear water to allow the last sediments to be transported. In order to estimate the quantity of sediment passing through the vegetation, a 250 ml flow sample was taken every 15 sec, from the sediment input to the end of the experiment. After the test run, the sediments deposited in the channel were collected. All the sampled sediments were oven-dried at 105°C for 48h and weighted. Particle granulometry was analysed using a LS 13 320 Beckman Coulter particle sizing analyser for the sediments deposited in the channel and the ones downstream the vegetation.

The total sediment quantity downstream the vegetation was calculated using a sequential calculation method, from each sample collected. The quantity trapped within the vegetation (S_{within}) was estimated as followed:

$$S_{within} = S_{input} - (S_{upstream} + S_{downstream}) \qquad (2)$$

where S_{input} is the total quantity of sediments integrated into the flow, $S_{upstream}$ is the quantity deposited in the channel and $S_{downstream}$ the quantity which passed through the vegetation.

The sediment retention capacity represented the quantity of sediments upstream and within the vegetation:

$$S_{retention} = S_{upstream} + S_{within} \qquad (3)$$

5.2.5. Leaf and stem trait measurements

Six aboveground plant morphological traits (stem – density, diameter, projected area; leaf – density, area and specific area), known to influence the hydraulic roughness and sediment retention (Kervroëdan et al. 2018), were measured on three levels along the stem: between 0 and 5 cm, 0 and 10 cm and 0 and 20 cm. Sampling collection, samples conservation and analyses methods were conducted following the standardised guidelines from (Pérez-Harguindeguy et al. 2013). The leaves were collected in sealed bags with moist tissue until measurements were performed and then, dried at 70°C for 72h. As all the plots presented a homogenous plant cover, the traits were all measured within one quadrat (10 by 10 cm) per monospecific community plot and one quadrat per species within the multi-specific community plots, due to the homogeneous plant cover within the plots. The leaf density (leaves.m^{-2}) was measured for each level along the stems by counting fresh and dry leaves. The leaf area (mm^{2}) and specific area (mm^{2}.mg^{-1}) were determined using six representative leaves, scanned at 600dpi resolution, and the images were analysed using Gimp 2.8. Pseudoculms for sedges species (Cyperaceae) and tillers for grass species were counted with the stems to measure the stem density (stems.m^{-2}). The stem diameter (mm) was measured for each level on three representative stems and was used to calculate the projected stem area (mm^{2}), using the rectangle area formula. The aboveground biomass (g) was estimated by collecting a 50 x 50 cm quadrat in each plot and dried during 72h at 70°C. The species biomass in the multi-specific plots were separated in order to determine the biomass productivity of each species.

Moreover, a density-weighted trait was calculated for each trait by multiplying the (1) leaf traits with the leaf density and (2) stem traits with the stem density; which corresponded to the density value of the traits and were dissociated from the traits with a “D” at the front of the trait appellations.

5.2.6. Characterisation of the complementarity

All multi-specific plots were planted with an equal abundance of each species, although these abundances changed over time. The abundance (%) of each species was estimated for each multi-specific plot.

The complementarity effect on the traits was determined using two metrics: the land equivalent ratio (LER) and the complementarity effect index. The LER represents the relative area required for monoculture to grow with the same productivity as when the species are in mixture (Mead and Willey 1980). The LER was calculated for each species trait in the multi-specific plots as follows:

$$LER = pLER_A + pLER_B = \frac{T_{A,multi-specific}}{T_{A,monospecific}} + \frac{T_{B,multi-specific}}{T_{B,monospecific}} \qquad (4)$$

with $pLER_A$ and $pLER_B$ being the partial LERs for the species A and B; $T_{A,\text{multi-specific}}$ and $T_{B,\text{multi-specific}}$ being the trait values of the species A and B in the multi-specific conditions; and $T_{A,\text{monospecific}}$ and $T_{B,\text{monospecific}}$ being the trait values of the species A and B in their respective monospecific conditions. If LER > 1, the multi-specific condition presents an advantage for the trait value compared when the species is in monospecific condition. On the contrary, if LER < 1, there is a detrimental effect on the trait of the multi-specific condition compare to the monospecific. The pLER allows to identify competitive effects between the species, within the multi-specific condition, using pLER < (1/n) or pLER > (1/n) as an indices, with n the species number (Mead and Willey 1980; Hector 1998; Darch et al. 2018).

The complementarity effect index (CEI) indicates the decrease or increase in trait values as a result of the species mixture in comparison to the monospecific condition (Loreau and Hector 2001; Darch et al. 2018):

$$CEI_A = n \times \left(pLER_A - \left(\frac{1}{n}\right)\right) \times T_{A,monospecific} \qquad (5)$$

where n is the number of species, pLER is the partial LER of the species A and $T_{A,\text{monospecific}}$ is the trait value of the species A when in monospecific condition.

The community-weighted traits (CWT) were calculated for each trait in the multi-specific plots by weighting each trait with the species abundance (Díaz et al. 2007a; Violle et al. 2007):

$$CWT_i = \sum_{k=1}^{n_i} A_{k,i}\ T_{k,i} \qquad (6)$$

with *CWT* CWT_i being the community-weighted value of the trait in the community i, $A_{k,i}$ and $T_{k,i}$ being, respectively, the relative abundance and the trait value of the species k in the community i and n_i being the number of species in the community i.

5.2.7. Data analysis

Comparative analyses using Mann-Whitney tests were performed on the USP, the sediments (quantities and granulometries) and the biomass productivity data, regrouped under “monospecific” and “multi-specific” categories, in order to identify if there was a complementarity or a selection effect of the diversity on these processes.

To identify differences between the communities, ANOVA and Kruskal-Wallis analyses were computed accordingly to the normality of the data on the USP, the sediments (quantities and granulometries), the biomass and the community-weighted traits data. The analyses’ respective post-hoc tests Tukey and Dunn’s were also performed.

As the aim of the analyses was to understand the effect of the plant species diversity on the tested variables, control data were excluded. All the statistical analyses were carried out using the statistical software R (version 3.3.2).

5.3. Results

5.3.1. Complementarity of the traits involved in hydraulic roughness and aboveground biomass productivity

The complementarity effect of the traits in the multi-specific communities was analysed using the land equivalent ratio (LER) and the complementarity effect index. Regarding the LER (Table 10), leaf density (0 – 5 cm; 0 – 10 cm and 0 – 20 cm) and density-weighted SLA (0 - 5 cm and 0 – 10 cm) were higher in the multi-specific communities, with LER > 1. The density-weighted stem projected area (0 – 5 cm) and density-weighted stem diameter (0 – 5 cm) did not show differences between monospecific and multi-specific communities, with LER = 1. The traits of *F. arundinacea* and *C. pendula* (only the leaf density (0 – 5 cm and 0 – 10 cm) and the density-weighted SLA (0 - 5 cm and 0 – 10 cm)) presented higher values in the multi-specific communities, with partial LER > 0.33.

Table 10. Land equivalent ratio (LER) and partial LER values for the traits and density-weighted (DW) traits of each species composing the multi-specific communities.

		LER	Partial LER		
			C. pendula	*F. arundinacea*	*T. vulgare*
Leaf density	0 - 5 cm	1.11	0.45	0.54	0.12
	0 - 10 cm	1.13	0.39	0.6	0.14
	0 - 20 cm	1.08	0.31	0.62	0.15
Leaf area		0.89	0.24	0.5	0.14
DW Leaf area	0 - 5 cm	0.95	0.31	0.55	0.09
	0 - 10 cm	0.99	0.27	0.61	0.1
	0 - 20 cm	0.96	0.22	0.63	0.11
DW specific leaf area	0 - 5 cm	1.1	0.5	0.49	0.1
	0 - 10 cm	1.1	0.44	0.54	0.12
DW projected stem area	0 - 5 cm	1	0.27	0.55	0.18
	0 - 10 cm	0.98	0.26	0.54	0.18
	0 - 20 cm	0.85	0.19	0.49	0.18
DW stem diameter	0 - 5 cm	1	0.27	0.55	0.18
	0 - 10 cm	0.98	0.26	0.54	0.18
	0 - 20 cm	0.98	0.25	0.54	0.18

The complementarity effect index (Table 11) showed the decrease of (1) leaf density (0 – 20 cm), leaf area, density-weighted lea area (0 – 5 cm; 0 – 10 cm and 0 – 20 cm), density-weighted stem diameter (0 – 5 cm; 0 – 10 cm and 0 – 20 cm) and density-weighted stem projected area (0 – 5 cm; 0 – 10 cm and 0 – 20 cm) of *C. pendula* when put in multi-specific conditions and (2) all the traits of *T. vulgare*. Only *F. arundinacea* showed an increase of all its trait values in the multi-specific plots.

Table 11. Complementarity effect index for the traits and density-weighted (DW) traits of each species composing the multi-specific communities as well as the index for the overall multi-specific communities (CEtotal).

		CEtotal	Complementarity index		
			C. pendula	*F. arundinacea*	*T. vulgare*
Leaf density (.m^{-2})	0 - 5 cm	859	2338	6884	-2249
	0 - 10 cm	1459	1922	14046	-2283
	0 - 20 cm	1422	-641	25071	-2544
Leaf area (mm^{2})		-630	-2339	2107	-3201
DW Leaf area (mm^{2}.m^{-2})	0 - 5 cm	-1474941	-3407478	29268128	-15234307
	0 - 10 cm	-148347	-14601078	59826600	-16002891
	0 - 20 cm	-3053363	-38977932	105448084	-18296399
DW specific leaf area (mm^{2}.mg^{-1}.m^{-2})	0 - 5 cm	11024	33986	77990	-57667
	0 - 10 cm	16114	33135	163750	-60171
DW projected stem area (mm^{2}.m^{-2})	0 - 5 cm	5297	-130346	941307	-213060
	0 - 10 cm	-22045	-286111	1713757	-403908
	0 - 20 cm	-420119	-1135325	2336153	-785182
DW stem diameter (mm.m^{-2})	0 - 5 cm	106	-2607	18826	-4261
	0 - 10 cm	-220	-2861	17138	-4039
	0 - 20 cm	-186	-2962	16460	-3926

The comparison analysis on the biomass productivity between the monospecific and the multi-specific conditions showed no significant difference (Figure 21.A). Analyses comparing each condition did not show any difference in biomass productivity, although there was a lower productivity for *T. vulgare* compared to the two other monospecific communities (Figure 21.B).

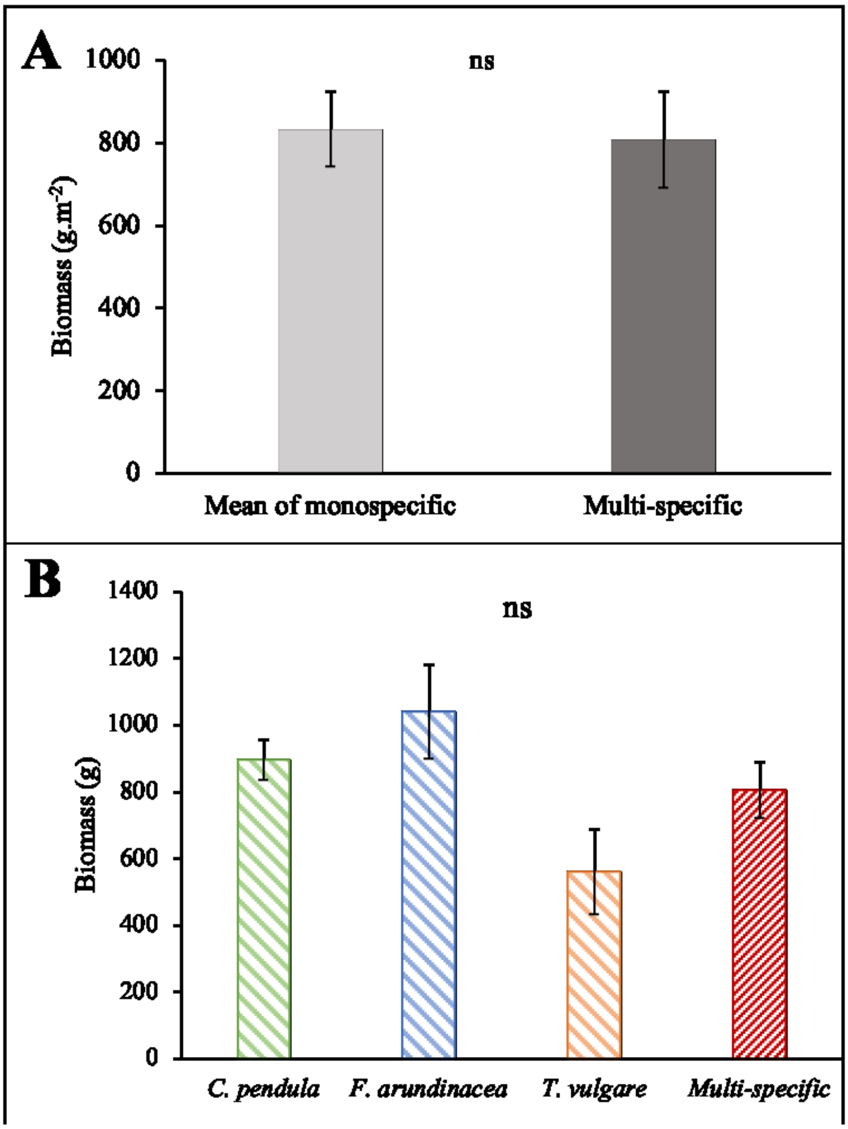

Figure 21. Differences in biomass productivity between (A) the mean of monospecific and the multi-specific communities and (B) each condition. The bars represent the mean ± standard error. The significance level “ns” means not significant.

5.3.2. Trait aggregation effects on unit stream power and sediment retention

The comparison analysis of the sediment quantities upstream, within and downstream the vegetation between the monospecific and the multi-specific conditions showed no significant difference (Figure 22.A). Similar results were found for the sediment particle sizes. Regarding the hydraulic roughness, there was no difference for the unit stream power between the monospecific and the multi-specific conditions (Figure 22.B).

The comparison analysis between each condition regarding the sediment retention (quantities upstream and within the vegetation) showed differences between the mixture and *T. vulgare*, which was also different from *C. pendula*. Similar results were found for the quantity of sediments downstream the vegetation, with *T. vulgare* having significantly more sediments downstream the vegetation than *C. pendula* and the mixture (Figure 23.A). Regarding the unit stream power, *T. vulgare* had a significantly lower hydraulic roughness than *C. pendula* and the mixture (Figure 23.B).

There was no difference between each condition for the sediment particle sizes. However, the particle size categories 20 µm – 50 µm and 50 µm – 100 µm upstream were different from the ones downstream of *C. pendula* (Figure 24.A). For the condition *T. vulgare*, the sediment quantity of the category 20 µm – 50 µm upstream the vegetation was significantly lower than the one downstream (Figure 24.C). The quantity of sediments between 100 µm and 200 µm was significantly higher upstream than downstream the multi-specific vegetation (Figure 24.D).

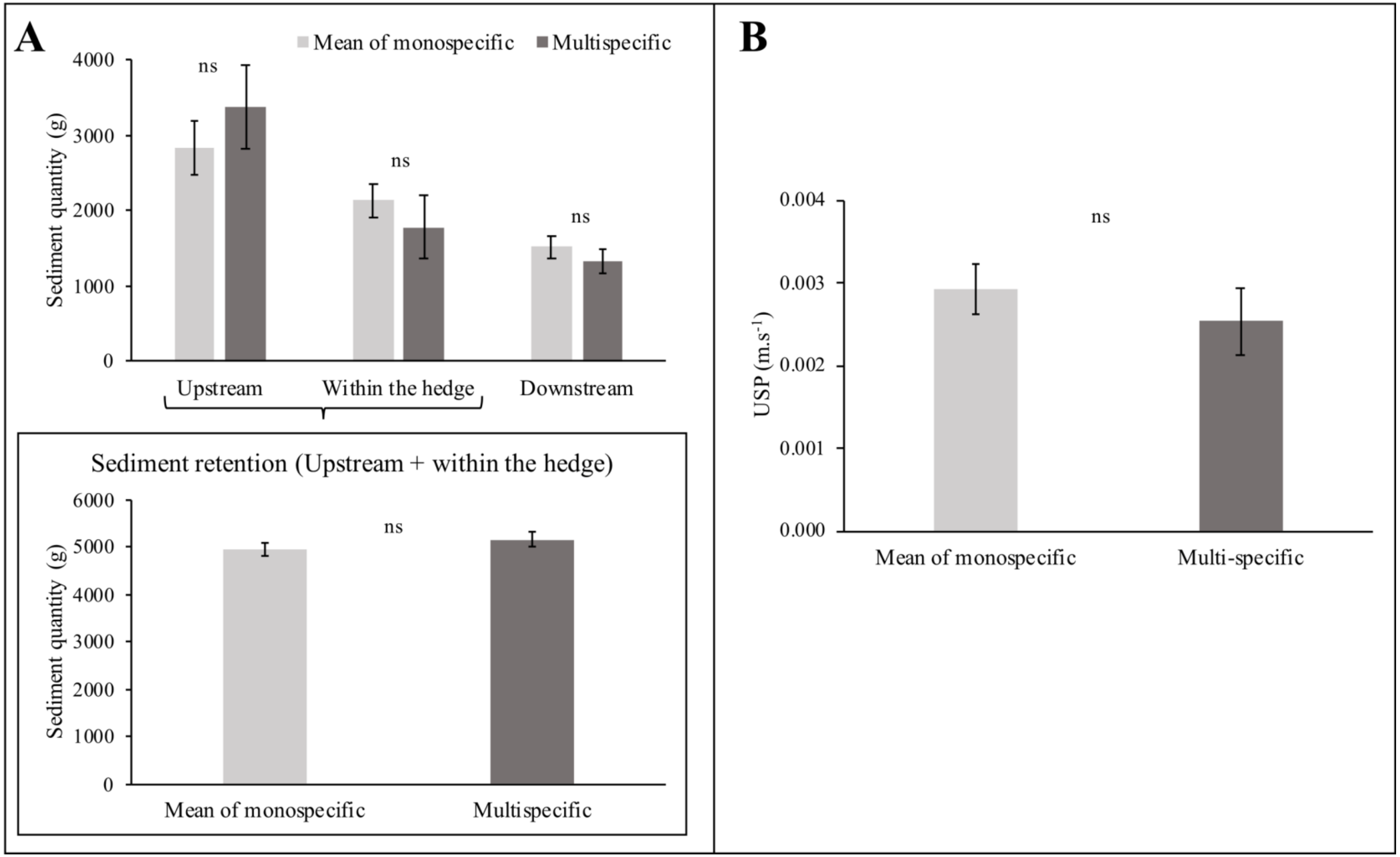

Figure 22. Differences between the mean of monospecific and the multi-specific communities for (A) the sediment quantities upstream, within and downstream the vegetation, as well as the sediment retention (upstream + within) and (B) the unit stream power. The bars represent the mean ± standard error. The significance level “ns” means not significant.

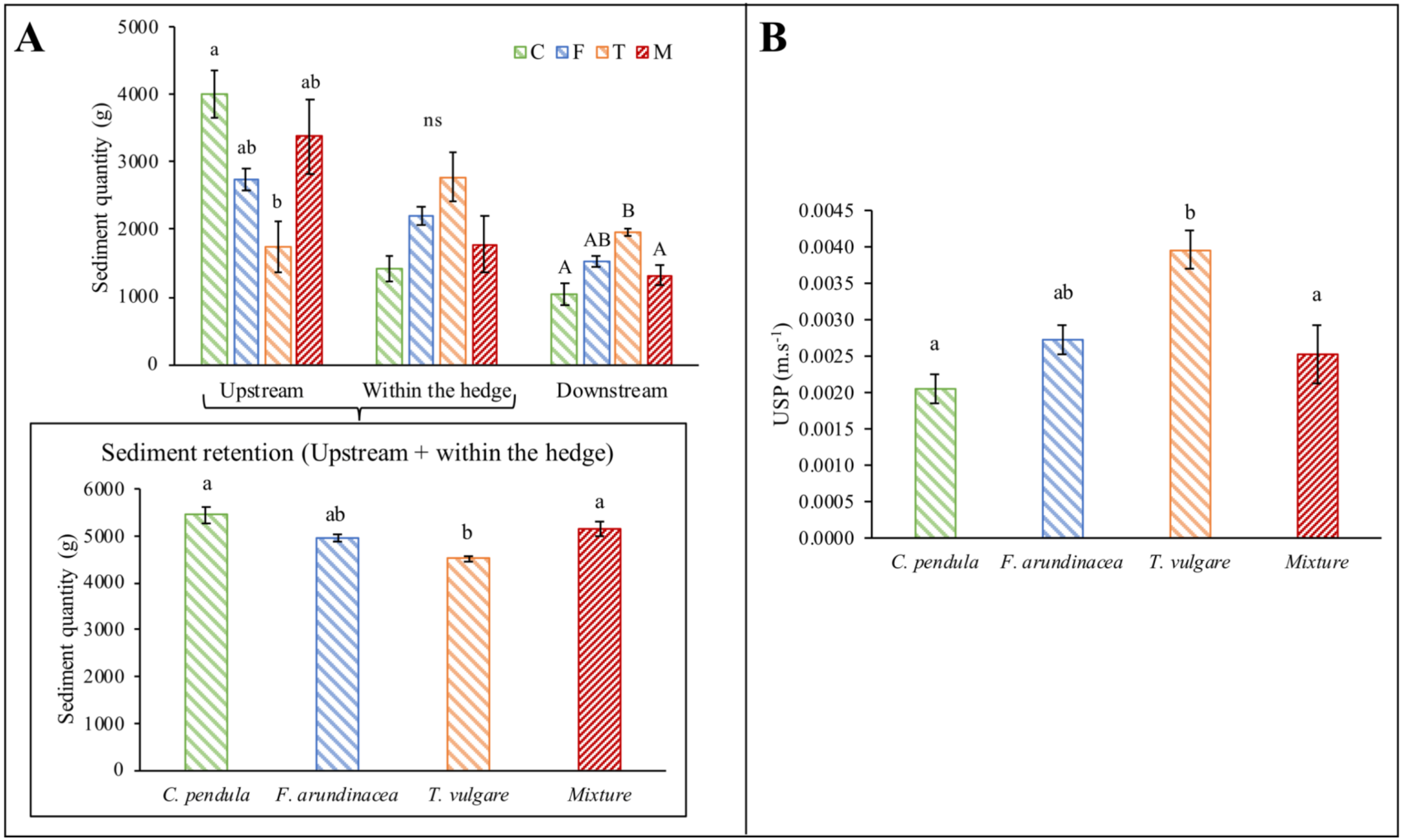

Figure 23. Differences between each community for (A) the sediment quantities upstream, within and downstream the vegetation, as well as the sediment retention (upstream + within) and (B) the unit stream power. The bars represent the mean ± standard error. The letters represent the significant differences between each condition according to Tukey post-hoc tests. The significance level “ns” means not significant.

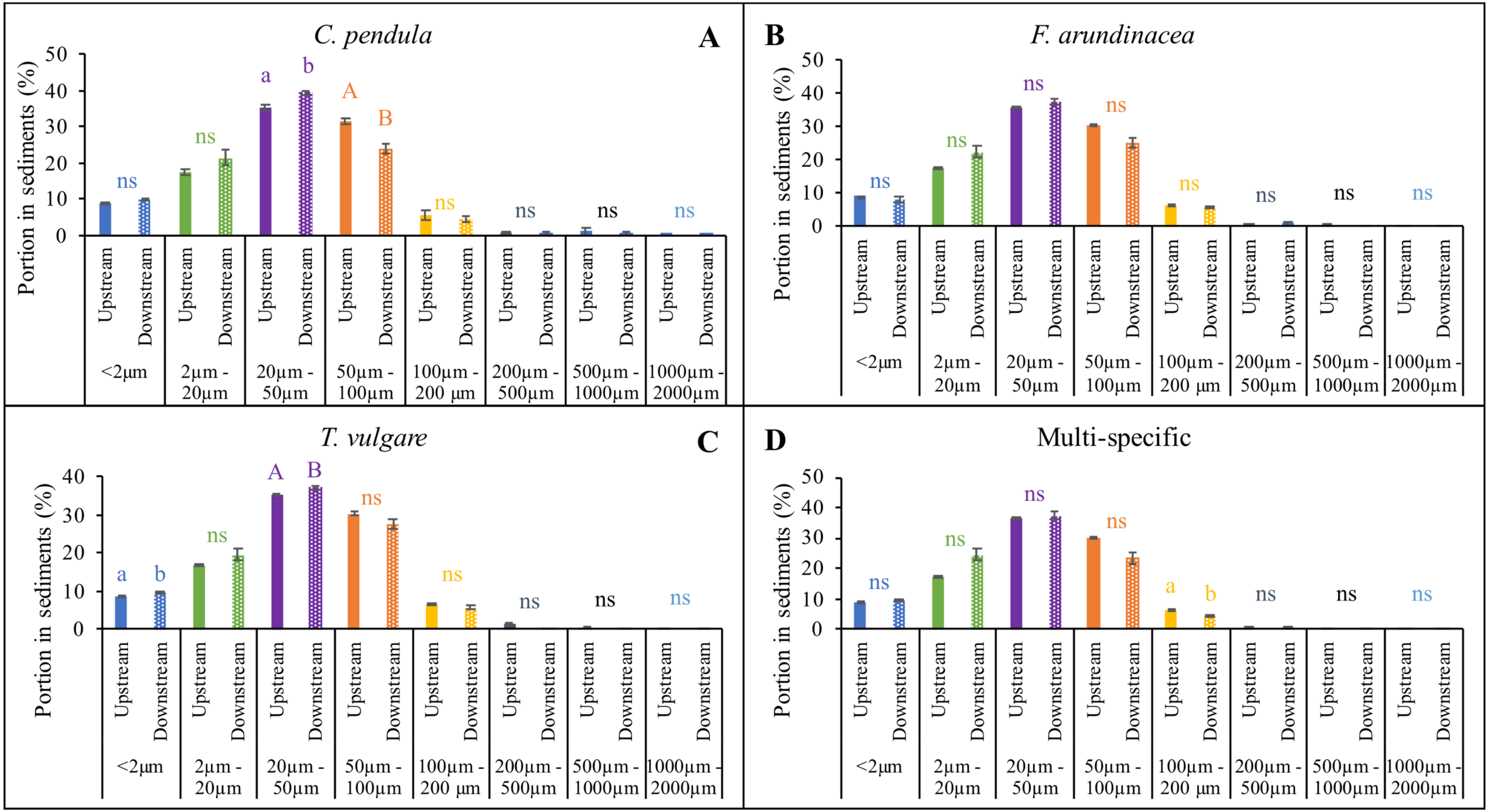

Figure 24. Differences in sediment quantities upstream and downstream the vegetation for each particle size category for (A) *C. pendula*; (B) *F. arundinacea*; (C) *T. vulgare* and (D) the multi-specific community. The bars represent the mean ± standard error. The letters represent the significant differences between the upstream and downstream sediment quantities at each size category according to Tukey and Dunn's post-hoc tests. The significance level "ns" means not significant.

5.4. Discussion

5.4.1. Complementarity of the traits but absence of complementarity effect on the hydraulic roughness and sediment retention

The complementarity effect of plant species was only highlighted on leaf density and density-weighted leaf specific area, both involved in hydraulic roughness increase. This advantage was driven by the traits of *F. arundinacea* and *C. pendula* in the multi-specific communities. However, while this complementary effect of the traits should have led to a greater hydraulic roughness, the results showed no significant increase in hydraulic roughness nor sediment retention for the multi-specific communities. Indeed, the complementarity hypothesis stipulates that the niche differentiation from the plant species diversity and trait variance influences ecosystem processes and leads to a more complete space and resources use (Loreau and Hector 2001). The absence of differences between the mean of the monospecific and the multi-specific communities indicated a dominant effect of the traits of specific species in the community on runoff and sediment transport capacity (Grime 1998; Lorentzen et al. 2008). These results are not in accordance with the complementarity effects of plant species diversity found on runoff, soil erosion and soil aggregation capacity in other studies (Pohl et al. 2009; Martin et al. 2010; Zhang et al. 2015). However, these studies focussed on non-herbaceous spontaneous plant communities of mountainous or semi-arid environments, which are usually characterised by more intense runoff and erosion episodes and adapted spontaneous vegetation towards these processes (Guerrero-Campo and Montserrat-Martí 2000). These opposing results could be explained by idiosyncratic effects (i.e. contrasting effects of the plant species diversity), impacted by species-traits and soil-plant interactions (Loreau 2000). The idiosyncratic effects could be influenced by the species combination and structure in the community (Parsons et al. 1996; Loreau 2000; Erktan et al. 2013), which is consistent with results showing the decrease of soil erosion resistance with the disappearance of species in the community (Berendse et al. 2015). Moreover, an increasing proportion of species with larger stem diameters would create preferential flow paths and further runoff intensity, which would impact the effect of plant species diversity effects on hydraulic roughness and sediment retention (Parsons et al. 1996; Erktan et al. 2013). This hypothesis is consistent with our results, showing the dominance of *T. vulgare*'s traits which presented large stem diameters and a lower hydraulic roughness and sediment retention capacity. Negative effects of species with larger stem diameters were also highlighted in the literature, highlighting their influence over the water path within the vegetation and the overall null effect of plant species diversity (Erktan et al. 2013). This postulate coincides with the dominant effect of the traits found regarding the size of the sediment particles deposited in the channel, as the preferential flow paths induced by the presence of larger stems would accelerate the velocity of the flow at the path's scale and further the transport of sediment particles. Indeed, while a wider range of sediment particle sizes were expected within the retained sediment by the multi-specific communities, there was no significant difference between the monospecific and the multi-specific communities for each particle size category. The analyses on the community-weighted traits emphasised the leading effect of leaf density and density-weighted leaf area of *T. vulgare,* traits identified to influence directly the hydraulic roughness (Kervroëdan et al. 2018). Perspective is to study the effects of plant species diversity on hydraulic roughness and sediment retention by using a gradient of functional structures and integrating a variation of trait abundances to understand how trait diversity impact sediment retention.

5.4.2. Non-complementarity effect on aboveground biomass productivity would explain no increase of sediment retention

The aboveground biomass productivity was not affected by plant species diversity, which would explain the non-complementarity effect of plant species diversity on sediment retention, as the aboveground biomass is positively related to sediment retention (Podwojewski et al. 2011; Burylo et al. 2012a). Similar results were obtained, showing selection effects of plant species diversity on biomass productivity, due to the presence of specific species in the community and suggesting that soil erosion reduction was not driven by niche complementarity (Berendse et al. 2015). On the contrary, complementarity effects on biomass productivity were found to appear and grow stronger through time (van Ruijven and Berendse 2003, 2005; Cardinale et al. 2007), which suggests that the effects of plant species diversity on sediment retention could change with an older vegetation community. Idiosyncratic effects could directly impact the biomass productivity by limiting the space use by the community (Loreau 2000; Dimitrakopoulos and Schmid 2004; Weigelt et al. 2008). The non-optimal space use for biomass productivity by the traits, as well as environmental factors, would thus lead to a limited effect of plant species diversity on hydraulic roughness and sediment retention (Bautista et al. 2007; Turnbull et al. 2008; Martin et al. 2010; Burylo et al. 2012a; Erktan et al. 2013; Hou et al. 2016). Perspective is to study the effects of plant species diversity with different combinations of species presenting traits involved in hydraulic roughness and sediment retention to understand which of the species present traits with major effects on biomass productivity and sediment retention. Testing these different combinations could lead to (1) the elimination of transient species (i.e. species with a high variability in trait and contributing poorly to the community (Grime 1998)) and (2) the identification of dominant and subordinate (i.e. species with a higher proportion but lower contribution than dominant species that they usually co-occur with (Grime 1998)) species to create efficient vegetation for erosion and runoff control.

5.5. Conclusions

This trait-based ecohydrology study allowed to further the understanding of plant species diversity effect on runoff and soil erosion processes. The results emphasised that there was a non-complementarity effect of plant species diversity on hydraulic roughness and sediment retention, driven by dominant traits in the community, identified as the leaf density and the density-weighted leaf area. This non-complementarity effect of plant species diversity could be explained by the non-increase in biomass productivity. The absence of negative effects on sediment retention suggests that multi-specific communities can be used to mitigate soil erosion and can be recommended because plant species and functional diversity could positively affect other ecosystem processes and services. Perspective is to understand the effects of plant species and functional diversity on different ecosystem processes integrating in plant-soil interactions, based on a multi-functional and meta-analysis.

Authors' Contributions

Léa Kervroëdan, Michel-Pierre Faucon and Romain Armand conceived the objectives and designed the methodology; Léa Kervroëdan and Mathieu Saunier collected the data; Léa Kervroëdan analysed the data; Léa Kervroëdan and Michel-Pierre Faucon led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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REFERENCES

Anten NPR (2004) Optimal Photosynthetic Characteristics of Individual Plants in Vegetation Stands and Implications for Species Coexistence. Annals of Botany 95:495–506. doi: 10.1093/aob/mci048

Bautista S, Mayor ÁG, Bourakhouadar J, Bellot J (2007) Plant Spatial Pattern Predicts Hillslope Runoff and Erosion in a Semiarid Mediterranean Landscape. Ecosystems 10:987–998. doi: 10.1007/s10021-007-9074-3

Berendse F, van Ruijven J, Jongejans E, Keesstra S (2015) Loss of plant species diversity reduces soil erosion resistance. Ecosystems 18:881–888. doi: 10.1007/s10021-015-9869-6

Boardman J, Poesen J (eds) (2006) Soil Erosion in Europe. John Wiley & Sons, Ltd

Burylo M, Rey F, Bochet E, Dutoit T (2012) Plant functional traits and species ability for sediment retention during concentrated flow erosion. Plant and Soil 353:135–144. doi: 10.1007/s11104-011-1017-2

Cadotte MW (2017) Functional traits explain ecosystem function through opposing mechanisms. Ecology Letters 20:989–996. doi: 10.1111/ele.12796

Caldeira MC, Ryel RJ, Lawton JH, Pereira JS (2001) Mechanisms of positive biodiversity±production relationships: insights provided by d13C analysis in experimental Mediterranean grassland plots. Ecology Letters 4:439–443

Cardinale BJ, Duffy JE, Gonzalez A, et al (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67. doi: 10.1038/nature11148

Cardinale BJ, Wright JP, Cadotte MW, et al (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of Sciences 104:18123–18128

Darch T, Giles CD, Blackwell MSA, et al (2018) Inter- and intra-species intercropping of barley cultivars and legume species, as affected by soil phosphorus availability. Plant and Soil 427:125–138. doi: 10.1007/s11104-017-3365-z

Díaz S, Lavorel S, Chapin FS, et al (2007) Functional Diversity — at the Crossroads between Ecosystem Functioning and Environmental Filters. In: Canadell JG, Pataki DE, Pitelka LF (eds) Terrestrial Ecosystems in a Changing World. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 81–91

Dillaha TA, Reneau RB, Mostaghimi S, Lee D (1989) Vegetative filter strips for agricultural nonpoint source pollution control. Transactions of the ASAE 32:513–0519

Dimitrakopoulos PG, Schmid B (2004) Biodiversity effects increase linearly with biotope space: Diversity effects increase with biotope space. Ecology Letters 7:574–583. doi: 10.1111/j.1461-0248.2004.00607.x

Erktan A, Cécillon L, Roose E, et al (2013) Morphological diversity of plant barriers does not increase sediment retention in eroded marly gullies under ecological restoration. Plant and Soil 370:653–669. doi: 10.1007/s11104-013-1738-5

Fargione J, Tilman D, Dybzinski R, et al (2007) From selection to complementarity: shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. Proceedings of the Royal Society B: Biological Sciences 274:871–876. doi: 10.1098/rspb.2006.0351

Garnier E, Navas M-L, Grigulis K (2016) Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties. Oxford University Press

Govers G (1992) Relationship between discharge, velocity and flow area for rills eroding loose, non-layered materials. Earth surface processes and landforms 17:515–528

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of ecology 86:902–910. doi: 10.1046/j.1365-2745.1998.00306.x

Guerrero-Campo J, Montserrat-Martí G (2000) Effects of soil erosion on the floristic composition of plant communities on marl in northeast Spain. Journal of Vegetation Science 11:329–336

Gyssels G, Poesen J, Bochet E, Li Y (2005) Impact of plant roots on the resistance of soils to erosion by water: A review. Progress in Physical Geography 29:189–217. doi: 10.1191/0309133305pp443ra

Hector A (1998) The Effect of Diversity on Productivity: Detecting the Role of Species Complementarity. Oikos 82:597. doi: 10.2307/3546380

Hou J, Wang H, Fu B, et al (2016) Effects of plant diversity on soil erosion for different vegetation patterns. CATENA 147:632–637. doi: 10.1016/j.catena.2016.08.019

Kervroëdan L, Armand R, Saunier M, et al (2018) Plant functional trait effects on runoff to design herbaceous hedges for soil erosion control. Ecological Engineering 118:143–151. doi: 10.1016/j.ecoleng.2018.04.024

Lambinon J, Delvosalle L, Duvigneaud J (2012) Nouvelle flore de la Belgique, du G.-D. de Luxembourg, du nord de la France et des régions voisines, 6th edn.

Loreau M (2000) Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91:3–17. doi: 10.1034/j.1600-0706.2000.910101.x

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76. doi: 10.1038/35083573

Lorentzen S, Roscher C, Schumacher J, et al (2008) Species richness and identity affect the use of aboveground space in experimental grasslands. Perspectives in Plant Ecology, Evolution and Systematics 10:73–87. doi: 10.1016/j.ppees.2007.12.001

Martin C, Pohl M, Alewell C, et al (2010) Interrill erosion at disturbed alpine sites: Effects of plant functional diversity and vegetation cover. Basic and Applied Ecology 11:619–626. doi: 10.1016/j.baae.2010.04.006

Mead R, Willey RW (1980) The Concept of a 'Land Equivalent Ratio' and Advantages in Yields from Intercropping. Experimental Agriculture 16:217–228. doi: 10.1017/S0014479700010978

Mekonnen M, Keesstra SD, Ritsema CJ, et al (2016) Sediment trapping with indigenous grass species showing differences in plant traits in northwest Ethiopia. Catena 147:755–763. doi: 10.1016/j.catena.2016.08.036

Naeem S, Thompson LJ, Lawler SP, et al (1994) Declining biodiversity can alter the performance of ecosystems. Nature 368:734–737. doi: 10.1038/368734a0

Parsons AJ, Abrahams AD, Wainwright J (1996) Responses of interrill runoff and erosion rates to vegetation change in southern Arizona. Geomorphology 14:311–317. doi: 10.1016/0169-555X(95)00044-6

Pérez-Harguindeguy N, Díaz S, Garnier E, et al (2013) New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61:167–234. doi: 10.1071/BT12225

Podwojewski P, Janeau JL, Grellier S, et al (2011) Influence of grass soil cover on water runoff and soil detachment under rainfall simulation in a sub-humid South African degraded rangeland. Earth Surface Processes and Landforms 36:911–922. doi: 10.1002/esp.2121

Pohl M, Alig D, Körner C, Rixen C (2009) Higher plant diversity enhances soil stability in disturbed alpine ecosystems. Plant and Soil 324:91–102. doi: 10.1007/s11104-009-9906-3

Rémy JC, Marin-Laflèche A (1974) L'analyse de terre : réalisation d'un programme d'interprétation automatique. Annales Agronomiques 25:607–632

Richet J-B, Ouvry J-F, Saunier M (2017) The role of vegetative barriers such as fascines and dense shrub hedges in catchment management to reduce runoff and erosion effects:

Experimental evidence of efficiency, and conditions of use. Ecological Engineering 103:455–469. doi: 10.1016/j.ecoleng.2016.08.008

Spehn EM, Hector A, Joshi J, et al (2005) Ecosystem effects of biodiversity manipulations in European grasslands. Ecological Monographs 75:37–63. doi: 10.1890/03-4101

Spehn EM, Joshi J, Schmid B, et al (2000) Above-ground resource use increases with plant species richness in experimental grassland ecosystems. Functional Ecology 14:326–337. doi: 10.1046/j.1365-2435.2000.00437.x

Tilman D (2001a) Diversity and Productivity in a Long-Term Grassland Experiment. Science 294:843–845. doi: 10.1126/science.1060391

Tilman D (2001b) Functional Diversity. In: Levin SA (ed) Encyclopedia of Biodiversity. Elsevier, New York, pp 109–120

Turnbull L, Wainwright J, Brazier RE (2008) A conceptual framework for understanding semi-arid land degradation: ecohydrological interactions across multiple-space and time scales. Ecohydrol 1:23–34. doi: 10.1002/eco.4

van Ruijven J, Berendse F (2005) Diversity-productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. Proceedings of the National Academy of Sciences 102:695–700. doi: 10.1073/pnas.0407524102

van Ruijven J, Berendse F (2003) Positive effects of plant species diversity on productivity in the absence of legumes. Ecology Letters 6:170–175. doi: 10.1046/j.1461-0248.2003.00427.x

Violle C, Navas M-L, Vile D, et al (2007) Let the concept of trait be functional! Oikos 116:882–892. doi: 10.1111/j.2007.0030-1299.15559.x

Weigelt A, Schumacher J, Roscher C, Schmid B (2008) Does biodiversity increase spatial stability in plant community biomass? Ecology Letters 11:338–347. doi: 10.1111/j.1461-0248.2007.01145.x

Yang CT (1972) Unit stream power and sediment transport. ASCE Journal of the Hydraulics Division 98:1805–1826

Zhang L, Wang J, Bai Z, Lv C (2015) Effects of vegetation on runoff and soil erosion on reclaimed land in an opencast coal-mine dump in a loess area. CATENA 128:44–53. doi: 10.1016/j.catena.2015.01.016

Zhu H, Fu B, Wang S, et al (2015) Reducing soil erosion by improving community functional diversity in semi-arid grasslands. Journal of Applied Ecology 52:1063–1072. doi: 10.1111/1365-2664.12442

Supplementary material 4. Community-weighted traits of each community for the identification of the traits driving the absence of complementarity. Data are the community-weighted (CW) mean values of traits (± standard deviation) and results of F (ANOVA) statistical tests. Significance levels: *** = $p < 0.001$; ** = $p < 0.01$ and * = $p < 0.05$. LA – leaf area; LD – leaf density; DLA – leaf area density; DSA – stem projected area density; DSDm – stem diameter density and DSLA – specific leaf area density. The letters represent the significant differences between each condition according to Tukey post-hoc tests. The greyed boxes indicate the significant different traits between the multi-specific and the other conditions.

	C. pendula	*F. arundinacea*	*T. vulgare*	Multi-specific	ANOVA
CW-LD5 (.m^{-2})	6433 (± 1350) ac	10767 (± 802) b	3567 (± 907) c	8830 (± 1248) ab	0.0002***
CW-LD10 (.m^{-2})	9967 (± 3007) ac	17567 (± 2203) b	3967 (± 1026) c	13903 (± 2634) ab	0.0006***
CW-LD20 (.m^{-2})	14233 (± 4474) ac	29300 (± 1836) b	4667 (± 1250) c	21264 (± 5590) ab	0.0003***
CW-LA (mm^{2})	8348 (± 828) a	4023 (± 345) b	5754 (± 966) c	4815 (± 121) bc	0.0002***
CW-DLA5 (mm^{2}.m^{-2})	53377423 (± 9750989) a	43482745 (± 6905142) a	21106361 (± 9097183) b	41569276 (± 3988928) a	0.0058**
CW-DLA10 (mm^{2}.m^{-2})	82002586 (± 18563792) a	70224699 (± 4523157) a	23482789 (± 10147761) b	64132335 (± 9170065) a	0.0015**
CW-DLA20 (mm^{2}.m^{-2})	116437381 (± 25458515) a	118141448 (± 15921698) a	27612478 (± 11833647) b	95909101 (± 21307422) a	0.0013**
CW-DSLA5 (mm^{2}.mg^{-1}.m^{-2})	66069 (± 16221) a	159920 (± 25732) b	84490 (± 39292) a	115283 (± 18030) ab	0.0115*
CW-DSLA10 (mm^{2}.mg^{-1}.m^{-2})	102601 (± 34986) a	258986 (± 31688) b	94433 (± 44594) a	181320 (± 36820) ab	0.002**
CW-DSA5 (mm^{2}.m^{-2})	702756 (± 172959) a	1422735 (± 271672) b	465461 (± 176758) a	968271 (± 235378) ab	0.0037**
CW-DSA10 (mm^{2}.m^{-2})	1366143 (± 329610) a	2775256 (± 537298) b	902756 (± 334177) a	1834676 (± 442368) ab	0.0034**
CW-DSA20 (mm^{2}.m^{-2})	2612215 (± 625510) a	4943043 (± 1090384) b	1770711 (± 640226) a	2939972 (± 746966) ab	0.0072**
CW-DSDm5 (mm.m^{-2})	14055 (± 3459) a	28455 (± 5433) b	9309 (± 3535) a	19365 (± 4708) ab	0.0037**
CW-DSDm10 (mm.m^{-2})	13661 (± 3296) a	27753 (± 5373) b	9028 (± 3342) a	18347 (± 4424) ab	0.0034**
CW-DSDm20 (mm.m^{-2})	13061 (± 3128) a	25909 (± 5317) b	8854 (± 3201) a	17328 (± 4149) ab	0.0048**

CHAPTER 3

6. FUNCTIONAL DIVERSITY EFFECTS OF HERBACEOUS VEGETATION ON RUNOFF TO DESIGN HERBACEOUS HEDGES FOR SEDIMENT RETENTION

Léa Kervroëdan, Romain Armand, Mathieu Saunier and Michel-Pierre Faucon

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Abstract

Functional diversity effects on ecosystem processes such as runoff and soil erosion, main natural processes influencing vegetation dynamics and ecosystem functioning, are not yet fully understood. In the north-west European agricultural landscapes, runoff and concentrated soil erosion are mainly reduced in small vegetation patches by the hydraulic roughness, which furthers sedimentation by reducing the flow velocity. Vegetation with important stem density, diameter (both negatively correlated), leaf area and density (both negatively correlated) impact the hydraulic roughness. The hypothesis is that a functional structure composed of these negatively correlated traits involved in the hydraulic roughness and sediment retention would constitute positive effects of the functional diversity. Runoff simulations were undertaken on four mono-specific and two multi-specific communities using plant species from north-west Europe, presenting six contrasting aboveground functional traits involved in the hydraulic roughness increase. The results showed an effect of dominant traits in the community on the hydraulic roughness, identified as the community-weighted leaf densities. The non-additive effect of the functional diversity on the hydraulic roughness could be explained by the absence of aboveground biomass productivity increase in plant communities with high functional diversity. We argued that the functional diversity effects on hydraulic roughness and biomass productivity could change due to idiosyncratic effects of the traits. This non-additive effect of the functional diversity on the hydraulic roughness constitutes a new advance in the understanding of plant trait assemblage on runoff and soil erosion processes.

Key-words

Biomass ratio hypothesis, functional diversity, hydraulic roughness, leaf and stem functional traits, plant-runoff interaction, soil erosion control

6.1. Introduction

Ecosystem processes are driven by plant functional traits in vegetation communities (Lavorel et al. 1997; Cadotte et al. 2011). The effects of vegetation on ecosystem processes and services have thus been exponentially analysed using the functional trait approach over the past decades (Lavorel et al. 1997; Lavorel and Garnier 2002; Mcgill et al. 2006; Faucon et al. 2017). More recently, studies have been focussing on the effects of the functional diversity on ecosystem processes and functioning, understanding if the effects were due to dominant species composing the community or to its functional diversity (Lavorel and Garnier 2002; Díaz et al. 2007a; Song et al. 2014; Cadotte 2017). The mass ratio hypothesis stipulates that ecosystem processes would be driven by the traits of the most abundant species in the community, characterised as dominant species, and is represented by the community-weighted mean traits (Grime 1998; Díaz et al. 2007b). On the contrary, the diversity hypothesis specifies that ecosystem processes are driven by the trait diversity composing the community, inducing complementarity effects among the species (Tilman et al. 1997a; Petchey 2003). Higher dissimilarity in traits in a community would lead to a more complete use of the resources and, thus, to higher productivity and impact on nutrient dynamics (Loreau and Hector 2001; Lambers et al. 2004; Petchey and Gaston 2006; Fornara and Tilman 2008; Cadotte 2017). While relationships between functional ecology and a number of ecosystem processes (e.g. net primary productivity, nutrient cycling and availability) have been highlighted, research is still needed to fully understand these relationships for other processes, such as runoff and soil erosion.

The relationships between plant functional diversity and soil erosion processes have recently appealed to the interest of the scientific community studying plant-soil erosion processes (Erktan et al. 2013; Zhu et al. 2015), although the results on functional diversity effects are controversial. However, these studies focussed on functional diversity effects of root traits of non-herbaceous communities on soil stabilisation and resistance in mountainous or semi-arid vegetation, which are community structures selected under the erosion processes specific to these soil and climatic contexts (Guerrero-Campo and Montserrat-Martí 2000; Martin et al. 2010; Zhu et al. 2015). The effects of aboveground functional diversity in herbaceous vegetation on hydraulic roughness still need to be understood for runoff and concentrated soil erosion processes. In landscape with important land use of annual crop fields (e.g. loamy soils of north-west Europe), runoff and concentrated soil erosion are mainly reduced by the hydraulic roughness in small vegetation patches (Styczen and Morgan 1995). The hydraulic roughness of herbaceous vegetation furthers sediment retention by reducing the flow velocity (Järvelä 2002; Hussein et al. 2007; Akram et al. 2014; Cantalice et al. 2015; Cao et al. 2015) and is influenced by the aboveground biomass and functional traits (Styczen and Morgan 1995; Burylo et al. 2012a; Akram et al. 2014). The effects of aboveground biomass was highlighted (Burylo et al. 2012a), showing that an increase in biomass productivity would further hydraulic roughness and sedimentation. Kervroëdan et al. (2018) identified the aboveground functional traits directly impacting the hydraulic roughness: vegetation with important leaf density, leaf area, stem diameter and stem projected area (stem area toward the flow direction) were found to be the most efficient. Nonetheless, these results emphasised the effects of negatively correlated trait combination (i.e. leaf density and area) on the hydraulic roughness increase, which suggested that multi-traits communities would reach the best trade-off to maximise the vegetation effects on hydraulic roughness (Kervroëdan et al. 2018).

In this study on trait-based plant ecohydrology, we aim to examine the effects of functional diversity on hydraulic roughness using monospecific and multi-specific communities, at different discharges. We predicted that functional diversity improves hydraulic roughness by exerting a synergetic effect. The stem and leaf traits involved in the hydraulic roughness increase (stem diameter and projected area; leaf density, area and specific area) would present a complementarity in the space use which is a competitive balance among the species in the community. Diverse communities with a high differentiation degree among these traits will use the aboveground space more efficiently and lead to an increase of productivity (Dimitrakopoulos and Schmid 2004; Yachi and Loreau 2007; Lorentzen et al. 2008).

6.2. Materials and methods

6.2.1. Plant material

Four plant species presenting contrasting aboveground functional traits involved in hydraulic roughness increase were chosen from an 76 candidate species list of indigenous plants from north-west Europe (Kervroëdan et al. 2018). This list resulted from six filters applied to the 3,500 spermatophyte species from north-west Europe (Lambinon et al. 2012), focussing on the selected functional types involved in mitigation of soil erosion in north-west Europe: (1) Raunkiaer's life-form categories of "herbaceous chamaephytes", "hemicryptophytes" and "geophytes", i.e. perennial herbaceous vegetation that provide an effective soil cover during all seasons; (2) the presence of fresh (i.e. herbaceous chamaephytes and caespitose hemicryptophytes) or dry (i.e. non-caespitose hemicryptophytes and geophytes) biomass in winter when soil erosion is observed in north-west Europe (Boardman and Poesen 2006); (3) the presence of rhizomes or stolon to ensure lateral spreading capacity and burial tolerance due to sediment deposition; (4) vegetative height ≥ 20 cm, as it is the water maximal level in the catchment in north-west Europe; (5) a broad ecological niche to select species able to grow in several silty agricultural soils; and (6) non-weed species to avoid their expansion in agricultural territories of north-west Europe.

In order to limit competition for light between the species tested in this study, a seventh filter was applied and only species within the same vegetative height range of a minimal height comprised between 20 and 60cm were chosen. These following species: *Carex flacca* (C), *Tanacetum vulgare* (T), *Festuca arundinacea* (F) and *Phalaris arundinacea* (P) were tested under monospecific and two multi-specific with contrasting traits communities (Figure 25) with four replicates. There were two types of multi-specific communities, one composed of *C. flacca, T. vulgare* and *F. arundinacea* (CTF); and the other with *C. flacca, T. vulgare, F. arundinacea* and *P. arundinacea* (CTFP).

In March 2016, three months before the experiments, the plants were collected *in natura* and planted in 60 x 30 x 15 cm plots made of a wooden frame and fence at the bottom to allow the roots' development. Multi-specific plots were composed of the same proportion of each species used, which were placed so the same species would not be in contact.

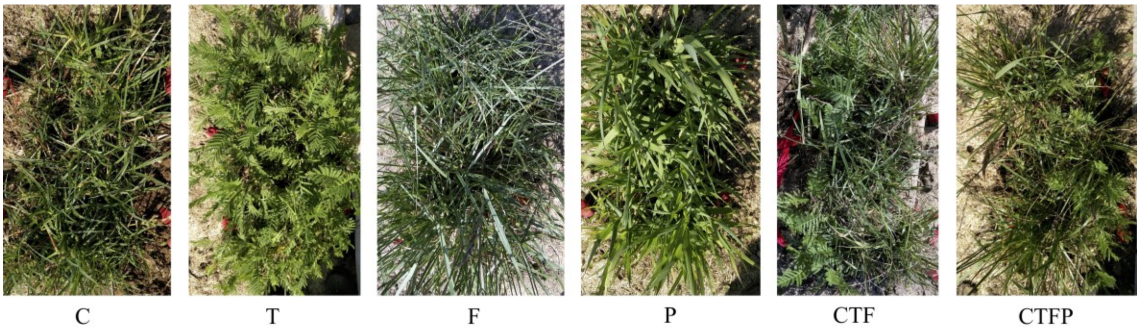

Figure 25. Three levels of plant functional diversity with four monospecific and two multi-specific conditions. Photos were taken 1.5 month prior experiments. C – *Carex flacca*, T – *Tanacetum vulgare*, F – *Festuca arundinacea* and P – *Phalaris arundinacea*; CTF – *Carex flacca* + *Tanacetum vulgare* + *Festuca arundinacea*; CTFP – *Carex flacca* + *Tanacetum vulgare* + *Festuca arundinacea* + *Phalaris arundinacea*.

6.2.2. Plant functional traits measurements

Six aboveground functional plant traits (stem – density, diameter, projected area; leaf – density, area and specific area), identified as influencing hydraulic roughness at the individual or the community level (Kervroëdan et al. 2018), were measured following the variation of inflow water level on three levels along the stem: between 0 and 5cm, 0 and 10cm and 0 and 20cm. Guidelines from Pérez-Harguindeguy et al. (2013) were followed regarding the sampling collection, samples conversation and analyses methods. As analyses could not be performed directly after sampling, the leaves were stored in sealed bags with moist tissue until measurements and were then dried at 70°C for 72h.

As the plots presented a homogeneous plant cover, all trait measurements were carried out on one quadrat (10 by 10 cm) per monospecific community plot and one quadrat per species within the multi-specific community plots. The determination of stem density included plant stems as well as pseudoculms for sedges species (Cyperaceae) and tillers for grass species which are considered here to have the same functional effect on hydraulic roughness as stems. The stem diameter was measured on three representative stems and was used to determine the stem projected area of each stem using the rectangle area formula. The leaf area and the specific leaf area (SLA) were estimated from six representative leaves which were scanned using a 600dpi resolution and images were processed using Gimp 2.8. The aboveground biomass of each plot was collected and then dried during 72h at 70°C.

Furthermore, a density value of traits within the quadrat was calculated through the product of (1) leaf traits by leaf density and (2) stem traits by stem density. These densities and the traits were dissociated by adding a "D" at the front of the trait appellations.

6.2.3. Characterisation of the community functional structure

Both multi-specific communities were created with an equal abundance of each species. The CTF communities accounted for 33% of each species (*C. flacca, T. vulgare* and *F. arundinacea*) and the CTFP communities accounted for 25% of each species (*C. flacca, T. vulgare, F. arundinacea* and *P. arundinacea*).

The community-weighted traits (CWT) were calculated, for each trait in both multi-specific communities, as the mean trait value after each trait was weighted by the abundance of each species composing the community (Violle et al. 2007; Díaz et al. 2007b):

$$CWT_i = \sum_{k=1}^{n_i} A_{k,i} \ T_{k,i} \qquad (1)$$

where CWT_i is the community-weighted value of the trait in the community i, $A_{k,i}$ and $T_{k,i}$ are, respectively, the relative abundance and the trait value of the species k in the community i and n_i is the number of species in the community i.

The functional variance (FD_{var}) was calculated for each trait in both multi-specific communities. FD_{var} represents the variance of the trait values of the species in the community (Mason, Mouillot, Lee, & Wilson, 2005):

$$FD_{var} = \frac{2}{\pi}\arctan[5 \sum_{i=1}^{N}[(\ln C_i - \overline{\ln x})^2 \ A_i] \qquad (2)$$

where C_i is the value of the trait i, $\overline{\ln x}$ is the abundance-weighted logarithmic mean of the trait and A_i is the abundance of the species with the trait i (Mason et al. 2003, 2005).

The Rao's quadratic entropy (FD_Q) (Rao 1982), a multidimensional index of functional diversity that is a generalized form of the diversity Simpson index (Leps et al. 2006) and combines a measure of the pairwise functional differences between species and the relative abundance of the species (Botta-Dukát 2005) . The FD_Q was determined using the package FD in R (version 3.3.2).

6.2.4. Hydraulic measurements

The effect of the functional diversity on the hydraulic roughness was measured using a runoff simulator that recreated a flow at set discharges in controlled conditions (Richet et al. 2017). The flow discharge was monitored through Venturi channels (flow range of 0.06-6 l/s) and ultrasound probes measuring the water level in the channels (± 1.26 mm) located in the upper and lower parts of the simulator. This system was manufactured by ISMA, France (Richet et al. 2017). Measures of hydrological processes were carried out in the central part of the simulator, a channel area which consisted of two 5.40 m galvanised iron sheets buried 60cm away from each others on a 5% levelled slope. The entire channel area was waterproofed using a tarpaulin to avoid water losses, such as leaks and infiltration in the ground, during the experiment. The plot was located 4 m away from the head of the channel in a 17 cm deep rectangular hole to level the plants with the channel. To measure the channel topography and the backwater level in front of the plants, five spacers were placed upstream the plot, from approximately 1.46 m from the channel head every 0.75 m. Each spacer was levelled and its elevation was measured to use them as elevation-known baselines for the water level measurements.

In order to investigate the communities' behaviour towards processes occurring more or less frequently, four discharges were chosen: 2, 4, 8 and 11 $L.s^{-1}.m^{-1}$ at ± 7% (observed approximately every 0.5, 1, 2 and 5 years, respectively, in 5 ha catchments with a 5 m-wide thalweg) (Richet et al. 2017). Discharges were continuously monitored through both upstream and downstream flowmeters. When upstream and downstream discharges were equivalent, water levels were measured as the perpendicular distance between the bottom of the spacer and the top of the water flow, using the closest spacer upstream of the plot. Seven vertical water profiles were made per discharge per plot, one every 10 cm along the spacer from the edges of the channel.

The hydraulic roughness was characterised by the unit stream power (USP), often used as a sediment transport capacity index (Yang 1972; Govers 1992) as it represents the "energy dissipation per unit of time and per unit of weight of the flow" (Govers 1992):

$$USP = V\ S \qquad (3)$$

where USP ($m.s^{-1}$) depends on V, the mean velocity of the flow ($m.s^{-1}$), and S, the slope of the channel ($m.m^{-1}$) (Morgan et al. 1998; Cao et al. 2015; Hessel et al. 2016). The USP negatively related to the hydraulic roughness: the lower it is, the higher the hydraulic roughness will be.

6.2.5. Data analysis

Mann Whitney and T tests were conducted on the functional diversity variance for each trait to analyse the variation of the functional structure between the two multi-specific communities.

After regrouping the data under the categories "monospecific" and "multi-specific", Kruskal-Wallis analyses were performed on the USP data to compare (1) the mean value of monospecific communities with the multi-specific communities and (2) both multi-specific communities. The monospecific P community data were excluded from the analysis for the comparison with the three-species communities (CTF). ANOVA and Tukey post-hoc tests were then computed on the USP data to examine the differences between each community category to understand if one species/community had more impact on the USP than another.

ANOVA and Kruskal-Wallis analyses as well as respective post-hoc tests Tukey and Mann-Whitney were used on the traits, the community-weighted traits and the biomass data, accordingly to the normality of the data, to examine the differences in trait and community-weighted trait composition between the communities. Moreover, after combining the data under “monospecific” and “multi-specific” categories, Mann-Whitney analyses were carried out on community-weighted trait data to compare the mean value of the monospecific communities with the multi-specific communities, as well as on the biomass data. For the analysis of the CTF communities, the monospecific P communities were removed from the data.

All the statistical analyses were computed using the statistical software R (version 3.3.2).

6.3. Results

6.3.1. Variation of functional diversity within the communities

The results on the functional variance showed significant differences and a higher variance of the traits in CTFP than in CTF, except for the leaf area and the density-weighted leaf area (0 – 5 cm) (Table 12). The values of FD_Q found for the community CTF was 10 and 11.25 for the community CTFP.

Table 12. Summary of the functional diversity variance FDvar for both multi-specific communities and results from the T and Mann-Whitney tests.

Traits	CTF	CTFP	t / **W**
LA (mm^2)	0.7454 (± 0.0836)	0.7614 (± 0.0735)	-0.24864 ns
LD5 (.dm^{-2})	0.9855 (± 0.0009)	0.9883 (± 0.0006)	-4.5579 *
LD10 (.dm^{-2})	0.9879 (± 0.0008)	0.9905 (± 0.0007)	-4.1791 *
LD20 (.dm^{-2})	0.9889 (± 0.0009)	0.9917 (± 0.001)	-3.6474 *
DSA5 (mm^2.dm^{-2})	0.9967 (± 0.0002)	0.9974 (± 0.0002)	-4.9464 *
DSA10 (mm^2.dm^{-2})	0.9972 (± 0.0002)	0.9979 (± 0.0001)	-5.5758 **
DSA20 (mm^2.dm^{-2})	0.9976 (± 0.0001)	0.9982 (± 0.0001)	-6.6792 **
DSDm5 (mm.dm^{-2})	0.9878 (± 0.0013)	0.9903 (± 0.0009)	-2.7224 °
DSDm10 (mm.dm^{-2})	0.9878 (± 0.0012)	0.9902 (± 0.0009)	-2.8 °
DSDm20 (mm.dm^{-2})	0.9878 (± 0.001)	0.9902 (± 0.0009)	-3.0036 *
DLA5 (mm^2.dm^{-2})	0.9986 (± 0.00003)	0.999 (± 0.00003)	**0 ns**
DLA10 (mm^2.dm^{-2})	0.9987 (± 0.00002)	0.9991 (± 0.0001)	-11.108 **
DLA20 (mm^2.dm^{-2})	0.9988 (± 0.00003)	0.9992 (± 0.0001)	-8.8503 **
DSLA5 (mm^2.mg^{-1}.dm^{-2})	0.9947 (± 0.0001)	0.9961 (± 0.0002)	-9.7441 **
DSLA10 (mm^2.mg^{-1}.dm^{-2})	0.9953 (± 0.0002)	0.9966 (± 0.0003)	-6.9083 **

Data are FDvar mean values (± standard deviation) and t values of T tests and W value of Mann-Whitney (in bold) test. CTF – *Carex flacca* + *Tanacetum vulgare* + *Festuca arundinacea*; CTFP – *Carex flacca* + *Tanacetum vulgare* + *Festuca arundinacea* + *Phalaris arundinacea*; LA – leaf area; LD – leaf density; DLA – leaf area density; DSA – stem area density; DSDm – stem diameter density and DSLA – specific leaf area density. Significance levels: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ° = $p < 0.1$; ns = not significant.

6.3.2. Variation of functional diversity and the unit stream power

The comparison analysis of the USP values for the monospecific communities and for the multi-specific communities, using Kruskal-Wallis tests, showed no significant differences for any of the combinations tested (Figure 26). Moreover, no difference was observed between both multi-specific communities and the USP did not show a decrease of its value with an increase of functional diversity in the communities (Figure 26). Similar results were found through all the tested discharges.

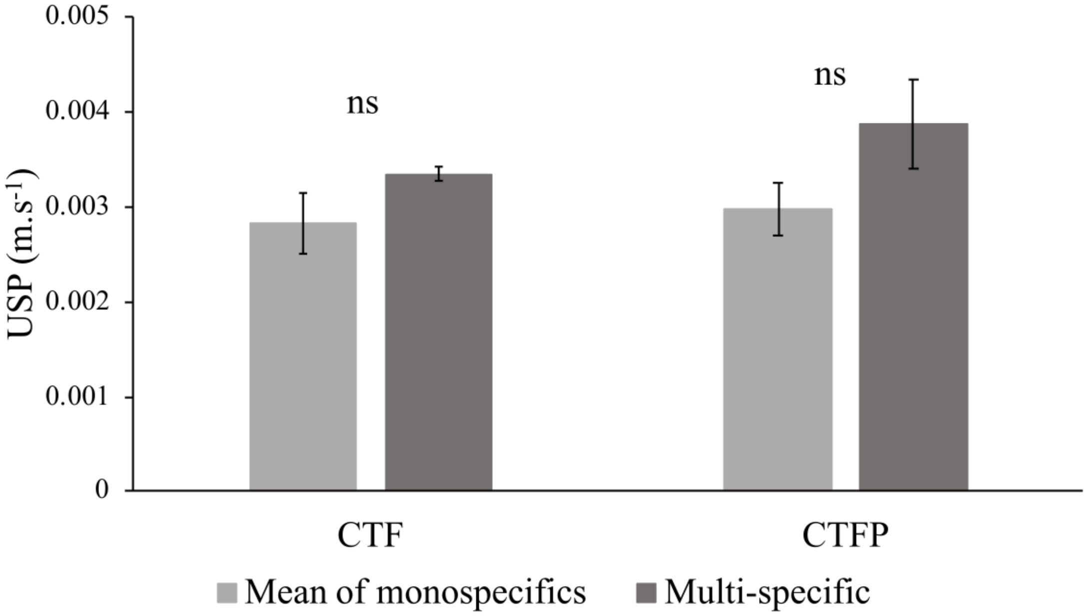

Figure 26. Differences between the mean of the monospecific and the multi-specific conditions at the discharge 2 L.s^{-1}.m^{-1}. The bars represent the mean ± standard error. Significance level: ns = not significant.

6.3.3. Variation of community-weighted trait and the unit stream power

According to the results from the comparison analyses between each community on the USP, only *F. arundinacea* in monoculture presented a significant difference to the other communities (Figure 27). Similar results were found at each tested discharge (Supplementary material 5). There were no significant differences between the other communities studied. Results on the aboveground biomass did not show any differences between the mean of the mono-specific with the multi-specific communities (Figure 28), showing a significant difference between *C. flacca* and *T. vulgare* (with a trend between *C. flacca* and all the other communities, as well as between *T. vulgare* and *F. arundinacea*, as the p-values from the Mann-Whitney tests were 0.057). Regarding the community-weighted trait analysis, all the ANOVA/Kruskal-Wallis tests were found to be significant (Table 13). Except for CW leaf area, CW leaf density (0 – 10cm), CW leaf density (0 – 20cm) and CW density-weighted SLA (0 – 10cm), both multi-specific communities had no significant difference with any of the monospecific communities. CW density-weighted stem projected and CW density-weighted stem diameter, for all levels along the stem, showed only a difference of *F. arundinacea* within the monospecific communities. Differences between *F. arundinacea* and the multi-specific communities were found for CW-LD20 (with both multi-specific communities) and CW-LD10 (only with CTFP).

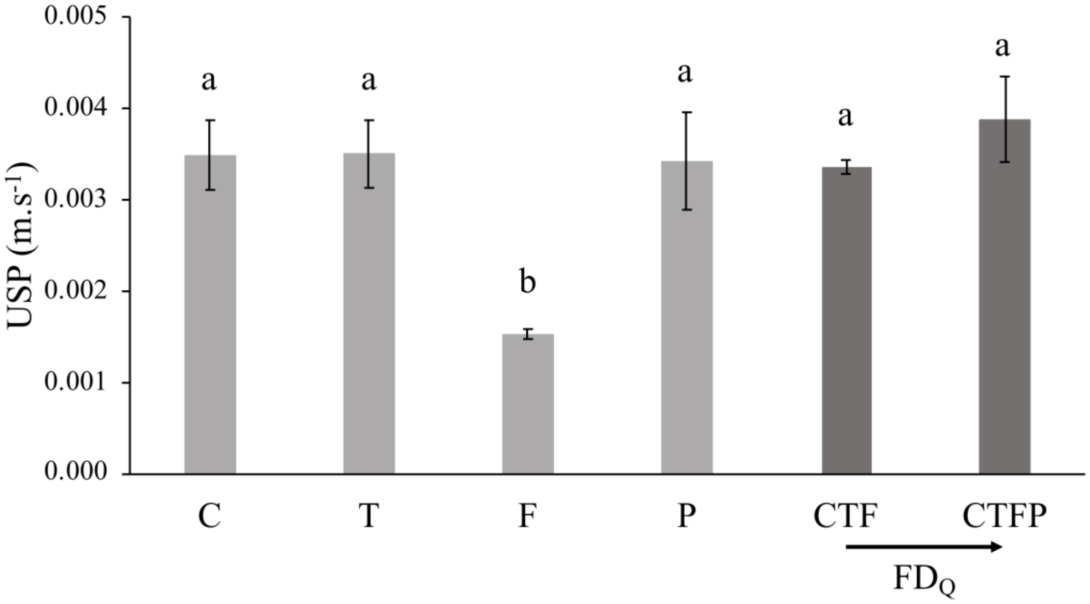

Figure 27. Differences between each community at the discharge 2 L.s^{-1}.m^{-1}. The bars represent the mean ± standard error. The letters represent the significant differences between each community according to the Tukey post-hoc tests. The arrow shows the direction of increasing functional diversity (with FD$_Q$ the Rao's quadratic entropy).

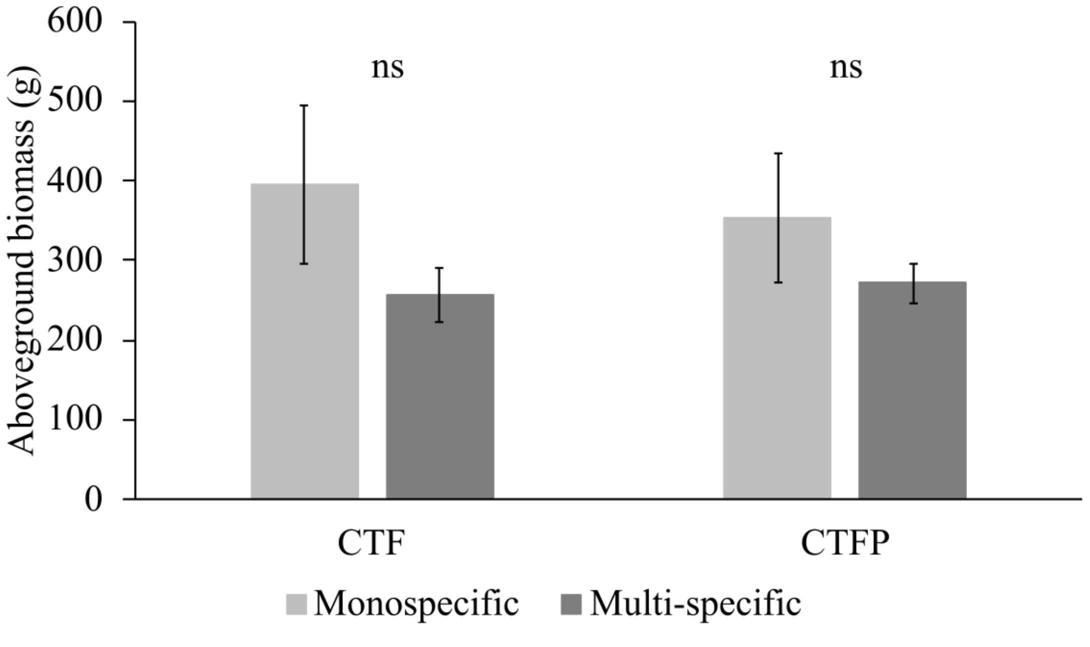

Figure 28. Differences in the biomass productivity between the mean of the monospecific communities and the multi-specific communities. The bars represent the mean ± standard error. The letters represent the significant differences between each community according to the Mann-Whitney post-hoc tests.

Table 13. Differences in community-weighted traits (CW) for each community tested.

	C	T	F	P	CTFP	CTF	ANOVA / **Kruskal-Wallis**
CW-LA (mm^2)	1575.8 (± 144.6) ^{a}	4168.5 (± 1049.5) ^{b}	3130 (± 298.4) ^{bc}	3054.4 (± 331.1) ^{bc}	3116.2 (± 605.6) ^{bc}	2715.9 (± 224.8) ^{ac}	9.28***
CW-LD5 (.dm^{-2})	96.3 (± 15.6) ^{a}	12 (± 2.6) ^{b}	193.1 (± 73.3) ^{c}	46.6 (± 24.5) ^{a}	91.2 (± 7.1) ^{abc}	111.2 (± 21.8) ^{abc}	**18.99****
CW-LD10 (.dm^{-2})	148.8 (± 30.8) ^{a}	20.8 (± 1.5) ^{b}	280.3 (± 79.6) ^{c}	74.9 (± 43.1) ^{ab}	154.8 (± 37.8) ^{a}	171.7 (± 31.4) ^{ac}	15.53***
CW-LD20 (.dm^{-2})	236.5 (± 43.4) ^{a}	38.8 (± 2.6) ^{b}	423.9 (± 61.4) ^{c}	108.5 (± 61.4) ^{bd}	214.8 (± 79.7) ^{ad}	212.8 (± 40.2) ^{ad}	24.89***
CW-DLA5 (mm^2.dm^{-2})	153175 (± 35395) ^{a}	50527 (± 20693) ^{b}	599417 (± 210360) ^{c}	147223 (± 90166) ^{ab}	229484 (± 25910) ^{abc}	251565 (± 59698) ^{abc}	**17.96****
CW-DLA10 (mm^2.dm^{-2})	236709 (± 61527) ^{a}	86420 (± 23545) ^{b}	868938 (± 216666) ^{c}	237161 (± 156858) ^{a}	406719 (± 121334) ^{abc}	389669 (± 77960) ^{abc}	**17.63****
CW-DLA20 (mm^2.dm^{-2})	376697 (± 93429) ^{a}	163234 (± 48516) ^{b}	1325651 (± 212015) ^{c}	343506 (± 223961) ^{ab}	573873 (± 251557) ^{abc}	474577 (± 79275) ^{abc}	**15.91****
CW-DSA5 (mm^2.dm^{-2})	4675.3 (± 1258.3) ^{a}	2263.4 (± 593.7) ^{a}	19926 (± 7469.9) ^{b}	3880.1 (± 2061) ^{a}	6088.6 (± 1345) ^{ab}	5579.4 (± 1499.8) ^{ab}	**15.48****
CW-DSA10 (mm^2.dm^{-2})	9226.5 (± 2471.1) ^{a}	4412.9 (± 1116.5) ^{a}	40673 (± 15603) ^{b}	7458.3 (± 3858.2) ^{a}	12040 (± 2561.4) ^{ab}	11169 (± 2975.2) ^{ab}	**15.95****
CW-DSA20 (mm^2.dm^{-2})	16841 (± 4587.3) ^{a}	8739.8 (± 2140.3) ^{a}	82565 (± 30896) ^{b}	14356 (± 7515.9) ^{a}	23190 (± 5038.9) ^{ab}	21497 (± 5331.6) ^{ab}	**16.09****
CW-DSDm5 (mm.dm^{-2})	93.5 (± 25.2) ^{a}	45.3 (± 11.9) ^{a}	398.5 (± 149.4) ^{b}	77.6 (± 41.2) ^{a}	121.8 (± 26.9) ^{ab}	111.6 (± 30) ^{ab}	**15.48****
CW-DSDm10 (mm.dm^{-2})	92.3 (± 24.7) ^{a}	44.1 (± 11.2) ^{a}	406.7 (± 156) ^{b}	74.6 (± 38.6) ^{a}	120.4 (± 25.6) ^{ab}	111.7 (± 29.8) ^{ab}	**15.95****
CW-DSDm20 (mm.dm^{-2})	91.5 (± 24) ^{a}	43.7 (± 10.7) ^{a}	412.8 (± 154.5) ^{b}	71.8 (± 37.6) ^{a}	119.2 (± 25.4) ^{ab}	110.6 (± 27.1) ^{ab}	**15.95****
CW-DSLA5 (mm^2.mg^{-1}.dm^{-2})	18.7 (± 1.4) ^{a}	18.9 (± 1.9) ^{a}	676.4 (± 1309.1) ^{ab}	180.1 (± 309.8) ^{b}	1731.8 (± 265.6) ^{ab}	1883.1 (± 344.9) ^{ab}	**15.72****
CW-DSLA10 (mm^2.mg^{-1}.dm^{-2})	1813.6 (± 386.8) ^{ac}	230.2 (± 71.7) ^{a}	4632.5 (± 1817.5) ^{b}	1215.3 (± 463) ^{ac}	2854.1 (± 886.5) ^{bc}	2895.4 (± 504) ^{bc}	11.33***

Data are CW mean values (± standard deviation) and results of F (ANOVA) and Chi-squared (Kruskal-Wallis, in bold) statistical tests. C – *Carex flacca*; T – *Tanacetum vulgare*; F – *Festuca arundinacea*; P – *Phalaris arundinacea*; CTF – *Carex flacca* + *Tanacetum vulgare* + *Festuca arundinacea*; CTFP – *Carex flacca* + *Tanacetum vulgare* + *Festuca arundinacea* + *Phalaris arundinacea*; LA – leaf area; LD – leaf density; DLA – leaf area density; DSA – stem area density; DSDm – stem diameter density and DSLA – specific leaf area density. The letters represent the significant differences between the communities, according to the Tukey and Mann-Whitney post-hoc tests. Significance levels: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant.

6.4. Discussion

Knowledge of the effects of aboveground functional structure on hydraulic roughness lacks research to understand the role of plant communities on runoff and soil erosion reduction. This study characterised for the first time the effects of functional structure of plant communities on the runoff and hydraulic roughness.

6.4.1. Non-additive effect of the functional diversity on the hydraulic roughness

An increasing functional diversity should lead to greater niche differentiation and could influence on ecosystem processes (Cadotte et al. 2011). Following this hypothesis, the differences in functional diversity of the traits observed among the communities should have led to an additive effect on the hydraulic roughness. However, the results did not show any additive effect, as with increasing functional diversity there was no increase of the hydraulic roughness. No significant difference between the mean of mono-specific populations and the multi-specific communities, nor between both multi-specific communities presenting different functional diversities (FD_Q) were found. These findings highlighted the dominant effect of community-weighted traits of specific species in the communities on runoff (Grime 1998; Lavorel and Garnier 2002; Díaz et al. 2007b) . The results have emphasised the community-weighted trait effects of *F. arundinacea* on the hydraulic roughness, being the only species significantly different from the other communities, which would be led by the CW leaf density (0 – 20cm) and the CW leaf density (0 – 10cm). In Kervroëdan et al. (2018), the leaf density was found to be a major trait impacting the hydraulic roughness. How is this non-additive effect of the functional diversity on the hydraulic roughness explained?

6.4.2. Complementarity between stem diameter, leaf area and density does not increase hydraulic roughness

The niche complementarity hypothesis stipulates that the diversity in trait attributes in a community influences the ecosystem processes, by inducing non-additive effects (i.e. complementarity or facilitation effects) among the coexisting species (Tilman et al. 1997a; Petchey and Gaston 2006). However, the results did not show any synergetic effect of the functional diversity on the hydraulic roughness with the presence of contrasting traits, which could be justified by the absence of complementarity between the traits. While similar results are found on soil retention when looking at different functional type mixtures (Erktan et al. 2013), additive effects of the functional diversity on erosion rates are also reported (Zhu et al. 2015). These opposing effects of the functional diversity on the hydraulic roughness and erosion rates could be explained by idiosyncratic effects, which represent contrasting effects of functional diversity affected by species and trait interactions and soil-plant interactions. Idiosyncratic effects could be influenced by the functional structure within the communities (Erktan et al. 2013). If the proportion of larger stem diameters is too high in the community, preferential flow paths will be taken by the water, limiting the effects of the denser individuals, which would impact the effect of the functional diversity on the hydraulic roughness (Styczen and Morgan 1995; Erktan et al. 2013). This hypothesis is consistent with results showing that the presence of functional types with larger stem diameters would influence the water path within a vegetation and, thus, displayed no effect of the community functional diversity (Erktan et al. 2013). Perspective is to study a gradient of functional structures, using a variation of abundances of large stem diameters, to confirm and show idiosyncratic effects of the functional diversity on the water flow.

6.4.3. The non-additive effect of functional diversity on aboveground biomass productivity would explain the absence of effects on the hydraulic roughness

The aboveground biomass of herbaceous vegetation positively influenced the hydraulic roughness, although the productivity was not impacted by the functional diversity. As positive relationships are found between the aboveground biomass and soil retention (Podwojewski et al. 2011; Burylo et al. 2012a), this absence of increase in productivity with the functional diversity would explain the non-additive effect of the functional diversity on the hydraulic roughness. The effects of the functional diversity on the biomass productivity can be contrasting and explained by idiosyncratic effects (Tilman et al. 1997a; Cardinale et al. 2007; Garnier et al. 2016; Cadotte 2017). Indeed, the biomass productivity efficiency depends on environmental factors (e.g. soil properties or the species combinations used), which can also influence the effects of diversity (specific and functional) on soil erosion processes (Lambers et al. 2004; Bautista et al. 2007; Turnbull et al. 2008; Pohl et al. 2009; Martin et al. 2010; Mueller et al. 2013; Erktan et al. 2013; Zhu et al. 2015; Hou et al. 2016; Mariotte et al. 2017). The absence of functional diversity effect on the biomass productivity can be explained by the non-optimal use of the functional space by the community (Lepik et al. 2004; Dimitrakopoulos and Schmid 2004), leading to a limited effect on the hydraulic roughness and sediment retention (Burylo et al. 2012a). Perspective is to understand the idiosyncratic effects on both the biomass productivity and the hydraulic roughness in order to unravel the contrasting effects of the functional diversity on the hydraulic roughness by studying a wider functional diversity gradient.

6.4.4. Implication to design herbaceous hedges for sediment retention

These findings constitute a first advancement in the understanding of community functional structure effects on runoff and the hydraulic roughness. The results highlighted that the presence of high leaf density species will tend to dominate the community effects on the hydraulic roughness and, thus, sediment retention. This response was found to be independent from the intensity of the event occurring as similar results were found for all the discharges tested.

In order to model the effects of multi-specific plant communities on runoff and sediment retention processes, the community-weighted mean value of traits could be implemented, as, depending on the functional structure of the community, non-additive effect of functional diversity can be found. The integration of the community-weighted traits into modelling vegetation effects would allow to take into account this dominance effect and model the community overall effects on runoff and soil erosion in herbaceous hedges involved essentially in sediment retention. Moreover, as an absence of negative effect of the functional diversity was found in this study, using combinations of species involved in the hydraulic roughness increase within the hedge design for soil erosion control is recommended. Indeed, using multi-specific communities would create multi-functional ecosystems that could offer other ecosystem services such as biodiversity conservation by the creation of new habitats and the enhancement of the ecological connectivity to mitigate biodiversity erosion (Ouin and Burel 2002).

6.5. Conclusions

This ecohydrology study allowed to identify the relationship between the aboveground functional structure and the hydraulic roughness. The results showed that there was no influence of the functional diversity on the hydraulic roughness but rather an effect of dominant traits in the community, identified as the community-weighted leaf densities. The absence of functional diversity effect on the hydraulic roughness would be explained by the non-increase in biomass productivity. Perspective is to study the functional diversity effects on a wider diversity gradient of candidate species involved in the increase of the hydraulic roughness, in order to explain the contrasting results found for the functional diversity effects on sediment retention and runoff processes.

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REFERENCES

Akram S, Yu B, Ghadiri H, et al (2014) The links between water profile, net deposition and erosion in the design and performance of stiff grass hedges. J Hydrol 510:472–479. doi: 10.1016/j.jhydrol.2014.01.001

Bautista S, Mayor ÁG, Bourakhouadar J, Bellot J (2007) Plant Spatial Pattern Predicts Hillslope Runoff and Erosion in a Semiarid Mediterranean Landscape. Ecosystems 10:987–998. doi: 10.1007/s10021-007-9074-3

Berendse F, van Ruijven J, Jongejans E, Keesstra S (2015) Loss of plant species diversity reduces soil erosion resistance. Ecosystems 18:881–888. doi: 10.1007/s10021-015-9869-6

Boardman J, Poesen J (eds) (2006) Soil Erosion in Europe. John Wiley & Sons, Ltd

Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J Veg Sci 16:533–540

Burylo M, Rey F, Bochet E, Dutoit T (2012) Plant functional traits and species ability for sediment retention during concentrated flow erosion. Plant Soil 353:135–144. doi: 10.1007/s11104-011-1017-2

Cadotte MW (2017) Functional traits explain ecosystem function through opposing mechanisms. Ecol Lett 20:989–996. doi: 10.1111/ele.12796

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. J Appl Ecol 48:1079–1087. doi: 10.1111/j.1365-2664.2011.02048.x

Cantalice JRB, Melo RO, Silva YJAB, et al (2015) Hydraulic roughness due to submerged, emergent and flexible natural vegetation in a semiarid alluvial channel. J Arid Environ 114:1–7. doi: 10.1016/j.jaridenv.2014.10.012

Cao L, Zhang Y, Lu H, et al (2015) Grass hedge effects on controlling soil loss from concentrated flow: A case study in the red soil region of China. Soil Tillage Res 148:97–105. doi: 10.1016/j.still.2014.12.009

Cardinale BJ, Wright JP, Cadotte MW, et al (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. Proc Natl Acad Sci 104:18123–18128

Díaz S, Lavorel S, Chapin FS, et al (2007a) Functional Diversity — at the Crossroads between Ecosystem Functioning and Environmental Filters. In: Canadell JG, Pataki DE, Pitelka LF (eds) Terrestrial Ecosystems in a Changing World. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 81–91

Díaz S, Lavorel S, de Bello F, et al (2007b) Incorporating plant functional diversity effects in ecosystem service assessments. Proc Natl Acad Sci 104:20684–20689. doi: 10.1073/pnas.0704716104

Dimitrakopoulos PG, Schmid B (2004) Biodiversity effects increase linearly with biotope space: Diversity effects increase with biotope space. Ecol Lett 7:574–583. doi: 10.1111/j.1461-0248.2004.00607.x

Erktan A, Cécillon L, Roose E, et al (2013) Morphological diversity of plant barriers does not increase sediment retention in eroded marly gullies under ecological restoration. Plant Soil 370:653–669. doi: 10.1007/s11104-013-1738-5

Faucon M-P, Houben D, Lambers H (2017) Plant functional traits: soil and ecosystem services. Trends Plant Sci 22:385–394. doi: 10.1016/j.tplants.2017.01.005

Fornara DA, Tilman D (2008) Plant functional composition influences rates of soil carbon and nitrogen accumulation. J Ecol 96:314–322. doi: 10.1111/j.1365-2745.2007.01345.x

Garnier E, Navas M-L, Grigulis K (2016) Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties. Oxford University Press

Govers G (1992) Relationship between discharge, velocity and flow area for rills eroding loose, non-layered materials. Earth Surf Process Landf 17:515–528

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910. doi: 10.1046/j.1365-2745.1998.00306.x

Guerrero-Campo J, Montserrat-Martí G (2000) Effects of soil erosion on the floristic composition of plant communities on marl in northeast Spain. J Veg Sci 11:329–336

Hessel R, Jetten VG, Liu B, Qiu Y (2016) Evaluating Effects of Soil and Water Management and Land Use Change on the Loess Plateau of China Using LISEM. In: Morgan RPC, Nearing M (eds) Handbook of Erosion Modelling. John Wiley and Sons, pp 223–248

Hou J, Wang H, Fu B, et al (2016) Effects of plant diversity on soil erosion for different vegetation patterns. CATENA 147:632–637. doi: 10.1016/j.catena.2016.08.019

Hussein J, Yu B, Ghadiri H, Rose C (2007) Prediction of surface flow hydrology and sediment retention upslope of a vetiver buffer strip. J Hydrol 338:261–272

Järvelä J (2002) Flow resistance of flexible and stiff vegetation: A flume study with natural plants. J Hydrol 269:44–54

Kervroëdan L, Armand R, Saunier M, et al (2018) Plant functional trait effects on runoff to design herbaceous hedges for soil erosion control. Ecol Eng 118:143–151. doi: 10.1016/j.ecoleng.2018.04.024

Lambers JHR, Harpole WS, Tilman D, et al (2004) Mechanisms responsible for the positive diversity-productivity relationship in Minnesota grasslands. Ecol Lett 7:661–668. doi: 10.1111/j.1461-0248.2004.00623.x

Lambinon J, Delvosalle L, Duvigneaud J (2012) Nouvelle flore de la Belgique, du G.-D. de Luxembourg, du nord de la France et des régions voisines, 6th edn.

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Funct Ecol 16:545–556

Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol Evol 12:474–478. doi: 10.1016/S0169-5347(97)01219-6

Lepik M, Liira J, Zobel K (2004) The space-use strategy of plants with different growth forms, in a field experiment with manipulated nutrients and light. Folia Geobot 39:113–127

Leps J, De Bello F, Lavorel S, Berman S (2006) Quantifying and interpreting functional diversity of natural communities: practical considerations matter. Preslia 78:481–501

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76. doi: 10.1038/35083573

Lorentzen S, Roscher C, Schumacher J, et al (2008) Species richness and identity affect the use of aboveground space in experimental grasslands. Perspect Plant Ecol Evol Syst 10:73–87. doi: 10.1016/j.ppees.2007.12.001

Mariotte P, Mehrabi Z, Bezemer TM, et al (2017) Plant–Soil Feedback: Bridging Natural and Agricultural Sciences. Trends Ecol Evol

Martin C, Pohl M, Alewell C, et al (2010) Interrill erosion at disturbed alpine sites: Effects of plant functional diversity and vegetation cover. Basic Appl Ecol 11:619–626. doi: 10.1016/j.baae.2010.04.006

Mason NWH, MacGillivray K, Steel JB, Wilson JB (2003) An index of functional diversity. J Veg Sci 14:571–578. doi: 10.1111/j.1654-1103.2003.tb02184.x

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118

Mcgill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends Ecol Evol 21:178–185. doi: 10.1016/j.tree.2006.02.002

Morgan RPC, Quinton JN, Smith RE, et al (1998) The EUROSEM model. In: Boardman J, Favis-Mortlock D (eds) Modelling Soil Erosion by Water. Springer Science and Business Media, pp 389–398

Mueller KE, Tilman D, Fornara DA, Hobbie SE (2013) Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. Ecology 94:787–793

Ouin A, Burel F (2002) Influence of herbaceous elements on butterfly diversity in hedgerow agricultural landscapes. Agric Ecosyst Environ 93:45–53

Pérez-Harguindeguy N, Díaz S, Garnier E, et al (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167–234. doi: 10.1071/BT12225

Petchey OL (2003) Integrating methods that investigate how complementarity influences ecosystem functioning. Oikos 101:323–330

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9:741–758. doi: 10.1111/j.1461-0248.2006.00924.x

Podwojewski P, Janeau JL, Grellier S, et al (2011) Influence of grass soil cover on water runoff and soil detachment under rainfall simulation in a sub-humid South African degraded rangeland. Earth Surf Process Landf 36:911–922. doi: 10.1002/esp.2121

Pohl M, Alig D, Körner C, Rixen C (2009) Higher plant diversity enhances soil stability in disturbed alpine ecosystems. Plant Soil 324:91–102. doi: 10.1007/s11104-009-9906-3

Rao CR (1982) Diversity and dissimilarity coefficients: A unified approach. Theor Popul Biol 21:24–43. doi: 0040-5809/82/010024-2OSO2.00/0

Richet J-B, Ouvry J-F, Saunier M (2017) The role of vegetative barriers such as fascines and dense shrub hedges in catchment management to reduce runoff and erosion effects: Experimental evidence of efficiency, and conditions of use. Ecol Eng 103:455–469. doi: 10.1016/j.ecoleng.2016.08.008

Song Y, Wang P, Li G, Zhou D (2014) Relationships between functional diversity and ecosystem functioning: A review. Acta Ecol Sin 34:85–91. doi: 10.1016/j.chnaes.2014.01.001

Styczen ME, Morgan RPC (1995) Engineering properties of vegetation. In: Morgan RPC, Rickson RJ (eds) Slope Stabilization and Erosion Control: A Bioengineering Approach. E & FN SPON, London, pp 4–60

Tilman D, Knops J, Wedin D, et al (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Turnbull L, Wainwright J, Brazier RE (2008) A conceptual framework for understanding semi-arid land degradation: ecohydrological interactions across multiple-space and time scales. Ecohydrology 1:23–34. doi: 10.1002/eco.4

Violle C, Navas M-L, Vile D, et al (2007) Let the concept of trait be functional! Oikos 116:882–892. doi: 10.1111/j.2007.0030-1299.15559.x

Yachi S, Loreau M (2007) Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities: Light-use complementarity and complementarity index. Ecol Lett 10:54–62. doi: 10.1111/j.1461-0248.2006.00994.x

Yang CT (1972) Unit stream power and sediment transport. ASCE J Hydraul Div 98:1805–1826

Zhu H, Fu B, Wang S, et al (2015) Reducing soil erosion by improving community functional diversity in semi-arid grasslands. J Appl Ecol 52:1063–1072. doi: 10.1111/1365-2664.12442

Supplementary material 5. Differences in unit stream power for each community tested at each discharge.

Discharges	C	T	F	P	CTF	CTFP	ANOVA
Q1 = 2 $L.s^{-1}.m^{-1}$	0.0035 (± 0.0008) ^{a}	0.0035 (± 0.0007) ^{a}	0.0015 (± 0.0001) ^{b}	0.0034 (± 0.0011) ^{a}	0.0033 (± 0.0001) ^{a}	0.0039 (± 0.0008) ^{a}	5.29**
Q2 = 4 $L.s^{-1}.m^{-1}$	0.0046 (± 0.0007) ^{a}	0.0051 (± 0.0009) ^{a}	0.0021 (± 0.0001) ^{b}	0.0046 (± 0.0011) ^{a}	0.0044 (± 0.0002) ^{a}	0.0053 (± 0.0008) ^{a}	8.8***
Q3 = 8 $L.s^{-1}.m^{-1}$	0.0066 (± 0.001) ^{a}	0.0083 (± 0.0013) ^{a}	0.0032 (± 0.0002) ^{b}	0.0067 (± 0.0013) ^{a}	0.0064 (± 0.0004) ^{a}	0.0077 (± 0.0015) ^{a}	10.92***
Q4 = 11 $L.s^{-1}.m^{-1}$	0.0078 (± 0.0011) ^{a}	0.0105 (± 0.0015) ^{a}	0.0038 (± 0.0001) ^{b}	0.0079 (± 0.0016) ^{a}	0.0077 (± 0.0006) ^{a}	0.009 (± 0.0017) ^{a}	12.64***

Data are USP mean values (± standard deviation) and results of statistical tests F in ANOVA. C – Carex flacca; T – *Tanacetum vulgare*; F – *Festuca arundinacea*; P – *Phalaris arundinacea*; CTF – *Carex flacca* + *Tanacetum vulgare* + *Festuca arundinacea*; CTFP – *Carex flacca* + *Tanacetum vulgare* + *Festuca arundinacea* + *Phalaris arundinacea*. The letters represent the significant differences between the communities, according to the Tukey post-hoc tests. Significance levels: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant.

DISCUSSION

7. DISCUSSION

7.1. Variations in the effects of plant functional traits on the hydraulic roughness and sediment retention

Herbaceous plants offer a protection and a control solution towards concentrated runoff and soil erosion processes by influencing the hydraulic roughness and furthering sediment retention. According to the first hypothesis regarding plant aboveground trait effects on runoff processes, hydraulic roughness and sediment retention were influenced by leaf and stem traits in herbaceous vegetation (Chapter 1). The analysis of the effects of 14 species presenting contrasting traits allowed to create a baseline for the identification of the traits linked to a high hydraulic roughness. Basing the analysis on the hydraulic roughness rather than soil detachment or sediment retention, as most studies did, allow to characterise the effects of traits on the hydrological components of soil erosion by runoff. Hydraulic roughness is correlated with sediment transport capacity and sediment retention (Isselin-Nondedeu and Bédécarrats 2007; Dabney et al. 2009; Lambrechts et al. 2014), which allowed to also use it as an index for the vegetation's efficiency towards the cited processes. Indeed, hydraulic roughness was found negatively correlated to sediment retention at 96% (Chapter 2). From the eight studied traits (i.e. leaf area, leaf density, specific leaf area, stem density, specific stem density, stem projected area and stem dry matter content), only two presented a significant effect on the hydraulic roughness: leaf area and leaf density. These results are consistent with other studies (Burylo et al. 2012a; Lambrechts et al. 2014). Stem density, main trait found to influence sediment retention, did not have a direct influence on the hydraulic roughness in the present study. Usually, only monocotyledon species are tested in the studies focussing on herbaceous vegetation (Meyer et al. 1995; Morgan and Duzant 2008; Dabney et al. 2009; Mekonnen et al. 2016), while our study comprised dicotyledon and monocotyledon species, which could explain the non-direct effect of stem density (Isselin-Nondedeu and Bédécarrats 2007).

The main advance in this research laid the greater effects of density-weighted traits (i.e. trait weighted by the trait's density) on hydraulic roughness, which have been scarcely considered in studies on plant trait effects on hydraulic roughness or sediment retention. This approach showed the effects of the density-weighted leaf area (i.e. leaf area x leaf density, in $mm^2.dm^{-2}$), the density-weighted stem diameter (i.e. stem diameter x stem density, in $mm.dm^{-2}$) and the density-weighted projected stem area (i.e. the projected area of the vegetation towards the flow; stem projected area x stem density, in $mm^2.dm^{-2}$) on the hydraulic roughness. Moreover, the study went further by identifying the most efficient combinations of density-weighted traits to increase hydraulic roughness: (1) the density-weighted leaf area with the density-weighted stem diameter and (2) the density-weighted leaf area with the density-weighted projected stem area. These results emphasise the indirect impact of stem density on hydraulic roughness, through the characterisation of the density-weighted stem diameter and projected stem area. Illustrating the relationship between plant traits and hydraulic roughness by including density-weighted traits would allow the characterisation of the trait effects at the vegetation's level, giving a more precise idea on how the plant community affects runoff and soil erosion processes.

Work is still needed to deepen the knowledge of traits and weighted traits on these processes. Including traits related to the plant biomechanical properties (e.g. leaf tensile strength, stem bending resistance, stem lignin and cellulose content) could also give more information regarding the physical resistance of the vegetation towards the flow (Meyer et al. 1995; Burylo et al. 2012a). Moreover, as variations in flow discharges can trigger different soil-plant-water interactions, trait responses towards hydraulic roughness and sediment retention could change (Temple et al. 1987; Dabney et al. 2004; Vieira and Dabney 2012). This hypothesis was validated with the changing responses in the effects of leaf density and leaf area depending on different discharges observed in the Chapter 1, which was also emphasised in the literature (Temple et al. 1987; Vieira and Dabney 2012). The leaf density was found influencing at important discharges (8 and 11 $L.s^{-1}.m^{-1}$) while the leaf area was efficient for small discharges (2 and 4 $L.s^{-1}.m^{-1}$). Similar contrasting responses were found for the stem stiffness, with an effect on sediment retention found for high discharges (from 11 to 43.7 $l.s^{-1}.m^{-1}$) (Meyer et al. 1995) but absent for lower discharges (from 1.6 to 11 $l.s^{-1}.m^{-1}$) (Chapter 1, Burylo et al. (2012a)). Using wider gradients of plant traits (including plant biochemical-related traits) and flow discharges would help build a better understanding and characterisation of the trait effects on runoff and soil erosion processes.

The understanding and characterisation of trait effects on hydraulic roughness and sediment retention can be implemented into (1) a first step in the selection of candidate herbaceous species related to a specific phyto-geographical territory following the selection filters listed in 3.2; and (2) existing erosion models assessing the vegetation effects on runoff and soil erosion.

7.1.1. Implication of trait effects on hydraulic roughness for selecting candidate species

A first implication of the characterisation of trait effects on the hydraulic roughness is the selection of candidate species that would be efficient for the phyto-geographical area of implantation. As the effects of functional traits can change depending on the flow characteristics (i.e. discharges), it is important to implement the trait's range for which there is an effect on the hydraulic roughness and sediment retention, depending on the flow discharges, into the design. The results obtained in this study give an insight of the contrasting effects of the traits depending on the discharge; which corresponds to a first step on the characterisation of the relationships between traits and flow rates under temperate climates.

Following the functional type approach for selective filters applied to north-west Europe indigenous spermaphyte species presented in the PhD methods (see 3.2), 76 potential candidate species were highlighted. The finalisation of the selection process requires the application of a filter integrating the traits involved in hydraulic roughness and sediment retention (Box 1: Implementation of trait effects into candidate species selection).

This method can be applied to any other phytogeographical territory than north-west Europe in order to select indigenous species able to reduce runoff and soil erosion processes encountered in these territories. Some particularities related to the erosion processes associated with the phytogeographical territories' climates would have to be modified in the selection method, as some traits and criteria would have more importance than others. For instance, under temperate climates, hydraulic resistance and sediment retention (through hydraulic roughness) are the main processes reducing runoff and soil erosion; while soil stabilisation and resistance (through e.g. soil detachment capacity, shear strength) are the main processes controlling runoff and soil erosion under semi-arid or Mediterranean climates (Meyer et al. 1995; Burylo et al. 2012b; Zhu et al. 2015). In semi-arid and Mediterranean ecosystems, where erosional precipitations are concentrated into one intense episode, functional root traits are highly efficient in the reduction of erosion rates, by reinforcing soil and slope stability by their effects on soil detachment capacity and soil shear strength (Ghestem et al. 2011; Burylo et al. 2012b; Stokes et al. 2014; Zhu et al. 2015; Mekonnen et al. 2016). Moreover, plants with the Raunkiaer's life-forms "chamaephytes" and "caespitose chameaphytes" would be more abundant (e.g. *Lavandula sp., Rosmarinus sp.*) and are found to reduce erosion rates with both aboveground and belowground traits (Bochet et al. 2006; Burylo et al. 2012a).

An interesting perspective to this selection process would be to (1) adapt the selection method according to the climate and erosion processes occurring; and (2) create frameworks for species selection in a multitude of phytogeographical territories under different climates. Identifying the aboveground and belowground traits impacting the hydrological and erosional processes occurring in different phytogeographical territories would allow the selection of species involved in the control of the targeted processes and help the practitioners in the design of effective measures for runoff and erosion control.

Box 1: Implementation of trait effects into candidate species selection

Considering the selection method used to identify the potential candidate species, traits and combination of traits emphasised as involved in the increase of hydraulic roughness and sediment retention should be the next selection step to find the candidate species for the design of efficient herbaceous hedges (Chapter 1).

Results from Chapter 1 showed the determinant effects of leaf and stem traits, at the individual and vegetation levels (Table 15). The threshold value from which an effect on the hydraulic roughness is found was identified for each trait and density-weighted trait, using the unit stream power critical value of 0.004 m.s^{-1} (Table 14). Although it is important to note that leaf area and density had different responses toward hydraulic roughness depending on the discharge; the combination of both traits was found to explain better the effect of hydraulic roughness for all discharges rather than the traits separately.

From the tested species (Chapter 1), the one with the highest hydraulic resistance for most discharges was *Carex pendula*; while the species with the lowest hydraulic resistance was *Origanum vulgare*. Both of these species presented a distinctive combination of trait values corresponding to their contrasting hydraulic resistance (Figure 29).

Table 15. Best model fits identifying the combinations of traits and density-weighted traits influencing the hydraulic roughness.

Discharge	Best model fits
2 L.s^{-1}.m^{-1}	USP ~ LA + LD USP ~ DLA + DSA USP ~ DLA + DSDm
4 L.s^{-1}.m^{-1}	USP ~ LA + LD USP ~ DLA + DSA USP ~ DLA + DSDm
8 L.s^{-1}.m^{-1}	USP ~ LA + LD USP ~ LD USP ~ DLA + DSDm USP ~ DLA + DSA
11 L.s^{-1}.m^{-1}	USP ~ LA + LD USP ~ LD USP ~ DLA + DSA USP ~ DLA + DSDm

LA: leaf area, LD: leaf density, "D": density-weighted, SA: projected stem area, SDm: stem diameter

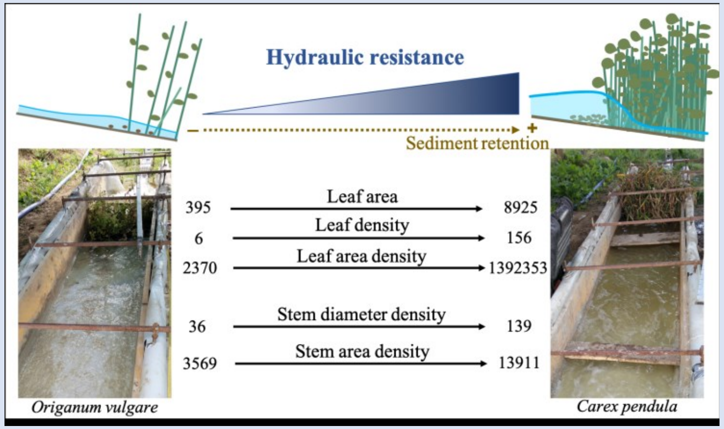

Figure 29. Two extremes from tested species with the lowest and highest hydraulic roughness: implementation of their aboveground trait values for candidate species selection.

By using both the efficient combinations and the identified threshold values, the 76-species list of potential candidate species can be narrowed down to the most interesting species to create herbaceous hedges in north-west Europe (Appendix A).

Table 14. Threshold values of each trait and density-weighted trait's range of efficiency on the hydraulic roughness.

	2 L.s^{-1}.m^{-1}	4 L.s^{-1}.m^{-1}	8 L.s^{-1}.m^{-1}	11 L.s^{-1}.m^{-1}
Leaf area (mm^2)	200	2200	6500	8200
Leaf density (dm^{-2})	0	70	250	310
D. leaf area (mm^2.dm^{-2})	2000	227500	820000	1000000
D. projected stem area (mm^2.dm^{-2})	2000	8400	18750	23500
D. stem diameter (mm.dm^{-2})	20	80	190	230

7.1.2. Necessity and study perspectives for the integration of trait effects on hydraulic roughness into modelling of vegetation effects for runoff and erosion control

A second implication of the identification of the traits involved in hydraulic roughness and sediment retention is their implementation into modelling the vegetation effects on runoff and soil erosion. The integration of plant trait effects into modelling allows to understand the effects of vegetation on hydraulic roughness and sediment retention from the local to the landscape scale and evaluate these effects in relation to the other components affecting runoff and soil erosion (e.g. soil properties, infiltration capacity, sediment properties). Comparisons of results obtained with a widely used model (VFS-MOD) with experimental results on sediment retention (Chapter 2) were made (Box 2: Modelling vegetation effects using VFS-MOD). VFS-MOD is an improved model comprising two older erosion models: GRASSF and SEDIMOT II, being respectively a model for suspended solids' filtration by grass and a hydrology and sedimentology catchment model (Munoz-Carpena et al. 1999). VFS-MOD was chosen following its recognised effectiveness in the (1) evaluation of vegetation effects on runoff and soil erosion processes and (2) design of efficient vegetation strips controlling erosional episodes related to the implantation area; as well as being an easy access and user-friendly model.

The comparison analysis showed a poor accuracy from the model. This inaccuracy was linked to the combination of hydrological and vegetation parameters. Indeed, the model is built to recreate shallow flows and does consider concentrated events for small runoff areas and vegetation widths (Fox et al. 2010; Muñoz Carpena and Parsons 2014). Integrating the characterisation of concentrated flows into the model, through the applicable dimensions of runoff area and vegetation width, could widen its use possibilities. The implementation of actual vegetation parameters using traits would give a more precise description of the plant community and its effects on the hydraulic roughness.

Box 2: Modelling vegetation effects using VFS-MOD

There are a number of soil erosion models characterising the effects of vegetation (Duzant 2008). VSF-MOD (Vegetative Filter Strip Modelling System), is a field and event-based model, developed by Muñoz Carpena and Parsons (2014), which evaluates the vegetation effects on hydrological and sediment transport processes through vegetative filter strips. This model is physically-based and simulates sediment retention resulting of vegetation's hydraulic roughness (i.e. Manning index). VFS-MOD uses data on rainfall, incoming water runoff and sediment characteristics to compute outflow, infiltration and sediment retention efficiency (Muñoz Carpena and Parsons 2014). However, VFS-MOD does not consider concentrated flows but simulates a uniform flow going through a vegetative filter strip (Duzant 2008). Although this model is widely used, the characterisation of the vegetation's hydraulic roughness is based on one plant trait: stem height (Muñoz Carpena and Parsons, 2014). The vegetation is also characterised within the model using the stem spacing, the vegetation's Manning roughness coefficient and the strip's width.

The experiment data from Chapter 2 were inputted into the model in order to compare the expected results from the model and the observed results (Table 16). The retention capacity determined through the model was significantly underestimated. From the vegetation parameters used in the model, stem spacing is the vegetation's most determinant component in the sediment efficiency characterisation, compared with the vegetation's height and Manning coefficient. A limitation to the use of stem spacing as parameter is the lack of definition (i.e. whether if it is the spacing between the external or the centre of the stem), and is derived from the stem density and attributed according to the plant species rather than being a measured value (Munoz-Carpena et al. 1999; Lambrechts et al. 2014).

Under a concentrated flow passing through a narrow object (i.e. herbaceous hedge), the model does not compute accurate sediment retention capacity values. Moreover, the characterisation of the vegetation, usually using constant or recommended values, does not recreate the accurate conditions. Adding traits controlling the hydraulic roughness in herbaceous hedges would increase the precision in modelling vegetative barriers efficiency and broaden the model's field of application. Therefore, improvements may apply to: (1) the estimation of sediment transport and retention capacities, and (2) the design of herbaceous vegetation by creating efficient vegetation for hydraulic processes encountered in the implantation landscape.

Table 16. Comparison between the observed sediment retention by the experimentations and the expected retention capacity by VFSMOD

Plots		Observed retention (%)	Expected retention (%)
Carex pendula	1	86.0	0
	2	78.9	0
	3	87.0	0
Tanacetum vulgare	1	71.2	0
	2	69.2	0
	3	68.8	0
Festuca arundinacea	1	77.7	0.1
	2	73.7	0.1
	3	77.2	1.0
Mixture	1	84.5	0
	2	77.0	0
	3	77.2	0

7.2. Functional and specific diversity effects on hydraulic roughness and sediment retention

Plant species diversity and functional diversity affect the hydraulic roughness and sediment retention, even though the results did not validate the original research hypotheses. Unlike the expected complementarity effect of the traits on hydraulic roughness and sediment retention when testing communities presenting contrasting traits, a dominant effect of the traits was found (Chapter 2). This result is not in accordance with other studies that showed a complementary effect of the traits in mountainous or semi-arid multi-specific communities on runoff and soil erosion resistance (Pohl et al. 2009; Martin et al. 2010), as well as for herbaceous vegetation of western Europe (Berendse et al. 2015). When using a gradient of functional structures, non-additive effects of functional diversity were found (Chapter 3). Contrasting results are found in the literature, showing dominant effects of traits in mountainous plant communities composed with different functional types (Erktan et al. 2013) and complementarity effect of functional diversity in semi-arid grassland communities (Zhu et al. 2015). In overall, leaf traits drove the dominant effects in both experiments: leaf density, density-weighted leaf area (Chapter 2) and leaf density (Chapter 3).

The non-impact of the functional diversity on hydraulic roughness using different discharges (ranged from 2 to 11 $L.s^{-1}.m^{-1}$) shows that the non-additive effects must have been linked to the traits and biomass productivity of the tested communities, rather than to the flow velocity. The results showed that low values of community-weighted leaf density and low values of community-weighted leaf area density limited the effects of the vegetation on hydraulic roughness and sediment retention (Chapter 2), while high values of community-weighted leaf density furthered the effects of the vegetation on these processes (Chapter 3). This emphasised the dominant effect of graminoid species (presenting a high density of long leaves) in a multi-specific community, which have also been highlighted in the literature (Morgan 2004; Isselin-Nondedeu and Bédécarrats 2007), and a limiting effect of dicotyledon species presenting low leaf density and leaf area at the vegetation scale. Moreover, integrating species with large stems with an excessive abundance in plant communities could inflect on the overall community efficiency towards runoff velocity reduction, as preferential path flows can be created by the presence of low stem density with large diameters (Erktan et al. 2013). A limited amount of species with set abundances have been tested in this research project (3 species at 33% or 4 species at 25%, Chapter 3), which imply that different effects could be found with different species combinations and abundances presenting a better use of the functional space.

The absence of effect of functional diversity on the aboveground biomass productivity also suggests that the space-use of the tested communities was non-optimal (Dimitrakopoulos and Schmid 2004; Weigelt et al. 2008) which could have led to the non-additive effects of functional diversity on hydraulic roughness and sediment retention, as aboveground biomass positively affects sediment retention (Podwojewski et al. 2011; Burylo et al. 2012a). Plant space-use strategy, as for biomass productivity, depends on the species used in the community, their growth form, the range of the niches they represent as well as the light and nutrient allocation (Lepik et al. 2004; Dimitrakopoulos and Schmid 2004; Spehn et al. 2005). Indeed, in nutrient-deficient soils, species in communities with high functional diversities will allocate different strategies in order to access the limiting resources, decreasing the competition for light between the aboveground traits, developing competitive acquisition strategies depending on their niche differentiation (e.g. depending on their optimal competitive abilities N:P ratios) and leading to an increase of the overall biomass productivity (Tilman et al. 1997b, 2014).

Furthering the present study by integrating a wider gradient of trait combinations and a variation of trait abundances in the community would give a great insight and deepen the knowledge on functional diversity effects of herbaceous vegetation on runoff and soil erosion control processes. The integration of symbiotic nitrogen fixation traits (i.e. legume species) in the community would increase the nitrogen availability for the non-legumes, increase the biomass productivity (Lambers et al. 2004; Spehn et al. 2005; Mueller et al. 2013; Mariotte et al. 2017) and should thus induce a greater hydraulic roughness and sediment retention. Moreover, even if the effect of dicotyledon species has been found lower and limiting on hydraulic roughness and sediment retention, their presence could enhance the space-use and productivity stability by the fast establishment of seedlings in gaps in-between graminoid species, post disturbance (Weigelt et al. 2008). In order to validate the hypothesis of preferential flows created by an important number of wide stems, the integration of individuals with large stems could be done following a variation of abundances. Although individuals presenting wide diameters could be included in the community as they could present a support action for the high-density individuals with smaller stems which would bend more easily under the flow pressure.

7.3. Designing herbaceous hedges from trait-based approach to control runoff and soil erosion

In agricultural areas, implanting vegetative barriers in the form of herbaceous hedges across the flow path reduces sheet and concentrated erosion (Dabney et al. 1995). Herbaceous hedges are narrow strips of dense and stiff perennial vegetation and present a high efficiency on the reduction of soil erosion caused by concentrated flows by furthering hydraulic roughness and sediment retention in concentrated flow paths (Dabney et al. 1995; Yuan et al. 2009). They represent a good complementary tool to the existing ones for erosion control (e.g., fascines, buffer strips), with a number of advantages: (1) the high efficiency in runoff velocity reduction and sediment retention for concentrated episodes; (2) the small area needed for implantation; (4) the limited maintenance after implantation; (3) the sustainability of the hedge with the vegetation growth above the retained sediments.

7.3.1. From field to hillslope: determining suitable localisations to implant herbaceous hedges using trait-based approach

Numerous soil and landscape processes can control runoff sources and pathways, which result in a spatially heterogeneous runoff erosion distribution (Vandaele and Poesen 1995). When designing herbaceous hedges, setting the expected levels of impacts regarding the rainfall properties and the reduction of suspended sediment are the main components. Sediment control is site specific and thus requires specific studies to target the efficiency of the herbaceous hedges (Tomer et al. 2008; Mekonnen et al. 2015). After selecting the species composing the herbaceous hedge, the specific catchment area (i.e. upslope area contributing to runoff generation), the soil characteristics (e.g. texture), the slope gradient and topographical features (e.g. thalwegs), the crops and the observed runoff pathways should be considered to design and locate efficient hedges (Dosskey et al. 2015; Carluer et al. 2017).

These factors can be implemented in a scoping tool (i.e. model) to help local planners to set-up the herbaceous hedges at the most efficient location (Tomer et al. 2008; Dosskey et al. 2011, 2015; Carluer et al. 2017). The capability of vegetated areas to reduce runoff and sediment transport through infiltration and sediment retention processes can be assessed by using soil and slopes properties to determine the infiltration capacity of the vegetated area, which allows to calculate indexes such as the 'Sediment Trapping Efficiency' of the herbaceous hedge (Dosskey et al. 2011).

The placement of the herbaceous hedges can also be determined by terrain analysis through GIS use, especially on elevation dataset (Digital Elevation Model), to predict runoff spatial patterns. The elevation dataset is processed to create flow direction and flow accumulation. The resulting data enables to map the hydrological network used by the runoff and to delineate the watersheds or specific catchment areas of previously selected places such as field limits or human infrastructures.

7.3.2. Designing herbaceous hedges: monospecific or multi-specific?

Effects of multi-specific herbaceous hedges on runoff and erosion control

Biodiversity generally leads to a more ecologically stable system, as a stable and healthy system would be less vulnerable to abiotic and biotic stress (Tilman 1999). Most of the studied herbaceous hedges through the literature were monospecific hedges (Meyer et al. 1995; Dabney et al. 2004; Cullum et al. 2007; Hussein et al. 2007; Lin et al. 2009; Huang et al. 2010; Cao et al. 2015; Mekonnen et al. 2016). However, the use of multi-specific vegetation to control runoff and soil erosion has been studied (Bautista et al. 2007; Turnbull et al. 2008; Pohl et al. 2009; Martin et al. 2010; Erktan et al. 2013; Zhang et al. 2015; Berendse et al. 2015; Zhu et al. 2015; Hou et al. 2016), but some of the studies focussed on the diversity of different functional types or within vegetation patches.

The effects of diversity within herbaceous hedges were found contradictory, but they did not show negative interactions with the efficiency of the hedges. Results obtained on the effect of plant morphological diversity used in vegetation barriers on bioengineering structures showed no increase of sediment retention (Erktan et al. 2013). This insinuates that even if plant species diversity and functional diversity do not negatively affect the efficiency of the hedges, the herbaceous hedges could be composed of only few species with the best traits involved in decreasing runoff, increasing sediment retention and mitigating soil erosion (Rey and Labonne 2015). Moreover, the integration of scattered trees or shrubs into the herbaceous hedge would enhance its infiltration capacity (Christen and Dalgaard 2013), as long as they are maintained at a low height and present a light foliage to avoid competition and reduction of the herbaceous species' development. The integration of a shrub hedge along the herbaceous hedge could also be beneficial – as long as the competition for light is limited between the two objects by a north-south positioning – in terms of (1) water infiltration and (2) protection against agricultural engines and treatments that could damage the herbaceous hedges (e.g. herbicides, ploughing), if the shrub hedge is placed upstream the herbaceous hedge.

As there were no negative effects of functional diversity on the hedges' efficiencies, developing multi-specific herbaceous hedges is recommended. Favouring species diversity in the herbaceous hedges would enable reducing the risks of failure of vegetation systems in case of loss of a species on a site due to abiotic/biotic factors (Doak et al. 1998; Berendse et al. 2015) and provide other ecosystem services (e.g. habitat creation, ecological connectivity enhancement, integrated pest control). It is thus necessary to quantify the different services provided by multi-specific herbaceous hedges.

Multi-specific herbaceous hedges would provide other ecosystem services

The assessment of the multi-scale effects of functional diversity in herbaceous hedges on other ecosystem processes and services would be an exciting perspective. In addition to the water quality, soil loss and erosion reduction, runoff reduction services, multi-specific herbaceous hedges could present effects on other ecosystem processes and provide different ecosystem services. The effects of integrating herbaceous hedges should be studied, using a multi-scale analysis, to characterise the other impacted ecosystem processes and identify the provided ecosystem services. For instance, herbaceous hedges would induce habitat creation at the local scale and a network of herbaceous hedges at the landscape scale would further the ecological connectivity for species dispersion and distribution (Woodcock et al. 2005; Smith et al. 2008; Delattre et al. 2010).

- At the local scale: habitat creation

The use of several indigenous species to create the herbaceous hedges allows interactions between the plant diversity and the animal and microbial indigenous diversity, due to their co-evolution within the north-west European biogeographical territory. Indeed, a number of studies have found a positive effect of field margin strips on a wide range of taxa (e.g. birds, pollinators, small mammals) (Ouin and Burel 2002; Woodcock et al. 2005; Carvell et al. 2007; Smith et al. 2008). Although the strips (circa 5m) were larger than herbaceous hedges, similar effects than field margins could be found for herbaceous hedges, especially if they present a high functional diversity. For instance, the tested hedges (Chapter 2) showed the presence of passerine bird nests (Figure 30) after a year of implantation: 4 nests in two multi-specific plots (1.3 nests per m^2 in average), one nest in a *Carex pendula* plot (0.3 nest per m^2 in average) and one in a *Festuca arundinacea* plot (0.3 nest per m^2 in average). It can be thus hypothesised that older and longer hedges would further the establishment of a number of species, especially if these hedges present a diversity of traits, as grass species like *Festuca arundinacea* can provide materials and anchorage for the nests with the long and resistant leaves; while *Tanacetum vulgare* present a protection and cover with the high stems. Herbaceous hedges would also positively affect insect diversity distribution by providing an herbaceous habitat along or within agricultural fields and developing the predator-prey ratios within the herbaceous vegetation, which can also impact auxiliaries species involved in pest control (Denys and Tscharntke 2002; Meek et al. 2002; Woodcock et al. 2005; Haaland et al. 2011).

To understand the effects of herbaceous hedges on insects and animal diversity and distribution and validate that they further biodiversity by being suitable habitats, a multi-temporal analysis could be done on the distribution of different taxa, using a network of herbaceous hedges in a catchment. This analysis would reference soil macrofaunal species before the implantation of the herbaceous hedges, which would provide a baseline of the taxa already present in the area.

After implantation, sampling of soil macrofauna within the herbaceous hedge, with replications along the hedge, would be done every year to assess the multi-temporal effects of the herbaceous hedges on the distribution of the species. Comparison analysis between the years of the development of the soil macrofauna communities would be done in order to identify the evolution of the distribution of the communities within each hedge.

Figure 30. Passerine nests found in an experimental multi-specific plot (left) and *Festuca arundinacea* plot (right). Photos: Léa Kervroëdan.

- At the landscape scale: restauration of ecological corridors and connectivity

The integration of multi-specific herbaceous hedges in agricultural catchment could also further and restore the landscape ecological connectivity for species dispersion (Delattre et al. 2010). Their connectivity effects would further the ecological continuity of herbaceous habitats in the landscape and target subordinate species of herbaceous vegetation with a limited dispersion capacity (Smith et al. 2008).

The assessment of the effects of herbaceous hedges on the landscape ecological connectivity would be done on the same network of multi-specific herbaceous hedges previously cited. The data collected on soil macrofauna in all herbaceous hedges would be compared at each year to identify the distribution of the soil macrofauna communities in the landscape. The analysis of the ecological connectivity would be performed using the software Conefor that calculates connectivity indices using the habitat areas, the intrapatch connectivity and the interpatch connectivity (Saura and Torné 2009). This tool would also allow to identify suitable areas to implant additional herbaceous hedges to further the ecological connectivity in the catchment.

7.4. How to explain the contrasting effects of functional diversity on soil-plant processes: a meta-analysis perspective

Contrasting results on the effects of functional diversity have been found on biomass productivity (Tilman et al. 1997a; Cardinale et al. 2007; Mokany et al. 2008; Cadotte 2017; Xu et al. 2018) and soil erosion processes (Erktan et al. 2013; Zhu et al. 2015), as well as a number of other soil processes (i.e. nutrient dynamics, microbial activity, carbon sequestration) (Fornara and Tilman 2008; Lange et al. 2015; Garnier et al. 2016; Zuo et al. 2016a, b). The responses of functional diversity towards ecosystem processes can be affected by idiosyncratic effects of the traits (i.e. contrasting effects of functional diversity influenced by abiotic/biotic factors, such as species-traits and soil-plant interactions), explaining the contrasting results found (Loreau 2000; Díaz et al. 2007b; Xu et al. 2018). The contrasting effects of functional diversity on ecosystem processes would be dependant of the abundance of particular traits in the community, being affected by interactions between the plant species in the community, or even with animals or micro-organisms (Shachak et al. 1987; Díaz et al. 2007b). These idiosyncratic effects of the traits would thus create an uncertainty in the prediction of the functional diversity effects on ecosystem processes (Díaz et al. 2007b).

Although contrasting results of functional diversity effects have been found for a number of plant-soil processes, there has not been any analysis to explain the drivers of these controversial results. An interesting perspective would be to perform a meta-analysis focussing on how the contrasting effects of functional diversity on plant-soil processes can be explained. This meta-analysis would unravel the contrasting effects of functional diversity on soil-plant processes to highlight the potential ecological factors explaining the idiosyncratic effects of the traits influencing the functional diversity effects. Multiple ecosystem processes related to plant-soil interactions can be influenced by the same idiosyncratic effects and impact each-other (e.g. the aboveground productivity being affected by idiosyncratic effects of the traits (e.g. trait combinations) and resulting in an effect on runoff velocity regulation); on another hand, some processes can only be influenced functional diversity. Understanding how idiosyncratic effects alter functional diversity effect on ecosystem processes would unravel the levels of impact these effects have on the entire network of processes occurring in the plant-soil ecosystem. It is hypothesised that traits' assembly in the community plays a major role in how functional diversity affects ecosystem processes and how these effects of trait combination in the community would drive the effects of functional diversity. The understanding of the different parameters influencing functional diversity would also allow the prediction of functional diversity effects on major ecosystem processes.

To answer the central question, the meta-analysis would focus on plant functional diversity effects on soil biological, physical and chemical properties; considering the most studied processes which will comprise a significant amount of data (e.g. biomass net productivity, nutrient cycling, soil organic carbon, litter decomposition, soil erosion). Each process would be analysed separately to unravel the contrasting effects to understand if they are influenced by (1) environmental factors (soil, climate, anthropogenic activities); (2) the species traits and functional types. The first aim would be to characterise the differences in the functional diversity effects regarding abiotic environmental factors such as edaphic and climatic conditions, as well as management practices applied to the study area (e.g. mowing, ploughing). The climatic conditions, especially regarding precipitations and temperatures, would influence traits' distribution in plant communities (Moor et al. 2015). The phytogeographic territory in which the studies are located could impact the functional traits and the functional diversity of plant communities. For instance, functional diversity would have different effects on plant-soil processes, such as biomass productivity or carbon sequestration, depending on the climate of the study area (Garnier et al. 2004; Cortez et al. 2007; Klumpp and Soussana 2009). Although climatic conditions impact the effects of functional diversity on ecosystem processes, edaphic conditions have been found to influence plants' distribution in a greater way (Van Landuyt et al. 2011). Indeed, the edaphic conditions in which the studies take place can influence the responses of the community's functional diversity; notably depending on soil quality types, as they induce differences in the physical and chemical properties of the soil (e.g. nutrient availability, nutrient retention capacity, workability) (Tilman et al. 1997b, 2014; Aerts et al. 2003; Fischer et al. 2012). Anthropic activities through the ecosystem management – such as mowing, agricultural practices or extensive/intensive pasture – would also impact the way functional diversity affect ecosystem processes within plant communities (Matson et al. 1997; Davari et al. 2010). The second aim of this meta-analysis would be to generalise the behaviour of functional diversity toward each process and understand how the effects of functional diversity vary depending on the functional traits composing the plant communities. Indeed, traits' combination in a community influences the effects of functional diversity on ecosystem processes (Hooper et al. 2005; de Bello et al. 2010; Erktan et al. 2013). For instance, symbiotic nitrogen fixation traits could induce different responses of functional diversity towards plant-soil processes; depending on the level of functional diversity and on the community-weighted stem and leaf traits, such as the vegetative height which would influence the community's competition for light (Lambers et al. 2004; Spehn et al. 2005; Mueller et al. 2013; Mariotte et al. 2017).

To assess the effects of functional diversity on plant-soil processes, a search for relevant studies would be performed into databases (e.g. Web of Science (1900-2018), Google Scholar). This search would be carried out using combinations of key words such as "plant functional diversity"*"plant-soil" which gave 5 results on the Web of Science database and 781 results on Google Scholar. The first step of this analysis would be the selection of the processes of interest, which should comprise enough data to allow a throughout analysis of the contrasting results of functional diversity and the factors influencing these results. The search should include different combinations of relevant key words for each process (Table 17).

Table 17. Number of publications found on Google Scholar and Web of Science depending on the combinations of key words

Key word combinations	Number of results	
	Google Scholar	Web of Science
"plant functional diversity"*"biomass productivity"	781	0
"plant functional diversity"*"litter decomposition"	712	14
"plant functional diversity"*"soil erosion"	402	3
"plant functional diversity"*"phosphorus cycling"	51	0
"plant functional diversity"*"nitrogen cycling"	403	3
"plant functional diversity"*"microbial activity"	338	1
"plant functional diversity"*"carbon sequestration"	687	10

Although studies comprising replications within their experiments would be preferred to studies with limited replication sizes, there would not be an exclusion of a study based on the replication size. Indeed, meta-analyses on studies presenting a range of replication sizes allow to weight or reduce the impact of the small replicated studies (Hillebrand and Cardinale 2010). Trait measurements should be available in the studies to be included in the meta-analysis, as well as the species composition and abundance data in the plant communities. These data would allow to compute functional diversity indices as well as the community-weighted mean values of traits, if they are not already included in the study. Each process would be analysed separately from each other, using models (e.g. linear, linear mixed, generalised linear; depending on the computed data) to (1) assess the generalised effects of functional diversity on the process and (2) evaluate the combinations of traits and factors that could influence the effects of functional diversity on the process. The use of models would allow the ranking of the different tested parameters depending on their influence on the effects of functional diversity.

REFERENCES

Aerts R, Caluwe HD, Beltman B (2003) Plant Community Mediated Vs. Nutritional Controls on Litter Decomposition Rates in Grasslands. Ecology 84:3198–3208. doi: 10.1890/02-0712

Bautista S, Mayor ÁG, Bourakhouadar J, Bellot J (2007) Plant Spatial Pattern Predicts Hillslope Runoff and Erosion in a Semiarid Mediterranean Landscape. Ecosystems 10:987–998. doi: 10.1007/s10021-007-9074-3

Berendse F, van Ruijven J, Jongejans E, Keesstra S (2015) Loss of plant species diversity reduces soil erosion resistance. Ecosystems 18:881–888. doi: 10.1007/s10021-015-9869-6

Bochet E, Poesen J, Rubio JL (2006) Runoff and soil loss under individual plants of a semi-arid Mediterranean shrubland: influence of plant morphology and rainfall intensity. Earth Surface Processes and Landforms 31:536–549. doi: 10.1002/esp.1351

Burylo M, Rey F, Bochet E, Dutoit T (2012a) Plant functional traits and species ability for sediment retention during concentrated flow erosion. Plant and Soil 353:135–144. doi: 10.1007/s11104-011-1017-2

Burylo M, Rey F, Mathys N, Dutoit T (2012b) Plant root traits affecting the resistance of soils to concentrated flow erosion. Earth Surface Processes and Landforms 37:1463–1470. doi: 10.1002/esp.3248

Cadotte MW (2017) Functional traits explain ecosystem function through opposing mechanisms. Ecology Letters 20:989–996. doi: 10.1111/ele.12796

Cao L, Zhang Y, Lu H, et al (2015) Grass hedge effects on controlling soil loss from concentrated flow: A case study in the red soil region of China. Soil and Tillage Research 148:97–105. doi: 10.1016/j.still.2014.12.009

Cardinale BJ, Wright JP, Cadotte MW, et al (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of Sciences 104:18123–18128

Carluer N, Lauvernet C, Noll D, Munoz-Carpena R (2017) Defining context-specific scenarios to design vegetated buffer zones that limit pesticide transfer via surface runoff. Science of the Total Environment 575:701–712. doi: 10.1016/j.scitotenv.2016.09.105

Carvell C, Meek WR, Pywell RF, et al (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. Journal of Applied Ecology 44:29–40. doi: 10.1111/j.1365-2664.2006.01249.x

Christen B, Dalgaard T (2013) Buffers for biomass production in temperate European agriculture: A review and synthesis on function, ecosystem services and implementation. Biomass and Bioenergy 55:53–67. doi: 10.1016/j.biombioe.2012.09.053

Cortez J, Garnier E, Pérez-Harguindeguy N, et al (2007) Plant traits, litter quality and decomposition in a Mediterranean old-field succession. Plant and Soil 296:19–34. doi: 10.1007/s11104-007-9285-6

Cullum RF, Wilson GV, McGregor KC, Johnson JR (2007) Runoff and soil loss from ultra-narrow row cotton plots with and without stiff-grass hedges. Soil and Tillage Research 93:56–63

Dabney SM, McGregor KC, Wilson GV, Cullum RF (2009) How management of grass hedges affects their erosion reduction potential. Soil Science Society of America Journal 73:241. doi: 10.2136/sssaj2007.0434

Dabney SM, Meyer LD, Harmon WC, et al (1995) Depositional patterns of sediment trapped by grass hedges. Transactions of the ASAE 38:1719–1729

Dabney SM, Shields Jr FD, Temple DM, Langendoen EJ (2004) Erosion processes in gullies modified by establishing grass hedges. Transactions of the ASAE 47:1561

Davari MR, Ram M, Tewari JC, Kaushish S (2010) Impact of agricultural practice on ecosystem services. International journal of Agronomy and Plant Production 1:11–23

de Bello F, Lavorel S, Díaz S, et al (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. Biodiversity and Conservation 19:2873–2893. doi: 10.1007/s10531-010-9850-9

Delattre T, Pichancourt J-B, Burel F, Kindlmann P (2010) Grassy field margins as potential corridors for butterflies in agricultural landscapes: A simulation study. Ecological Modelling 221:370–377. doi: 10.1016/j.ecolmodel.2009.10.010

Denys C, Tscharntke T (2002) Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. Oecologia 130:315–324. doi: 10.1007/s004420100796

Díaz S, Lavorel S, de Bello F, et al (2007) Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences 104:20684–20689. doi: 10.1073/pnas.0704716104

Dimitrakopoulos PG, Schmid B (2004) Biodiversity effects increase linearly with biotope space: Diversity effects increase with biotope space. Ecology Letters 7:574–583. doi: 10.1111/j.1461-0248.2004.00607.x

Doak DF, Bigger D, Harding EK, et al (1998) The Statistical Inevitability of Stability-Diversity Relationships in Community Ecology. The American Naturalist 151:264–276. doi: 10.1086/286117

Dosskey MG, Neelakantan S, Mueller TG, et al (2015) AgBufferBuilder: A geographic information system (GIS) tool for precision design and performance assessment of filter strips. Journal of Soil and Water Conservation 70:209–217. doi: 10.2489/jswc.70.4.209

Dosskey MG, Qiu Z, Helmers MJ, Eisenhauer DE (2011) Improved indexes for targeting placement of buffers of Hortonian runoff. Journal of Soil and Water Conservation 66:362–372. doi: 10.2489/jswc.66.6.362

Erktan A, Cécillon L, Roose E, et al (2013) Morphological diversity of plant barriers does not increase sediment retention in eroded marly gullies under ecological restoration. Plant and Soil 370:653–669. doi: 10.1007/s11104-013-1738-5

Fischer G, Nachtergaele FO, Prieler S, et al (2012) Global Agro-ecological Zones. IIASA, Laxenburg, Austria and FAO, Rome, Italy

Fornara DA, Tilman D (2008) Plant functional composition influences rates of soil carbon and nitrogen accumulation. Journal of Ecology 96:314–322. doi: 10.1111/j.1365-2745.2007.01345.x

Fox GA, Muñoz-Carpena R, Sabbagh GJ (2010) Influence of flow concentration on parameter importance and prediction uncertainty of pesticide trapping by vegetative filter strips. Journal of Hydrology 384:164–173. doi: 10.1016/j.jhydrol.2010.01.020

Garnier E, Cortez J, Billès G, et al (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology 85:2630–2637. doi: 10.1890/03-0799

Garnier E, Navas M-L, Grigulis K (2016) Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties. Oxford University Press

Ghestem M, Sidle RC, Stokes A (2011) The Influence of Plant Root Systems on Subsurface Flow: Implications for Slope Stability. BioScience 61:869–879. doi: 10.1525/bio.2011.61.11.6

Haaland C, Naisbit RE, Bersier L-F (2011) Sown wildflower strips for insect conservation: a review. Insect Conservation and Diversity 4:60–80. doi: 10.1111/j.1752-4598.2010.00098.x

Hillebrand H, Cardinale BJ (2010) A critique for meta-analyses and the productivity–diversity relationship. Ecology 91:2545–2549. doi: 10.1890/09-0070.1

Hooper DU, Chapin FS, Ewel JJ, et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge.

Ecological Monographs 75:3–35. doi: 10.1890/04-0922

Hou J, Wang H, Fu B, et al (2016) Effects of plant diversity on soil erosion for different vegetation patterns. CATENA 147:632–637. doi: 10.1016/j.catena.2016.08.019

Huang D, Han JG, Wu JY, et al (2010) Grass hedges for the protection of sloping lands from runoff and soil loss: An example from Northern China. Soil and Tillage Research 110:251–256. doi: 10.1016/j.still.2010.08.013

Hussein J, Yu B, Ghadiri H, Rose C (2007) Prediction of surface flow hydrology and sediment retention upslope of a vetiver buffer strip. Journal of Hydrology 338:261–272

Isselin-Nondedeu F, Bédécarrats A (2007) Influence of alpine plants growing on steep slopes on sediment trapping and transport by runoff. Catena 71:330–339. doi: 10.1016/j.catena.2007.02.001

Klumpp K, Soussana J-F (2009) Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect trait approach. Global Change Biology 15:2921–2934. doi: 10.1111/j.1365-2486.2009.01905.x

Lambers JHR, Harpole WS, Tilman D, et al (2004) Mechanisms responsible for the positive diversity-productivity relationship in Minnesota grasslands. Ecology Letters 7:661–668. doi: 10.1111/j.1461-0248.2004.00623.x

Lambrechts T, François S, Lutts S, et al (2014) Impact of plant growth and morphology and of sediment concentration on sediment retention efficiency of vegetative filter strips: Flume experiments and VFSMOD modeling. Journal of Hydrology 511:800–810. doi: 10.1016/j.jhydrol.2014.02.030

Lange M, Eisenhauer N, Sierra CA, et al (2015) Plant diversity increases soil microbial activity and soil carbon storage. Nature Communications 6:. doi: 10.1038/ncomms7707

Lepik M, Liira J, Zobel K (2004) The space-use strategy of plants with different growth forms, in a field experiment with manipulated nutrients and light. Folia Geobotanica 39:113–127

Lin C, Tu S, Huang J, Chen Y (2009) The effect of plant hedgerows on the spatial distribution of soil erosion and soil fertility on sloping farmland in the purple-soil area of China. Soil and Tillage Research 105:307–312. doi: 10.1016/j.still.2009.01.001

Loreau M (2000) Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91:3–17. doi: 10.1034/j.1600-0706.2000.910101.x

Mariotte P, Mehrabi Z, Bezemer TM, et al (2017) Plant–Soil Feedback: Bridging Natural and Agricultural Sciences. Trends in ecology & evolution

Martin C, Pohl M, Alewell C, et al (2010) Interrill erosion at disturbed alpine sites: Effects of plant functional diversity and vegetation cover. Basic and Applied Ecology 11:619–626. doi: 10.1016/j.baae.2010.04.006

Matson PA, Parton WJ, Power AG, Swift MJ (1997) Agricultural Intensification and Ecosystem Properties. Science 277:504–509. doi: 10.1126/science.277.5325.504

Meek B, Loxton D, Sparks T, et al (2002) The effect of arable field margin composition on invertebrate biodiversity. Biological Conservation 106:259–271. doi: 10.1016/S0006-3207(01)00252-X

Mekonnen M, Keesstra SD, Ritsema CJ, et al (2016) Sediment trapping with indigenous grass species showing differences in plant traits in northwest Ethiopia. Catena 147:755–763. doi: 10.1016/j.catena.2016.08.036

Mekonnen M, Keesstra SD, Stroosnijder L, et al (2015) Soil Conservation Through Sediment Trapping: A Review. Land Degrad Develop 26:544–556. doi: 10.1002/ldr.2308

Meyer LD, Dabney SM, Harmon WC (1995) Sediment-trapping effectiveness of stiff-grass hedges. ASAE 38:809–815

Mokany K, Ash J, Roxburgh S (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland: Determinants of ecosystem processes. Journal of Ecology 96:884–893. doi: 10.1111/j.1365-2745.2008.01395.x

Moor H, Hylander K, Norberg J (2015) Predicting climate change effects on wetland ecosystem services using species distribution modeling and plant functional traits. AMBIO 44:113–126. doi: 10.1007/s13280-014-0593-9

Morgan RPC (2004) Vegetative-Based Technologies for Erosion Control. In: Stokes A, Spanos I, Norris JE, Cammeraat E (eds) Eco- and Ground Bio-Engineering: The Use of Vegetation to Improve Slope Stability. Springer, Dordrecht, The Netherlands, pp 265–272

Morgan RPC, Duzant JH (2008) Modified MMF (Morgan–Morgan–Finney) model for evaluating effects of crops and vegetation cover on soil erosion. Earth Surface Processes and Landforms 33:90–106. doi: 10.1002/esp.1530

Mueller KE, Tilman D, Fornara DA, Hobbie SE (2013) Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. Ecology 94:787–793

Muñoz Carpena R, Parsons JE (2014) VFSMOD - Vegetative filter strips modelling system. University of Florida

Munoz-Carpena R, Parsons JE, Gilliam JW (1999) Modeling hydrology and sediment transport in vegetative filter strips. Journal of Hydrology 214:111–129

Ouin A, Burel F (2002) Influence of herbaceous elements on butterfly diversity in hedgerow agricultural landscapes. Agriculture, ecosystems & environment 93:45–53

Podwojewski P, Janeau JL, Grellier S, et al (2011) Influence of grass soil cover on water runoff and soil detachment under rainfall simulation in a sub-humid South African degraded rangeland. Earth Surface Processes and Landforms 36:911–922. doi: 10.1002/esp.2121

Pohl M, Alig D, Körner C, Rixen C (2009) Higher plant diversity enhances soil stability in disturbed alpine ecosystems. Plant and Soil 324:91–102. doi: 10.1007/s11104-009-9906-3

Rey F, Labonne S (2015) Resprout and survival of willow (*Salix*) cuttings on bioengineering structures in actively eroding gullies in marls in a mountainous Mediterranean climate: A large-scale experiment in the Francon catchment (southern Alps, France). Environmental Management 56:971–983. doi: 10.1007/s00267-015-0542-9

Saura S, Torné J (2009) Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. Environmental Modelling & Software 24:135–139. doi: 10.1016/j.envsoft.2008.05.005

Shachak M, Jones CG, Granot Y (1987) Herbivory in Rocks and the Weathering of a Desert. Science 236:1098–1099. doi: 10.1126/science.236.4805.1098

Smith J, Potts S, Eggleton P (2008) The value of sown grass margins for enhancing soil macrofaunal biodiversity in arable systems. Agriculture, Ecosystems & Environment 127:119–125. doi: 10.1016/j.agee.2008.03.008

Spehn EM, Hector A, Joshi J, et al (2005) Ecosystem effects of biodiversity manipulations in European grasslands. Ecological Monographs 75:37–63. doi: 10.1890/03-4101

Stokes A, Douglas GB, Fourcaud T, et al (2014) Ecological mitigation of hillslope instability: ten key issues facing researchers and practitioners. Plant and Soil 377:1–23. doi: 10.1007/s11104-014-2044-6

Temple DM, Robinson KM, Ahring RM, Davis AG (1987) Stability Design of Grass-Lined Open Channels. U.S. Department of Agriculture, Washington, D.C.

Tilman D (1999) The ecological consequences of changes in biodiversity: A search for general principles. Ecology 80:1455–1474. doi: 10.1890/0012-9658(1999)080[1455:TECOCI]2.0.CO;2

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and Ecosystem Functioning.

Annual Review of Ecology, Evolution, and Systematics 45:471–493. doi: 10.1146/annurev-ecolsys-120213-091917

Tilman D, Knops J, Wedin D, et al (1997a) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Tilman D, Lehman CL, Thomson KT (1997b) Plant diversity and ecosystem productivity: theoretical considerations. Proceedings of the national academy of sciences 94:1857–1861

Tomer MD, Dosskey MG, Burkart MR, et al (2008) Methods to prioritize placement of riparian buffers for improved water quality. Agroforest Syst: 10 p

Turnbull L, Wainwright J, Brazier RE (2008) A conceptual framework for understanding semi-arid land degradation: ecohydrological interactions across multiple-space and time scales. Ecohydrol 1:23–34. doi: 10.1002/eco.4

Van Landuyt W, Vanhecke L, Hoste I, Bauwens D (2011) Do the distribution patterns of vascular plant species correspond to biogeographical classifications based on environmental data? A case study from northern Belgium. Landscape and Urban Planning 99:93–103. doi: 10.1016/j.landurbplan.2010.08.020

Vandaele K, Poesen J (1995) Spatial and temporal patterns of soil erosion rates in an agricultural catchment, central Belgium. CATENA 25:213–226. doi: 10.1016/0341-8162(95)00011-G

Vieira DAN, Dabney SM (2012) Two-dimensional flow patterns near contour grass hedges. Hydrological Processes 26:2225–2234. doi: 10.1002/hyp.8262

Weigelt A, Schumacher J, Roscher C, Schmid B (2008) Does biodiversity increase spatial stability in plant community biomass? Ecology Letters 11:338–347. doi: 10.1111/j.1461-0248.2007.01145.x

Woodcock BA, Westbury DB, Potts SG, et al (2005) Establishing field margins to promote beetle conservation in arable farms. Agriculture, Ecosystems & Environment 107:255–266. doi: 10.1016/j.agee.2004.10.029

Xu Z, Li M-H, Zimmermann NE, et al (2018) Plant functional diversity modulates global environmental change effects on grassland productivity. Journal of Ecology 106:1941–1951. doi: 10.1111/1365-2745.12951

Yuan Y, Bingner RL, Locke MA (2009) A Review of effectiveness of vegetative buffers on sediment trapping in agricultural areas. Ecohydrology 2:321–336. doi: 10.1002/eco.82

Zhang L, Wang J, Bai Z, Lv C (2015) Effects of vegetation on runoff and soil erosion on reclaimed land in an opencast coal-mine dump in a loess area. CATENA 128:44–53. doi: 10.1016/j.catena.2015.01.016

Zhu H, Fu B, Wang S, et al (2015) Reducing soil erosion by improving community functional diversity in semi-arid grasslands. Journal of Applied Ecology 52:1063–1072. doi: 10.1111/1365-2664.12442

Zuo X, Wang S, Lv P, et al (2016a) Plant functional diversity enhances associations of soil fungal diversity with vegetation and soil in the restoration of semiarid sandy grassland. Ecology and Evolution 6:318–328. doi: 10.1002/ece3.1875

Zuo X, Zhang J, Lv P, et al (2016b) Plant functional diversity mediates the effects of vegetation and soil properties on community-level plant nitrogen use in the restoration of semiarid sandy grassland. Ecological Indicators 64:272–280. doi: 10.1016/j.ecolind.2016.01.012

APPENDICES

APPENDICES

Appendix A – Candidate species to create herbaceous hedges to control runoff and soil erosion.

+ to ++++ represent the gradient of effectiveness to increase hydraulic roughness from poorly to highly efficient, identified as an estimation based on the traits involved in hydraulic roughness increase and botanical field observations. These gradients represent the effectiveness of the species in monospecific conditions and would change if the species are placed in multi-specific conditions.

Family	Species name	Efficient for discharges	
		Small	High
Adoxaceae	*Sambucus ebulus L.*	+	++
Apiaceae	*Anthriscus sylvestris (L.) Hoffmann*	+	+
	Bupleurum falcatum L.	+	+
	Heracleum sphondylium L.	+	+
Asteraceae	*Achillea ptarmica L.*	+	+
	Artemisia verlotiorum	+	+
	Artemisia vulgaris L.	+	+
	Aster laevis L.	+	+
	Aster salignus Willd.	+	+
	Eupatorium cannabinum L.	+	++
	Hieracium piloselloides Vill.	+	+
	Senecio jacobaea L.	+	+
	Tanacetum corymbosum L.	+	+
	Tanacetum parthenium L.	+	+
	Tanacetum vulgare L.	+	+
Caryophyllaceae	*Saponaria officinalis L.*	+	
Clusiaceae	*Hypericum perforatum L.*	+	+
Cyperaceae	*Carex acutiformis Ehrh.*	++++	++++
	Carex binervis Smith	++	+
	Carex brizoides L.	++	++
	Carex canescens L.	++	++
	Carex otrubae Podp.	++	++
	Carex diandra Schrank	++	+
	Carex distans L.	+	+
	Carex divulsa Stokes	++++	+++
	Carex elongata L.	++++	+++
	Carex flacca Schreb.	++	+
	Carex flava L.	+	+
	Carex paniculata L.	++++	+++
	Carex pendula Huds.	++++	++++
	Carex pilosa Scop.	+	+
	Carex pseudocyperus L.	++++	++++
	Carex remota Jusl. ex L.	++	+
	Carex spicata Huds.	+	+

	Carex strigosa Huds.	++	+
	Carex sylvatica Huds.	+++	++
	Carex vulpina L.	++	+
Lamiaceae	*Calamintha nepeta (L.) Savi*	+	+
	Clinopodium vulgare L.	+	+
	Mentha longifolia L.	+	+
	Mentha spicata L.	+	+
	Mentha suaveolens Ehrh.	+	+
	Origanum vulgare L.	+	+
Linaceae	*Linum perenne L.*	+	
Papaveraceae	*Meconopsis cambrica (L.) Vig.*	+	+
Poaceae	*Agrostis gigantea*	+++	++
	Arrhenatherum elatius L.	+++	++
	Brachypodium pinnatum (L.) Beauv.	+++	+++
	Brachypodium sylvaticum (Huds.) Beauv.	++	+
	Bromus erectus Huds.	+++	++
	Bromus inermis Leyss.	+++	++
	Bromus ramosus Huds.	+	+
	Calamagrostis arundinacea (L.) Roth	++++	++++
	Calamagrostis epigejos (L.) Roth	++++	++++
	Calamagrostis varia (Schrad.) Host	++++	++++
	Calamagrostis villosa (Chaix ex Vill.) J.F. Gmel.	+++	++
	Cynosurus cristatus L.	+++	++
	Dactylis glomerata L.	++++	++++
	Deschampsia cespitosa (L.) Beauv.	++++	++++
	Deschampsia flexuosa (L.) Trin.	++	++
	Festuca arundinacea Schreb.	++++	++++
	Festuca gigantea (L.) Vill.	+++	++
	Festuca heteropachys (St-Yves) Patzke ex Auquier	++	+
	Festuca heterophylla Lam.	++	+
	Festuca longifolia Thuill.	++	+
	Festuca marginata (Hack.) K. Richt.	+	+
	Festuca polesica Zapal.	+	+
	Festuca pratensis Huds.	++++	++++
	Festuca rubra L.	+++	+++
	Koeleria pyramidata (Lam.) Beauv.	++	+
	Melica ciliata L.	+	
	Melica nutans L.	+	
	Melica uniflora Retz.	+	
	Milium effusum L.	+	+
	Phalaris arundinacea L.	+++	+++
Rosaceae	*Filipendula ulmaria (L.) Maxim.*	+	+

Appendix B – List of publications and communications

Articles published in international peer-reviewed journals

Kervroëdan, L., Armand, R., Saunier, M., Ouvry, J.-F., Faucon, M.-P., 2018. Plant functional trait effects on runoff to design herbaceous hedges for soil erosion control. Ecol. Eng. 118, 143–151. https://doi.org/10.1016/j.ecoleng.2018.04.024.

Manuscripts submitted in international peer-reviewed journals

Kervroëdan, L., Armand, R., Saunier, M., Faucon, M.-P.. Functional diversity effects of herbaceous vegetation on runoff to design herbaceous hedges for sediment retention. Ecohydrology.

Kervroëdan, L., Armand, R., Rey, F., Faucon, M.-P.. Plant functional traits effects of herbaceous vegetation on runoff mitigation, sediment retention and soil erosion control in agricultural landscapes under temperate climates. A review. Agronomy for sustainable development.

Manuscripts under finalisation before submission in international peer-reviewed journals

Kervroëdan, L., Armand, R., Saunier, M., Faucon, M.-P.. Non-complementarity effects of plant species diversity on runoff and sediment retention in herbaceous vegetation. Plant and Soil.

Posters in national and international congresses

Kervroëdan, L., Armand, R., Saunier, M., Faucon, M.-P., 2017. Understanding soil erosion processes within herbaceous vegetation using plant functional traits approach in North-West Europe. European Geosciences Union (EGU) General Assembly 2017, 23/04/2017 – 28/04/2017, Vienna, Austria.

Oral communications in national and international congresses

Kervroëdan, L., Armand, R., Saunier, M., Ouvry, J.-F., Faucon, M.-P., 2016. Plant functional traits approach on hydraulic brake and soil erosion in north-western Europe. ECOSUMMIT 2016, 29/08/2016 – 02/09/2016, Montpellier, France.

Kervroëdan, L., Armand, R., Saunier, M., Ouvry, J.-F., Faucon, M.-P., 2017. Effects of aboveground plant functional traits on hydraulic roughness, implication in soil erosion reduction. Journées des Jeunes Chercheurs Condorcet 2017, 19/01/2017 – 20/01/2017, Amiens, France.

Kervroëdan, L., Armand, R., Saunier, M., Faucon, M.-P., 2017. Understanding functional diversity effects of aboveground functional traits on runoff in herbaceous vegetation. British Ecological Society (BES) Annual Meeting 2017, 11/12/2017 – 14/12/2017, Ghent, Belgium.

Kervroëdan, L., Armand, R., Saunier, M., Faucon, M.-P., 2018. Effet de la diversité fonctionnelle des haies herbacées sur l'érosion. Journées d'études des sols (JES) 2018, Rouen, France.

Appendix C – Plant functional trait effects on runoff to design herbaceous hedges for soil erosion control

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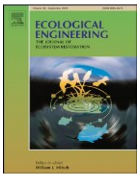

Plant functional trait effects on runoff to design herbaceous hedges for soil erosion control

Léa Kervroëdan[a,b,*], Romain Armand[a], Mathieu Saunier[b], Jean-François Ouvry[b],
Michel-Pierre Faucon[a]

[a] AGHYLE (SFR Condorcet FR CNRS 3417), UniLaSalle, 19 Rue Pierre Waguet, 60026 Beauvais, France
[b] AREAS, 2 avenue Foch, 76460 St Valéry en Caux, France

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ABSTRACT

Vegetation controls concentrated runoff and erosion in the European loess belt by increasing hydraulic roughness and sediment retention. Studies of plant effects on runoff velocity are usually based on a taxonomical characterisation and do not consider the effects of aboveground plant functional traits in attempts to understand soil erosion by water. This trait-based plant study investigates aboveground plant functional trait effects of herbaceous hedges on the hydraulic roughness to understand soil erosion. Eight aboveground morphological traits were measured on fourteen indigenous and perennial plant species (caespitose or comprising dry biomass in winter) from north-west Europe with a high morphological variability. For each trait, density-weighted traits were calculated. The effects of traits and density-weighted traits were examined using a runoff simulator with four discharges. The leaf density and area, as well as density-weighted stem and leaf areas, stem diameter and specific leaf area were positively correlated with the hydraulic roughness. Generalised linear models defined the best combinations of traits and density-weighted traits: (1) leaf density and leaf area, (2) density-weighted leaf area and density-weighted projected stem area, and (3) density-weighted leaf area and density-weighted stem diameter. Moreover, the effects of leaf density, leaf area and density-weighted specific leaf area, varied depending on the discharge. This study is one of the first characterisation of aboveground trait effects on hydraulic roughness and highlights that vegetation with large stem density, diameter and leaf area plays a significant role in minimising soil erosion. The selection of plant species can derive from these plant trait effects to design reconstructed herbaceous hedges to minimise soil erosion.

1. Introduction

Soil erosion by water is influenced by precipitation, soil texture and structure, slopes that can generate intense discharges, and plant and litter covers which vary according to cultural practices in cultivated areas. Intense runoff and soil erosion are frequently found in north-western European catchments where the sloping loamy soils are intensively tilled and cultivated with annual crops (Boardman and Poesen, 2006; Gobin et al., 2003). In the European loess belt, erosion can be mitigated by both (1) tillage reduction and the establishment of cover crops during sensitive seasons which increase the crop residue quantity on soil surface and thus, reduce the rill and inter-rill soil erosion (Knapen et al., 2007), and (2) establishment of vegetative barriers across the thalweg to mitigate rill and ephemeral gully erosion (Richet et al., 2017). Richet et al. (2017) demonstrated the effects of fascines (i.e. vegetative barriers made of bundles of stems) on hydraulic roughness and soil erosion mitigation however, their short lifetime and high cost represent a main limitation. Herbaceous hedges, defined as narrow strips of dense and stiff perennial vegetation, constitute a major interest to develop vegetative barriers with a high efficiency on the reduction of soil erosion at lower cost against concentrated flows (Dabney et al., 1995; Yuan et al., 2009). Besides, herbaceous hedges composed of indigenous plant species could offer other ecosystem services than regulating services such as the provision of habitats and their ecological connectivity in these catchments (Ouin and Burel, 2002; Smith et al., 2008).

The effects of herbaceous vegetation on runoff and soil erosion have been studied over the past decades (Haan et al., 1994; Lambrechts et al., 2014; Ludwig et al., 2005; Temple et al., 1987). Blanco-Canqui et al. (2006), Dosskey et al. (2010), Lambrechts et al. (2014), Le Bissonnais et al. (2005), Ruiz-Colmenero et al. (2013) and Stokes et al. (2014) noted the direct effects of vegetation cover on splash

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[*] Corresponding author at: UniLaSalle, 19 Rue Pierre Waguet, 60026 Beauvais, France.
E-mail address: lea.kervroedan@unilasalle.fr (L. Kervroëdan).

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detachment and inter-rill erosion reduction. The impact of plant roots on infiltration capacity and resistance of soils to erosion by water has been well documented (Berendse et al., 2015; Dabney et al., 2009; De Baets et al., 2006; De Baets and Poesen, 2010; Gyssels et al., 2005; Isselin-Nondedeu and Bédécarrats, 2007; Lambrechts et al., 2014). The influence of vegetation on sediment retention was highlighted (Burylo et al., 2012; Dabney et al., 2009; Dillaha et al., 1989; Haan et al., 1994; Isselin-Nondedeu and Bédécarrats, 2007; Lowrance et al., 1995). The relationship between vegetation and sediment retention can be understood only if the vegetation effects on hydraulic roughness, which is the frictional resistance due to the contact of runoff with the vegetation, are characterised, as it is the main process with gravity furthering sediment retention. This effect has been previously investigated (Akram et al., 2014; Cantalice et al., 2015; Cao et al., 2015; Haan et al., 1994; Järvelä, 2002; Temple et al., 1987). The presence of herbaceous vegetation has positive impacts on hydraulic roughness, as it reduces flow velocity and increases backwater depth (Akram et al., 2014; Cantalice et al., 2015; Hussein et al., 2007), thereby increasing sediment retention due to its linear relationship with backwater depth (Dabney et al., 1995; Hussein et al., 2007; Meyer et al., 1995). Plant effects on hydraulic roughness are highly variable among species and are difficult to explain without characterisation of all aboveground morphological traits (Cantalice et al., 2015; Cao et al., 2015; Dabney et al., 1995). The relationship between aboveground plant morphology and hydraulic roughness should be specified to globally understand runoff and soil erosion processes.

One of the challenges to improving the understanding in plant and vegetation (e.g. herbaceous hedges) effects on hydraulic roughness and soil erosion is the development of a functional trait-based approach (Faucon et al., 2017). This approach, which allows for characterising trait effects on ecosystem processes and services (Lavorel and Garnier, 2002), has been developed with the establishment of the relationship between the soil detachment ratio and root length density for underground biomass (De Baets and Poesen, 2010; Mekonnen et al., 2016; Vannoppen et al., 2015). Concerning aboveground characteristics, trait-based approaches highlighted the relationships between stem density, diameter and stiffness, and between leaf area and density with sediment retention (Bochet et al., 2000; Burylo et al., 2012; Mekonnen et al., 2016; Zhu et al., 2015). Because the hydraulic roughness is one of the main process influencing sediment retention, plant functional traits known to influence sediment retention could influence the hydraulic roughness. Those traits, such as the stem and tiller density (Hayes et al., 1978; Isselin-Nondedeu and Bédécarrats, 2007; Morgan and Duzant, 2008; Temple, 1982), stem diameter (Bochet et al., 2000; Meyer et al., 1995; Morgan and Duzant, 2008), stem stiffness (Dabney et al., 2009; Meyer et al., 1995), specific leaf area (Graff et al., 2005), leaf area (Burylo et al., 2012) and leaf density (Lambrechts et al., 2014), should be considered to specifically characterise the effect of aboveground traits on hydraulic roughness. In addition to characterising vegetation effects on hydrological processes and, notably, hydraulic roughness, the weight of traits in the vegetation should be considered (Garnier and Navas, 2012) to improve the overall understanding of soil erosion.

Plant functional trait effects on hydraulic roughness should vary according to water discharge and different hydraulic processes (Cao et al., 2015). Vieira and Dabney (2012) showed that flow resistance of vegetation changed with flow depth. Temple et al. (1987) and Van Dijk et al. (1996) found that for low flows, the mean flow velocity was dependent on the vegetation density. However, for higher flows, when the flow depth was higher than the deflecting vegetation height, the leaf structures had less impact and the flow resistance was primarily dependent on the stem density and length and on the stem diameter and stiffness (Meyer et al., 1995; Temple et al., 1987).

It is thus expected that high discharges would challenge the mechanical resistance through the stiffness, the density and the diameter of the stems, while low discharges would be impacted by the overall vegetation density. The challenge is to highlight plant functional trait effects on hydraulic roughness at several discharges that are representative of those present in catchments of north-west Europe.

This study of trait-based plant ecohydrology examined the relationship between aboveground plant traits with the hydraulic roughness at different discharges in fourteen perennial plant species presenting contrasting aboveground morphological traits. The objectives are (1) to highlight the major morphological traits influencing hydraulic roughness and (2) to examine the effect of discharges on the relationship between plant morphological traits and hydraulic roughness to improve the understanding of soil erosion and select candidate species to create reconstructed herbaceous ecosystems to mitigate soil erosion in north-west Europe.

2. Materials and methods

2.1. Plant materials

Fourteen plant species that display contrasting aboveground morphological traits were chosen from 76 candidate species, resulting in six filters of selected functional types involved in the mitigation of soil erosion in north-west Europe applied to the 3500 spermatophyte species from north-west Europe (Lambinon et al., 2012). These selective filters were as follows: (1) Raunkiaer's life-form categories of "herbaceous chamaephytes", "hemicryptophytes" and "geophytes", i.e., perennial herbaceous vegetation that provide an effective soil cover during all seasons; (2) the presence of fresh (i.e., herbaceous chamaephytes and caespitose hemicryptophytes) or dry (i.e., non-caespitose hemicryptophytes and geophytes) biomass in winter when soil erosion is observed in north-west Europe (Boardman and Poesen, 2006); (3) the presence of rhizomes or stolon to ensure lateral spreading capacity and burying tolerance due to sediment deposition; (4) vegetative height ≥ 20 cm, as it is the water maximal level in the catchment in north-west Europe; (5) a broad ecological niche to select species able to grow in several silty agricultural soils; and (6) non-weed species to prohibit their expansion in agricultural territories of north-west Europe.

Thirteen of the tested species were from the list of candidates (*Carex sylvatica*, *Carex flacca*, *Carex acutiformis*, *Carex pendula*, *Artemisia vulgaris*, *Origanum vulgare*, *Lolium perene*, *Senecio jacobaea*, *Tanacetum vulgare*, *Festuca arundinacea*, *Dactylis glomerata*, *Melica nutans*, *Phalaris arundinacea*) (Table 1). An exotic species, *Miscanthus sinensis*, was also tested along the thirteen indigenous species as it is considered a model plant in studies of plant hydraulic properties and erosion mitigation (Dabney et al., 2009). These species, varying in leaf and stem traits (e.g., density, area and specific area – density, diameter, specific density and dry matter content), were chosen to establish a range of traits to highlight the effect of aboveground plant traits on hydraulic roughness. The species were collected *in natura*, selecting only established individuals, and planted in 60 × 30 × 15 cm plots in early April 2016, creating 14 monospecific herbaceous hedges. These vegetation plots consisted of a wooden frame with a 1.5 cm grid fence at the bottom and were buried for three months prior the experiments to allow the full development of the plants and roots. The plot design allowed for both plant growth and plot extraction for the experiments in the runoff simulator.

2.2. Plant morphological trait measurements

Eight aboveground plant morphological traits (leaf – area, density and specific area; stem – density, diameter, specific density, area and dry matter content), potentially involved in increasing hydraulic roughness, were measured (Table 2) at three levels along the stem – between 0 and 5 cm, 0 and 10 cm, and 0 and 20 cm – related to the variation of the water flow depth. Sampling collection and process methods followed recognised sampling guidelines (Pérez-Harguindeguy et al., 2013). The leaves and stems were wrapped in moist paper and sealed in bags to limit water loss until the measures were complete, and

Table 1
List of the species used for the study and basic information.

Category	Species name	Family	Life form	Vegetative height (m)
Graminoid	*Dactylis glomerata L.*	Poaceae	Hemicryptophyte	0.96 (± 0.11)
	Festuca arundinacea Schreb.	Poaceae	Hemicryptophyte	0.54 (± 0.14)
	Lolium perenne L.	Poaceae	Hemicryptophyte	0.34 (± 0.02)
	Melica nutans L.	Poaceae	Hemicryptophyte	0.28 (± 0.02)
	Miscanthus sinensis	Poaceae	Hemicryptophyte; Geophyte	1.03 (± 0.26)
	Phalaris arundinacea L.	Poaceae	Hemicryptophyte	0.49 (± 0.11)
Herb	*Artemisia vulgaris L.*	Asteraceae	Hemicryptophyte	0.96 (± 0.17)
	Origanum vulgare L.	Lamiaceae	Chamaephyte; Hemicryptophyte	0.48 (± 0.06)
	Senecio jacobaea L.	Asteraceae	Hemicryptophyte	0.98 (± 0.04)
	Tanacetum vulgare L.	Asteraceae	Hemicryptophyte	0.64 (± 0.07)
Sedge	*Carex acutiformis Ehrh.*	Cyperaceae	Hemicryptophyte	0.17 (± 0.03)
	Carex flacca Schreb.	Cyperaceae	Hemicryptophyte	0.31 (± 0.04)
	Carex pendula Huds.	Cyperaceae	Caespitose hemicryptophyte	0.23 (± 0.15)
	Carex sylvatica Huds.	Cyperaceae	Caespitose hemicryptophyte	0.12 (± 0.03)

The stem height values represent the mean values (± standard deviation) measured on the experimental plots.

Table 2
List of the measured traits, their abbreviations and formulas used.

Morphological trait	Abbreviation	Unit	Formula[a]	Abbreviation after density-weighting
Stem density	SD	stems.dm^{-2}	–	–
Leaf density	LD	leaves.dm^{-2}	–	–
Leaf area	LA	mm^2	–	WLA
Specific leaf area	SLA	mm^2.mg^{-1}	$SLA = LA\ (Leaf\ mass_{dry})^{-1}$	WSLA
Stem diameter	SDm	mm	–	WSDm
Specific stem density	SSD	mg.mm^{-3}	$SSD = Mass_{oven\ dry}\ (Stem\ volume)^{-1}$	WSSD
Stem dry matter content	SDMC	–	$SDMC = Mass_{oven\ dry}\ (Mass_{fresh})^{-1}$	WSDMC
Projected stem area	SA	mm^2	$SA = L\ SDm$	WSA

[a] Volume formulas used were (1) for cylindrical stems: $V = \pi L [(SDm)\ (0.5)]^2$ and (2) for triangular stems (*Carex* sp.): $V = [\sqrt{(3)/4}]\ SDm^2\ L$ with L = height of the stem portion on which the concerned trait is measured.

they were then dried at 70 °C for 72 h.

Trait measurements were performed within two 10 × 10 cm quadrats in each plot, to ensure representative sampling. Stem density was measured within each quadrat, defining pseudoculms in sedge species (Cyperaceae) and tillers in grass species as stems. Fresh and dry leaves were counted to determine the leaf density at each level along the stems in the quadrats. Specific leaf area (SLA) and leaf area were calculated from three mature leaves per quadrat. The leaves were scanned while fresh using a 600 dpi resolution, and the images were then analysed using the software Gimp 2.8 to determine the leaf area. The SLA was calculated by dividing the leaf area by the oven-dry mass of the leaf. Stem diameter, stem specific density and stem dry matter content were measured on three stems per quadrat. Stem diameter (mm) was measured three times along each vertical level of the fresh stem using a calliper. From the measurements of stem diameter, the projected stem area was calculated using the rectangle area formula and represented the contact area of a stem toward the flow direction. The stem specific density (mg.mm^{-3}) was calculated by dividing the oven-dry mass of the first 20 cm of the stem by the volume of the stem, measured when still fresh. The volume of the stems was calculated using the formula for the volume of a cylinder, except for the sledge species, which have triangular stems, and for which we used the formula for the volume of a triangular prism. The stem specific density of each height level along the stem was estimated using the volume of each level by assuming the density was homogeneous within the stem section. The stem specific density, representing the structural strength of a stem, was used as the estimation of the plant resistance to the water flow (Burylo et al., 2012; Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). The stem dry matter content was calculated from the ratio of the oven dry-mass of the first 20 cm of the stem and the fresh mass of the stem. The mean values of the measured traits are listed in Appendices A1, A2 and A3.

To characterise the effect of the herbaceous hedge on hydraulic roughness, the density-weighted mean of the trait values was calculated for each trait as the mean value of the trait multiplied by the proportion of the trait, here by the stem density for stem traits and by leaf density for leaf traits. This method does not include plant cover, given that all monospecific vegetation plot presented 100% cover and more precisely characterise the abundance of traits from stem and leaf densities. These density-weighted traits were determined for each vertical level along the stem (i.e. 0–5 cm, 0–10 cm and 0–20 cm).

2.3. Hydraulic measurements

We used the same runoff simulator as Richet et al. (2017) to quantify the effect of plant morphological traits on hydraulic roughness (Fig. 1). The simulator allowed the recreation of a flow at chosen discharges and the measurement of hydrological parameters resulting from the presence of plants. The upper and lower parts of the simulator are equipped with flowmeters made of Venturi channels with a flow range of 0.06 L.s^{-1}–6 L.s^{-1}, comprising ultrasound probes that measure the water level in the channel at ± 1.26 mm. This system was manufactured by ISMA, France (Richet et al., 2017). The water was circulating within the system, with the aid of two pumps and a reservoir, in a closed circuit. The central part of the simulator is a channel setup with two galvanised iron sheets. The channel was 60 cm wide and 5.40 m long along a 5% slope. The entire channel was waterproofed using a plastic tarpaulin to avoid any water loss during the experiments. The tarpaulin was placed in order to obtain a smooth channel bottom and limit bottom roughness as much as possible. The roughness of the tarpaulin was determined by experiment using a control plot without any plants and represented a small percentage of the roughness created by the plants (Appendix B). The vegetation was placed 4 m away from the head of the channel, in a 17 cm deep rectangular hole to level the ground with the flow and the slope. The tarpaulin used in the upper

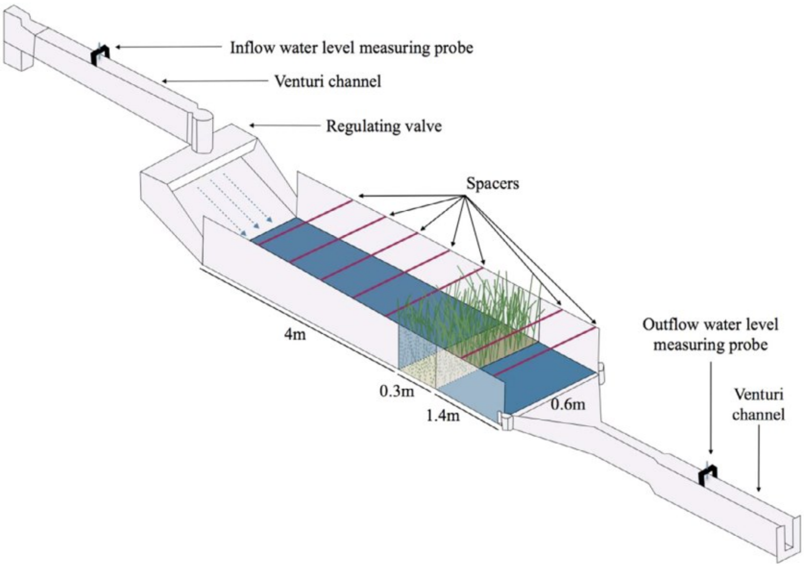

Fig. 1. Runoff simulator used during the study.

part of the channel was placed continually underneath the plot and through the lower part of the channel to avoid water loss by infiltration. The boundary effects were minimal as the plants were left in the wooden frame where they grew, and a wooden plank was placed along each side the entire channel. The small gap areas along the base of the planks and the bottom of the channel were sealed using clay. Along the channel, 7 spacers were set up to measure the topography of the channel bed and the water heights in the backwater and downstream of the plot. Five were located upstream of the plants and two were located downstream. Approximately 1.46 m from the channel head, the spacers were spaced at 0.75 m.

The four discharges used in this study were 2, 4, 8 and 11 L.s^{-1}.m^{-1} at ± 7%. The tested discharges are observed approximately every 0.5, 1, 2 and 5 years, respectively, in 5 ha catchments in the European loess belt with a 5 m-wide thalweg, as precised by Richet et al. (2017). Both upstream and downstream discharges were continuously monitored. Water level were measured when the upstream and downstream discharges were equivalent. No infiltration occurred as the soil in the plots was saturated in water. The backwater and downstream flow levels were measured using the spacers as elevation-known baselines. The levels were determined by measuring the distance between the top of the water flow and the spacer every 10 cm from the edges of the channel, corresponding to seven vertical profiles.

To express the hydraulic resistance related to the plant presence, we used the unit stream power (*USP*), a sediment transport capacity index (Govers, 1992; Yang, 1972). USP is defined as the "energy dissipation per unit of time and per unit of weight of the flow" (Govers, 1992), depending on its velocity and the slope:

$$USP = VS \tag{1}$$

where *USP* is expressed in m.s^{-1}, V is the mean velocity (m.s^{-1}), and S is the channel slope (m.m^{-1}) (Cao et al., 2015; Hessel et al., 2016; Morgan et al., 1998). The lower the *USP* is, the greater the hydraulic roughness will be. The mean velocity was calculated using the water levels measured at the closest spacer upstream of the plot. Govers (1990) determined a *USP* critical value of 0.004 m.s^{-1} that indicates that the threshold from which soil is most likely to erode in the loamy soils found in the European loess belt. Govers (1990) established this critical value for bare loess soils with a D_{50} from 58 µm to 218 µm, at slopes ranging from 1° to 8° and for discharges varying from 0.2 to 10 L.s^{-1}.m^{-1}. The *USP*, Manning coefficients and backwater depths are presented in Appendix B.

2.4. Data analysis

Principal component analysis (PCA) was conducted to examine the link between each trait. Data used for the PCA included the measured traits in the two quadrats within the plots. Generalised linear models (GLM) for the inverse-link gamma family were then processed to examine the effect of plant morphological traits on the *USP* at each discharge.

Another analysis using GLMs were then used to analyse the relationship between the *USP* and the significant traits and density-weighted traits identified in the previous step between 0 and 10 cm. These models were run separately for each discharge to highlight differences of trait effects among the discharge levels. To avoid autocorrelation within the models, traits and density-weighted traits were processed in separate models. Due to the small sample size n and ratio $n/K < 40$ (where K the number of parameters used in the models), second order Akaike's Information Criterion (AICc) and ΔAICc were used to assess the model performance, as recommended in Burnham and Anderson (2002). ΔAICc is the difference between the AICc of a model i and the model with the lowest AICc (also characterised as the best model fit). Burnham and Anderson (2002) recognise the models with a ΔAICc $<$ 2 as models with substantial support, which are identified as the best model fits in this study. Models with ΔAICc varying between 2 and 7, indicating less support, were also analysed as recommended by Burnham et al. (2011). Akaike weights (wAICc) were used in this study to assess the relative likelihood of the models, as this indicates the probability of a model i being the best among the set of tested models (Brown et al., 2011; Burnham and Anderson, 2002).

All the data in this study were analysed using the statistical software R (version 3.3.2).

3. Results

3.1. Variations of plant morphological traits

Covariation among the eight traits of the 14 species studied were analysed using a PCA (Fig. 2), which showed that the first two principal

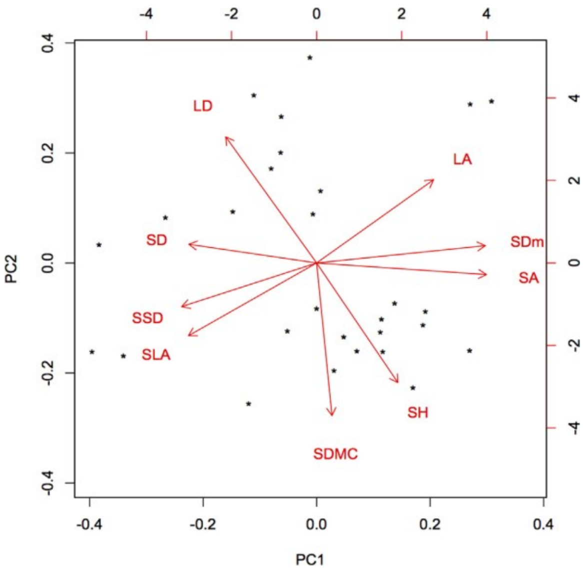

Fig. 2. Principal component analysis of nine morphological traits measured on 14 plant species. PC1 explained 47% of the variance and PC2 explained 24.9%. LA = leaf area, LD = leaf density, SA = projected stem area, SD = stem density, SDm = stem diameter, SDMC = stem dry matter content, SLA = specific leaf area, SSD = stem specific density. The vegetative stem height (SH) was added to the other traits for this analysis.

components explained 71.9% of the variance. The first principal component (PC1) accounted for 47% of the total variance and was associated with the projected stem area, the stem diameter and the stem density. The variance of PC1 was explained by the leaf area, the stem specific density and the specific leaf area. Two groups of variables were observed along the PC1 axis: the projected stem area and the stem diameter on the positive end and the stem density on the negative end. The second principal component (PC2) accounted for 24.9% of the total variance and was explained by the stem dry matter content, which was found on the negative end of the axis. The variance of PC2 was explained by the leaf density and the stem height.

3.2. *Effect of morphological traits on the unit stream power*

The effects of traits on hydraulic roughness were analysed using GLMs to show the traits affecting the *USP* at each discharge (Table 3). The leaf densities (0–5 cm and 0–10 cm) were correlated to the *USP* for the four discharge levels. The leaf area had a significant relationship with the *USP* at discharges Q1 and Q2, while the leaf density (0–20 cm) was significant with the *USP* at discharges Q3 and Q4. The weighted leaf area (0–5 cm, 0–10 cm and 0–20 cm), the weighted projected stem area (0–5 cm, 0–10 cm and 0–20 cm), the weighted stem diameter (0–5 cm, 0–10 cm and 0–20 cm) and the weighted SLA (0–5 cm) were correlated to the *USP* at discharges Q1, Q2, Q3 and Q4. The weighted SLA (0–10 cm) influenced the *USP* at discharges Q2, Q3 and Q4.

From the results in Table 3, GLMs were used to highlight traits and density-weighted traits (0–10 cm) that have a greater impact on the *USP* within the traits previously identified as significantly impacting the *USP* (Fig. 3, Tables 4 and 5). The GLMs for single traits (Table 4) highlighted that the combination of leaf area and leaf density was the best model fit for all discharges (wAICc > 0.50), although the leaf density was also a good fit for the data at discharges Q3 and Q4 (wAICc = 0.39 and wAICc = 0.34, respectively). The results of the density-weighted trait GLMs (Table 5) showed that models USP ~ WLA + WSA and USP ~ WLA + WSDm were the best fit for all discharges, with cumulative wAICc ranging from 0.75 at discharge Q1 to 0.84 at Q4, showing a growing significance along with the discharge gradient. However, the ranking of importance changed with the discharges, as USP ~ WLA + WSA was greater for discharges Q1 and Q4, USP ~ WLA + WSDm was greater for Q3 and both combinations were equivalent for Q2.

4. Discussion

Contrary to processes of soil detachment by water flow (De Baets and Poesen, 2010; Vannoppen et al., 2015) and sediment retention (Burylo et al., 2012), the effect of morphological plant traits on hydraulic roughness corresponds to a lack of research to understand the role of plant and vegetation on soil erosion. This study examined the effects of plant morphological traits on hydraulic roughness for four discharges.

4.1. *Effect of morphological traits and density-weighted traits on hydraulic roughness*

Stem and leaf traits influenced hydraulic roughness, given that they constitute a hydraulic brake on water flows. However, some stem and leaf traits may have a greater effect on hydraulic roughness. This study has highlighted that, among the considered aboveground traits involved in soil erosion (i.e., leaf area, SLA, leaf density, stem density, stem diameter, stem specific density, projected stem area and stem dry matter content), only the leaf area and the leaf density presented a significant effect on hydraulic roughness. The leaf traits have a better impact on hydraulic roughness than stem traits, regarding non-weighted traits. The GLMs showed that the combination of leaf density and leaf area better explained the effect on hydraulic roughness than these traits alone for any discharge used. Plant individuals with better trade-off between leaf density and leaf area, meaning high leaf density and long leaves, such as some graminoid species, would have a great impact on mitigating the unit stream power and thus increase hydraulic roughness. These results are in agreement with other studies highlighting the efficiency of several graminoid species in soil erosion mitigation (Isselin-Nondedeu and Bédécarrats, 2007; Morgan, 2004). The absence of the stem density effect on hydraulic roughness is not in agreement with the literature where the stem density is considered a main trait impacting flow velocity and soil erosion (Isselin-Nondedeu and Bédécarrats, 2007; Mekonnen et al., 2016; Meyer et al., 1995; Morgan and Duzant, 2008; Temple et al., 1987). This contradiction could be explained by the lack of a standard characterisation of all stem and leaf traits involved in hydraulic roughness and soil erosion (e.g. defining the tillers and pseudoculms as stems when characterising the stem density). The stem density is one of the main traits included in hydraulic and soil erosion models such as VFSMOD (Muñoz Carpena and Parsons, 2014) and in studies focusing on the relationship between vegetation and hydraulic roughness or sediment retention (Morgan, 2004; Temple, 1982; Van Dijk et al., 1996; Xiao et al., 2011), which could be improved by considering the effect of other stem traits (e.g., stem diameter). In the trait-based approach, the importance of stem density in the plant-hydraulic roughness relationship lays in its use in the calculation of weighted stem trait values in the vegetation. Indeed, this approach highlighted that mainly density-weighted traits influenced hydraulic roughness. Specifically, all the GLMs included weighted leaf area, indicating its great importance in the increase of hydraulic roughness. Projected stem area or stem diameter showed no significance on the hydraulic roughness at the trait level but, by considering weighted stem traits, weighted projected stem area and weighted stem diameter showed highly significant effects on the unit stream power. The GLMs showed that the best fit model was WSA + WLA (weighted projected stem area + weighted leaf area) as these traits represent the interception area of the leaves and stems with the water flow in the vegetation, i.e., a hydraulic brake. As the stem diameter, projected stem area and leaf area were negatively associated

Table 3
Morphological trait effects on USP for each discharge used. Generalised linear models (GLM) of each trait and density-weighted trait at each stem level in relation to the *USP* for each discharge. LA = leaf area, LD = leaf density, SA = projected stem area, SD = stem density, SDm = stem diameter, SDMC = stem dry matter content, SLA = specific leaf area, SSD = stem specific density. The density-weighted traits were named by adding "W" at the beginning of their existing abbreviations.

Traits	Level along the stem	$Q1 = 2\ L.s^{-1}.m^{-1}$		$Q2 = 4\ L.s^{-1}.m^{-1}$		$Q3 = 8\ L.s^{-1}.m^{-1}$		$Q4 = 11\ L.s^{-1}.m^{-1}$	
		AIC	β	AIC	β	AIC	β	AIC	β
LA		−158.15	**0.04***	−147.27	**0.03***	−131.38	0.02 ns	−125.83	0.02 ns
LD	0–5 cm	−159.11	**1.33***	−150.06	**1.07****	−135.45	**0.78****	−131.14	**0.76****
	0–10 cm	−157.68	**0.81***	−148.34	**0.65***	−134.21	**0.49***	−129.23	**0.46****
	0–20 cm	−154.49	0.44 ns	−145.21	0.37 ns	−131.54	**0.29***	−126.12	**0.27***
SA	0–5 cm	−152.71	0.46 ns	−141.33	0.22 ns	−126.83	0.11 ns	−120.93	0.1 ns
	0–10 cm	−152.55	0.22 ns	−141.25	0.11 ns	−126.78	0.05 ns	−120.87	0.05 ns
	0–20 cm	−151.70	0.08 ns	−140.75	0.02 ns	−126.51	0.0048 ns	−120.58	0.0037 ns
SD		−151.71	0.73 ns	−142.22	0.84 ns	−128.89	0.77 ns	−122.19	0.57 ns
SDC		−153.37	−707.3 ns	−143.40	−571.4 ns	−130.15	−475.66 ns	−124.26	−429.54 ns
SDm	0–5 cm	−152.70	22.9 ns	−141.33	11.02 ns	−126.83	5.54 ns	−120.93	5.18 ns
	0–10 cm	−152.58	22.47 ns	−141.27	10.76 ns	−126.79	5.32 ns	−120.89	4.96 ns
	0–20 cm	−152.41	21.78 ns	−141.15	9.93 ns	−126.72	4.72 ns	−120.80	4.33 ns
SLA		−154.96	−7.87 ns	−142.59	−4.47 ns	−127.46	−2.39 ns	−121.92	−2.46 ns
SSD	0–5 cm	−153.46	−128.71 ns	−142.06	−75.4 ns	−127.63	−49.26 ns	−121.86	−46.93 ns
	0–10 cm	−153.64	−277 ns	−141.95	−151.2 ns	−127.38	−91.26 ns	−121.75	−93.63 ns
	0–20 cm	−153.33	−569.8 ns	−141.35	−251.1 ns	−126.88	−134.38 ns	−121.05	−134.77 ns
WLA	0–5 cm	−163.29	**0.0004****	−154.63	**0.0003****	−138.44	**0.0002****	−136.08	**0.0002****
	0–10 cm	−163.26	**0.0003****	−153.79	**0.0002****	−137.69	**0.0001****	−135.63	**0.0001****
	0–20 cm	−163.44	**0.0002****	−153.65	**0.0001****	−137.78	**0.0001****	−136.37	**0.0001****
WSA	0–5 cm	−161.43	**0.02****	−154.14	**0.02****	−141.02	**0.02****	−133.45	**0.01****
	0–10 cm	−160.97	**0.01****	−153.49	**0.01****	−140.30	**0.0081****	−132.81	**0.0071****
	0–20 cm	−158.44	**0.0055***	−149.75	**0.0046***	−136.37	**0.0036****	−129.07	**0.0031***
WSDMC		−151.38	1.72 ns	−141.76	2.31 ns	−128.25	2.14 ns	−121.66	1.51 ns
WSDm	0–5 cm	−161.43	**1.25****	−154.14	**1.05****	−141.02	**0.82****	−133.45	**0.71****
	0–10 cm	−161.06	**1.24****	−153.64	**1.05****	−140.46	**0.82****	−132.96	**0.71****
	0–20 cm	−160.46	**1.21***	−152.56	**1.01****	−139.27	**0.79****	−131.86	**0.68****
WSLA	0–5 cm	−157.33	**0.06***	−148.47	**0.05***	−134.37	**0.04***	−129.65	**0.04****
	0–10 cm	−154.34	0.03 ns	−145.19	**0.03***	−131.64	**0.02***	−125.92	**0.02***
	0–20 cm	−151.38	0.0058 ns	−141.71	0.0076 ns	−128.17	0.007 ns	−122.10	0.0061 ns
WSSD	0–5 cm	−151.10	0.12 ns	−141.05	0.22 ns	−127.32	0.23 ns	−121.02	0.15 ns
	0–10 cm	−151.07	0.19 ns	−141.03	0.41 ns	−127.32	0.45 ns	−120.99	0.28 ns
	0–20 cm	−151.04	0.23 ns	−141.00	0.8 ns	−127.33	0.91 ns	−121.00	0.58 ns

N = 14; AIC = Aikake's Information Criterion; β = regression coefficient; *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant. The significant correlations are indicated in bold.

with the stem density, trade-offs among these stem and leaf traits can be considered to improve herbaceous hedge effects on hydraulic roughness. The effect of weighted SLA, when associated with weighted leaf area and weighted stem diameter or weighted leaf area and weighted projected stem area, was also observed ($3 < \Delta AICc < 5$). Overall, vegetation presenting the best trade-off between stem density and weighted stem diameter, as well as between leaf density and leaf area, will have a greater efficiency to increase hydraulic roughness. Herbaceous hedges that present these weighted leaf and stem traits would be partly composed of graminoid species, given that these present large leaf density, leaf area, stem diameter and a greater hydraulic roughness than non-graminoid species (Isselin-Nondedeu and Bédécarrats, 2007). Stem and leaf densities should be considered to calculate weighted-traits in herbaceous hedges and quantify the effects on soil erosion. Characterisation of trait weights in herbaceous hedges vegetation allowed to highlight the main morphological aboveground traits and their combinations involved in hydraulic roughness, as well as the importance of stem density as a plant marker to examine the effect of vegetation on runoff. As a result, this trait-based approach can be effectively applied at the vegetation level to understand and model runoff and soil erosion.

4.2. Effects of morphological traits on hydraulic roughness depending on runoff processes

Flow rate variations can trigger different soil-plant-water processes (Dabney et al., 2004; Temple et al., 1987; Vieira and Dabney, 2012). The results here are consistent with the hypothesis that the influence of aboveground traits on hydraulic roughness can change with the discharge. The effect of leaf density (0–20 cm) and leaf area on hydraulic roughness varied with the discharge. The results showed the importance of leaf density in increasing hydraulic roughness at higher discharges ($\Delta AIC < 2$). However, for lower discharges, a combination of leaf area and leaf density should be considered rather than the traits alone. The results for the leaf area are in accordance with the one found by Temple et al. (1987) showing a decreasing impact of the leaf structure with an increasing discharge. At a small discharge ($2\ L.s^{-1}.m^{-1}$), weighted SLA (0–10 cm) did not present an effect on the hydraulic roughness, but a positive influence was observed at $4\ L.s^{-1}.m^{-1}$. Differences in the influence of leaf density and weighted SLA among the discharges may be interpreted as the water depth being too low to enter into contact with all the leaves between 0 and 20 cm of each individual and with large SLA until 5 cm of the vegetation at small discharges. Herbaceous hedges, playing a key role in hydraulic roughness, present the best trade-off between stem density and diameter, as well as leaf density and area at low discharges, and with increasing water discharge, larger basal leaf density and basal SLA. This study indicates that some trait and density-weighted trait effects on hydraulic roughness are linked to the flow water level. The characterisation of these effects according to flow depth constitutes an advance to model water flows and soil erosion in ecosystems and landscapes.

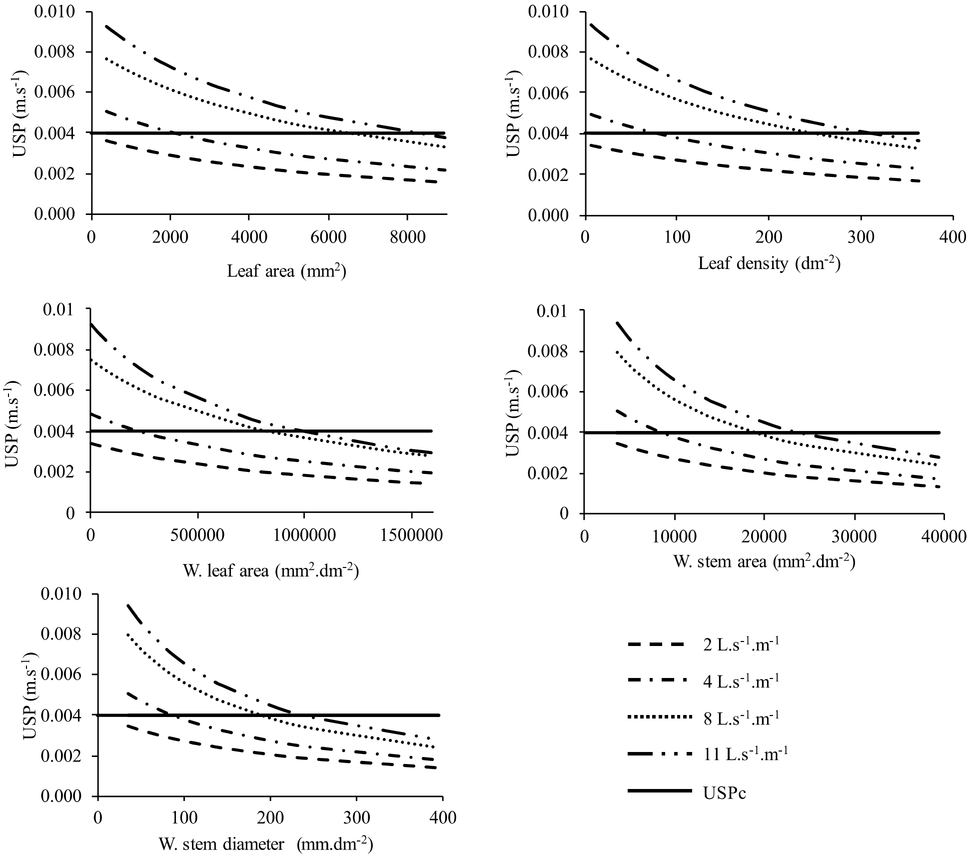

Fig. 3. Relationship between *USP* and traits and density-weighted traits identified as the best fit to hydraulic roughness at 0–10 cm. USPc represents the threshold of 0.004 m.s^{-1} from which soil is likely to erode in loamy soils found in the European loess belt (Govers, 1990).

Table 4
Selected GLMs fitted to *USP* and two traits as estimation variables for each discharge used. The models are sorted from the smallest ΔAICc to the highest ΔAICc at each discharge used.

Discharge	Models	AICc	ΔAICc	wAICc
Q1 = 2 L.s^{-1}.m^{-1}	USP ~ LA + LD	−158.68	0.0	0.707
	USP ~ LA	−155.75	2.9	0.164
	USP ~ LD	−155.28	3.4	0.129
	USP ~ LA + LD	−148.93	0.0	0.737
Q2 = 4 L.s^{-1}.m^{-1}	USP ~ LD	−145.94	3.0	0.166
	USP ~ LA	−144.87	4.1	0.097
	USP ~ LA + LD	−132.34	0.0	0.512
Q3 = 8 L.s^{-1}.m^{-1}	USP ~ LD	−131.81	0.5	0.393
	USP ~ LA	−128.98	3.4	0.096
	USP ~ LA + LD	−127.94	0.0	0.595
Q4 = 11 L.s^{-1}.m^{-1}	USP ~ LD	−126.83	1.1	0.342
	USP ~ LA	−123.43	4.5	0.063

Full model was: USP ~ LA + LD; LD from (0–10 cm). AICc = second order Aikake's Information Criterion; see text for more details on ΔAICc and wAICc. LA = leaf area and LD = leaf density.

4.3. Consequences on sediment retention

As hydraulic roughness is linked to sediment retention and transport capacities (Dabney et al., 2009; Isselin-Nondedeu and Bédécarrats, 2007; Lambrechts et al., 2014; Munoz-Carpena et al., 1999), plant morphological traits, which have positive effects on hydraulic roughness, can be discussed with studies highlighting plant trait effects on sediment retention. Indeed, results showed the positive effect of the leaf area on hydraulic roughness, whereas there was no effect of stem specific density at small discharges, such as 2 L.s^{-1}.m^{-1}, which is consistent with Burylo et al. (2012) on the sediment retention capacity for more intense erosion processes. Results display the greater impact of density-weighted traits, which were previously not considered in studies on plant trait effects on sediment retention. The density-weighted trait approach is therefore important in understanding the plant-soil interactions involved in soil erosion.

Application of this trait-based approach in ecohydrology involves using the results to manage the reduction of soil erosion. Use of the unit stream power allows to characterise the plant efficiency with regard to sediment retention, with a critical *USP* (USPc) value of 0.004 m.s^{-1} determined by (Govers, 1990), which indicates the threshold from which soil is most likely to erode in loamy soils found in the European loess belt. From identified traits and density-weighted traits presenting an effect on hydraulic roughness and their values ($USP <$ 0.004 m.s^{-1}), plant species selection could be performed to create new herbaceous ecosystems that will be efficient to reduce runoff and further sediment retention on degraded areas (e.g., bare soils in degraded agroecosystems, urban and mining habitats) (Fig. 3).

5. Conclusions

This trait-based ecohydrology study allows the identification of important plant traits that influence the hydraulic roughness. The results indicate the stronger effect of density-weighted traits, showing that communities with the best trade-offs between stem density,

Table 5

Selected GLMs fitted to USP and four density-weighted traits as estimation variables for each discharge used. The models are sorted from the smallest ΔAICc to the highest ΔAICc for each discharge used.

Discharge	Models	AICc	ΔAICc	wAICc
Q1 = 2 $L.s^{-1}.m^{-1}$	USP ~ WLA + WSA	−165.33	0.00	0.377
	USP ~ WLA + WSDm	−165.29	0.04	0.370
	USP ~ WLA + WSLA + WSDm	−161.93	3.40	0.069
	USP ~ WLA + WSA + WSLA	−161.92	3.41	0.069
	USP ~ WLA	−160.86	4.47	0.040
	USP ~ WLA + WSDm + WSA	−160.48	4.85	0.033
	USP ~ WSDm	−158.66	6.67	0.013
	USP ~ WSA	−158.57	6.76	0.013
	USP ~ WLA + WSA	−160.22	0.00	0.412
	USP ~ WLA + WSDm	−160.22	0.00	0.412
Q2 = 4 $L.s^{-1}.m^{-1}$	USP ~ WLA + WSLA + WSDm	−156.45	3.77	0.063
	USP ~ WLA + WSA + WSLA	−156.38	3.84	0.060
	USP ~ WLA + WSDm + WSA	−155.16	5.05	0.033
	USP ~ WLA + WSDm	−143.44	0.00	0.405
	USP ~ WLA + WSA	−143.44	0.01	0.404
	USP ~ WLA + WSLA + WSDm	−138.78	4.67	0.039
Q3 = 8 $L.s^{-1}.m^{-1}$	USP ~ WLA + WSA + WSLA	−138.73	4.71	0.038
	USP ~ WLA + WSDm + WSA	−138.39	5.06	0.032
	USP ~ WSDm	−138.06	5.39	0.027
	USP ~ WSA	−137.9	5.55	0.025
	USP ~ WLA + WSA	−140.87	0.00	0.423
	USP ~ WLA + WSDm	−140.86	0.02	0.419
	USP ~ WLA + WSLA + WSDm	−136.7	4.17	0.053
Q4 = 11 $L.s^{-1}.m^{-1}$	USP ~ WLA + WSA + WSLA	−136.68	4.20	0.052
	USP ~ WLA + WSDm + WSA	−135.85	5.03	0.034

Full model was: USP ~ WLA + WSA + WSLA + WSDm. All variables are for traits (0–10 cm). AICc = second order Aikake's Information Criterion; see text for more details on ΔAICc and wAICc. WLA = weighted leaf area, WSA = weighted projected stem area, WSDm = weighted stem diameter, WSLA = weighted specific leaf area.

diameter and leaf area are the key to mitigate soil erosion. This new knowledge in the relationship between plant functional traits with hydraulic roughness and soil erosion constitutes a new advancement for modelling vegetation effects on soil erosion and creating new herbaceous ecosystems in degraded areas (e.g. bare soils of agroecosystems, mining and urban habitats). These newly reconstructed herbaceous ecosystems will play an important role in soil erosion mitigation. Future work should (1) include these relationships between aboveground traits and hydraulic roughness in existing models to estimate the transport and sediment retention capacities of flows and design herbaceous hedges to mitigate soil erosion and (2) examine the effect of functional diversity on runoff and soil erosion, as it could influence hydraulic roughness by ecologically complementing aboveground biomass and, more precisely, by limiting vegetation lodging.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2018.04.024.

References

Akram, S., Yu, B., Ghadiri, H., Rose, C., Hussein, J., 2014. The links between water profile, net deposition and erosion in the design and performance of stiff grass hedges. J. Hydrol. 510, 472–479. http://dx.doi.org/10.1016/j.jhydrol.2014.01.001.

Berendse, F., van Ruijven, J., Jongejans, E., Keesstra, S., 2015. Loss of plant species diversity reduces soil erosion resistance. Ecosystems 18, 881–888. http://dx.doi.org/10.1007/s10021-015-9869-6.

Blanco-Canqui, H., Gantzer, C.J., Anderson, S.H., 2006. Performance of grass barriers and filter strips under interrill and concentrated flow. J. Environ. Qual. 35, 1969. http://dx.doi.org/10.2134/jeq2006.0073.

Boardman, J., Poesen, J. (Eds.), 2006. Soil Erosion in Europe. John Wiley & Sons, Ltd.

Bochet, E., Poesen, J., Rubio, J.L., 2000. Mound development as an interaction of individual plants with soil, water erosion and sedimentation processes on slopes. Earth Surf. Process. Landf. 25, 847–867.

Brown, K.A., Flynn, D.F.B., Abram, N.K., Ingram, J.C., Johnson, S.E., Wright, P., 2011. Assessing natural resource use by forest-reliant communities in Madagascar using functional diversity and functional redundancy metrics. PLoS ONE 6, e24107. http://dx.doi.org/10.1371/journal.pone.0024107.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer, New York.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35. http://dx.doi.org/10.1007/s00265-010-1029-6.

Burylo, M., Rey, F., Bochet, E., Dutoit, T., 2012. Plant functional traits and species ability for sediment retention during concentrated flow erosion. Plant Soil 353, 135–144. http://dx.doi.org/10.1007/s11104-011-1017-2.

Cantalice, J.R.B., Melo, R.O., Silva, Y.J.A.B., Cunha Filho, M., Araújo, A.M., Vieira, L.P., Bezerra, S.A., Barros, G., Singh, V.P., 2015. Hydraulic roughness due to submerged, emergent and flexible natural vegetation in a semiarid alluvial channel. J. Arid Environ. 114, 1–7. http://dx.doi.org/10.1016/j.jaridenv.2014.10.012.

Cao, L., Zhang, Y., Lu, H., Yuan, J., Zhu, Y., Liang, Y., 2015. Grass hedge effects on controlling soil loss from concentrated flow: a case study in the red soil region of China. Soil Tillage Res. 148, 97–105. http://dx.doi.org/10.1016/j.still.2014.12.009.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51, 335–380.

Dabney, S.M., McGregor, K.C., Wilson, G.V., Cullum, R.F., 2009. How management of grass hedges affects their erosion reduction potential. Soil Sci. Soc. Am. J. 73, 241. http://dx.doi.org/10.2136/sssaj2007.0434.

Dabney, S.M., Meyer, L.D., Harmon, W.C., Alonso, C.V., Foster, G.R., 1995. Depositional patterns of sediment trapped by grass hedges. Trans. ASAE 38, 1719–1729.

Dabney, S.M., Shields Jr, F.D., Temple, D.M., Langendoen, E.J., 2004. Erosion processes in gullies modified by establishing grass hedges. Trans. ASAE 47, 1561.

De Baets, S., Poesen, J., 2010. Empirical models for predicting the erosion-reducing effects of plant roots during concentrated flow erosion. Geomorphology 118, 425–432. http://dx.doi.org/10.1016/j.geomorph.2010.02.011.

De Baets, S., Poesen, J., Gyssels, G., Knapen, A., 2006. Effects of grass roots on the erodibility of topsoils during concentrated flow. Geomorphology 76, 54–67. http://dx.doi.org/10.1016/j.geomorph.2005.10.002.

Dillaha, T.A., Reneau, R.B., Mostaghimi, S., Lee, D., 1989. Vegetative filter strips for agricultural nonpoint source pollution control. Trans. ASAE 32, 513–0519.

Dosskey, M.G., Vidon, P., Gurwick, N.P., Allan, C.J., Duval, T.P., Lowrance, R., 2010. The role of riparian vegetation in protecting and improving chemical water quality in streams. J. Am. Water Resour. Assoc. 1–18. http://dx.doi.org/10.1111/j.1752-1688.2010.00419.x.

Faucon, M.-P., Houben, D., Lambers, H., 2017. Plant functional traits: soil and ecosystem services. Trends Plant Sci. 22, 385–394. http://dx.doi.org/10.1016/j.tplants.2017.01.005.

Garnier, E., Navas, M.-L., 2012. A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A Rev. Agron. Sustain. Dev. 32, 365–399.

Gobin, A., Govers, G., Jones, R., Kirkby, M., Kosmas, C., Gentile, A.R., 2003. Assessment and reporting on soil erosion: background and workshop report. (Technical No. 94). European Environment Agency, Copenhagen.

Govers, G., 1992. Relationship between discharge, velocity and flow area for rills eroding loose, non-layered materials. Earth Surf. Process. Landf. 17, 515–528.

Govers, G., 1990. Empirical relationships for the transport capacity of overland flow. Int. Assoc. Hydrol. Sci. 189, 45–63.

Graff, C.D., Sadeghi, A.M., Lowrance, R.R., Williams, R.G., 2005. Quantifying the sensitivity of the riparian ecosystem management model (REMM) to changes in climate and buffer characteristics common to conservation practices. Trans. ASAE 48, 1377–1387.

Gyssels, G., Poesen, J., Bochet, E., Li, Y., 2005. Impact of plant roots on the resistance of soils to erosion by water: a review. Prog. Phys. Geogr. 29, 189–217. http://dx.doi.org/10.1191/0309133305 pp443ra.

Haan, C.T., Barfield, B.J., Hayes, J.C., 1994. Design Hydrology and Sedimentology for Small Catchments. Academic Press.

Hayes, J.C., Barfield, B.J., Barnhisel, R.I., 1978. Evaluation of grass characteristics related to sediment filtration. ASAE 78–2513, 21.

Hessel, R., Jetten, V.G., Liu, B., Qiu, Y., 2016. Evaluating effects of soil and water management and land use change on the Loess Plateau of China using LISEM. In: Morgan, R.P.C., Nearing, M. (Eds.), Handbook of Erosion Modelling. John Wiley and Sons, pp.

223–248.
Hussein, J., Yu, B., Ghadiri, H., Rose, C., 2007. Prediction of surface flow hydrology and sediment retention upslope of a vetiver buffer strip. J. Hydrol. 338, 261–272.
Isselin-Nondedeu, F., Bédécarrats, A., 2007. Influence of alpine plants growing on steep slopes on sediment trapping and transport by runoff. Catena 71, 330–339. http://dx.doi.org/10.1016/j.catena.2007.02.001.
Järvelä, J., 2002. Flow resistance of flexible and stiff vegetation: a flume study with natural plants. J. Hydrol. 269, 44–54.
Knapen, A., Poesen, J., Govers, G., Gyssels, G., Nachtergaele, J., 2007. Resistance of soils to concentrated flow erosion: a review. Earth-Sci. Rev. 80, 75–109. http://dx.doi.org/10.1016/j.earscirev.2006.08.001.
Lambinon, J., Delvosalle, L., Duvigneaud, J., 2012. Nouvelle flore de la Belgique, du G.-D. de Luxembourg, du nord de la France et des régions voisines, 6th ed.
Lambrechts, T., François, S., Lutts, S., Muñoz-Carpena, R., Bielders, C.L., 2014. Impact of plant growth and morphology and of sediment concentration on sediment retention efficiency of vegetative filter strips: Flume experiments and VFSMOD modeling. J. Hydrol. 511, 800–810. http://dx.doi.org/10.1016/j.jhydrol.2014.02.030.
Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556.
Le Bissonnais, Y., Cerdan, O., Lecomte, V., Benkhadra, H., Souchère, V., Martin, P., 2005. Variability of soil surface characteristics influencing runoff and interrill erosion. CATENA 62, 111–124. http://dx.doi.org/10.1016/j.catena.2005.05.001.
Lowrance, R.R., Altier, L.S., Newbold, J.D., Schnabel, R.R., Groffman, P.M., Denver, J.M., Correll, D.L., Gilliam, J.W., Robinson, J.L., Brinsfield, R.B., Staver, K.W., Lucas, W., Todd, A.H., 1995. Water quality functions of riparian forest buffer systems in the Chesapeake Bay watershed (Technology transfer report No. EPA 903-R-95-004). U.S. Environmental Protection Agency, Chesapeake Bay Program.
Ludwig, J.A., Wilcox, B.P., Breshears, D.D., Tongway, D.J., Imeson, A.C., 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. Ecology 86, 288–297. http://dx.doi.org/10.1890/03-0569.
Mekonnen, M., Keesstra, S.D., Ritsema, C.J., Stroosnijder, L., Baartman, J.E.M., 2016. Sediment trapping with indigenous grass species showing differences in plant traits in northwest Ethiopia. Catena 147, 755–763. http://dx.doi.org/10.1016/j.catena.2016.08.036.
Meyer, L.D., Dabney, S.M., Harmon, W.C., 1995. Sediment-trapping effectiveness of stiff-grass hedges. Am. Soc. Agric. Eng. 38, 809–815.
Morgan, R.P.C., 2004. Vegetative-based technologies for erosion control. In: Stokes, A., Spanos, I., Norris, J.E., Cammeraat, E. (Eds.), Eco- and Ground Bio-Engineering: The Use of Vegetation to Improve Slope Stability. Springer, Dordrecht, The Netherlands, pp. 265–272.
Morgan, R.P.C., Duzant, J.H., 2008. Modified MMF (Morgan–Morgan–Finney) model for evaluating effects of crops and vegetation cover on soil erosion. Earth Surf. Process. Landf. 33, 90–106. http://dx.doi.org/10.1002/esp.1530.
Morgan, R.P.C., Quinton, J.N., Smith, R.E., Govers, G., Poesen, J.W.A., Chisci, G., Torri, D., 1998. The EUROSEM model. In: Boardman, J., Favis-Mortlock, D. (Eds.), Modelling Soil Erosion by Water. Springer Science and Business Media, pp. 389–398.
Muñoz Carpena, R., Parsons, J.E., 2014. VFSMOD – Vegetative Filter Strips Modelling System (Model Documentation and user's manual No. 6.x). University of Florida.
Munoz-Carpena, R., Parsons, J.E., Gilliam, J.W., 1999. Modeling hydrology and sediment transport in vegetative filter strips. J. Hydrol. 214, 111–129.
Ouin, A., Burel, F., 2002. Influence of herbaceous elements on butterfly diversity in hedgerow agricultural landscapes. Agric. Ecosyst. Environ. 93, 45–53.
Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167–234. http://dx.doi.org/10.1071/BT12225.
Richet, J.-B., Ouvry, J.-F., Saunier, M., 2017. The role of vegetative barriers such as fascines and dense shrub hedges in catchment management to reduce runoff and erosion effects: Experimental evidence of efficiency, and conditions of use. Ecol. Eng. 103, 455–469. http://dx.doi.org/10.1016/j.ecoleng.2016.08.008.
Ruiz-Colmenero, M., Bienes, R., Eldridge, D.J., Marques, M.J., 2013. Vegetation cover reduces erosion and enhances soil organic carbon in a vineyard in the central Spain. Catena 104, 153–160. http://dx.doi.org/10.1016/j.catena.2012.11.007.
Smith, J., Potts, S., Eggleton, P., 2008. The value of sown grass margins for enhancing soil macrofaunal biodiversity in arable systems. Agric. Ecosyst. Environ. 127, 119–125. http://dx.doi.org/10.1016/j.agee.2008.03.008.
Stokes, A., Douglas, G.B., Fourcaud, T., Giadrossich, F., Gillies, C., Hubble, T., Kim, J.H., Loades, K.W., Mao, Z., McIvor, I.R., Mickovski, S.B., Mitchell, S., Osman, N., Phillips, C., Poesen, J., Polster, D., Preti, F., Raymond, P., Rey, F., Schwarz, M., Walker, L.R., 2014. Ecological mitigation of hillslope instability: ten key issues facing researchers and practitioners. Plant Soil 377, 1–23. http://dx.doi.org/10.1007/s11104-014-2044-6.
Temple, D.M., 1982. Flow Retardance of Submerged Grass Channel Linings. Trans. ASAE 25, 1300–1303. https://doi.org/10.13031/2013.33717.
Temple, D.M., Robinson, K.M., Ahring, R.M., Davis, A.G., 1987. Stability Design of Grass-Lined Open Channels. Agriculture Handbook. U.S, Department of Agriculture, Washington, D.C.
Van Dijk, P.M., Kwaad, F.J.P.M., Klapwijk, M., 1996. Retention of water and sediment by grass strips. Hydrol. Process. 10, 1069–1080. http://dx.doi.org/10.1002/(SICI)1099-1085(199608)10:8<1069::AID-HYP412>3.0.CO;2-4.
Vannoppen, W., Vanmaercke, M., De Baets, S., Poesen, J., 2015. A review of the mechanical effects of plant roots on concentrated flow erosion rates. Earth-Sci. Rev. 150, 666–678. http://dx.doi.org/10.1016/j.earscirev.2015.08.011.
Vieira, D.A.N., Dabney, S.M., 2012. Two-dimensional flow patterns near contour grass hedges. Hydrol. Process. 26, 2225–2234. http://dx.doi.org/10.1002/hyp.8262.
Xiao, B., Wang, Q., Wang, H., Dai, Q., Wu, J., 2011. The effects of narrow grass hedges on soil and water loss on sloping lands with alfalfa (Medicago sativa L.) in Northern China. Geoderma 167–168, 91–102. http://dx.doi.org/10.1016/j.geoderma.2011.09.010.
Yang, C.T., 1972. Unit stream power and sediment transport. ASCE J. Hydraul. Div. 98, 1805–1826.
Yuan, Y., Bingner, R.L., Locke, M.A., 2009. A Review of effectiveness of vegetative buffers on sediment trapping in agricultural areas. Ecohydrology 2, 321–336. http://dx.doi.org/10.1002/eco.82.
Zhu, H., Fu, B., Wang, S., Zhu, L., Zhang, L., Jiao, L., Wang, C., 2015. Reducing soil erosion by improving community functional diversity in semi-arid grasslands. J. Appl. Ecol. 52, 1063–1072. http://dx.doi.org/10.1111/1365-2664.12442.

Appendix D – Plant functional traits effects of herbaceous vegetation on runoff mitigation, sediment retention and soil erosion control in agricultural landscapes under temperate climates. A review

Léa Kervroëdan, Romain Armand, Freddy Rey and Michel-Pierre Faucon

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Abstract

Soil degradation by concentrated runoff and erosion induce major environmental and economic damages, notably in agricultural areas under temperate climates. Management of runoff by herbaceous vegetation is a key feature to reduce soil loss and erosion by furthering infiltration and hydraulic roughness, main processes inducing sediment retention by slowing the flow velocity. Using plant trait-based approach, unlike taxonomical approach, allows to understand and characterise the direct effects of the vegetation on infiltration, runoff and sediment retention. Here we review the following for agricultural catchments under temperate climates: (1) effects of plant belowground functional traits on the infiltration capacity of herbaceous vegetation, (2) influence of plant aboveground functional types and traits of herbaceous vegetation on hydraulic roughness and sediment retention, (3) contrasting effects of the functional diversity on hydraulic roughness and sediment retention and (4) applications of the trait-based approach to design and manage herbaceous hedges for sediment retention and erosion control. This review synthesises recent advances regarding the effects of functional traits on runoff and sediment retention and defines a trait-based selection method of plant species for erosion control.

Key words

Agroecological engineering; hydraulic roughness; plant functional traits; plant-soil interactions; runoff-plant interactions; soil conservation; herbaceous hedges.

1. Introduction

Soil erosion by water is a frequently observed natural hazard in tropical, Mediterranean and temperate oceanic areas leading to soil degradation, and is accentuated by anthropogenic factors, especially by agriculture (Poesen 2018). Soil degradation due to water erosion leads to long-term negative effects on soil fertility, but also to wider environmental damages through runoff, sediment transport, pollutant transfer in water bodies, eutrophication and muddy floods (Le Bissonnais et al. 2004; Morgan 2009; Evrard et al. 2010). Water soil erosion is mainly influenced by the soil texture and structure, precipitations, slopes as well as plant and litter covers and soil organic matter, depending on the agricultural practices. Mitigation of soil erosion using herbaceous plants has been established for the past decades and their various effects on soil erosion processes (Figure 1) have been intensively studied (Haan et al. 1994; Ludwig et al. 2005; Mekonnen et al. 2015). Indeed, plants reduce soil erosion by protecting soil against raindrops impacts, furthering infiltration, stabilising and reinforcing soil, increasing surface roughness, reducing runoff velocity, boosting evapo-transpiration and inducing sediment retention (Haan et al. 1994; Styczen and Morgan 1995; Morgan 2009). However, plant efficiency towards runoff and soil erosion reduction changes depending on the species used, stressing the need to use another approach than taxonomy to identify efficient vegetation (Hayes et al. 1984; Cao et al. 2015). The effects of plant root density, length density, tensile strength, area ratio and system morphology on soil and slope stabilisation as well as on soil shear strength have been thoroughly analysed (De Baets et al. 2006, 2009; Stokes 2007; Stokes et al. 2014). The reduction of soil detachment rate under the “splash” effects has also been well documented, showing the positive effect of plant canopy on the decrease of the raindrop kinetic energy (Styczen and Morgan 1995; Morgan 2004; Gyssels et al. 2005). At the vegetation patch scale, the two main processes reducing soil loss, through sediment retention, are the infiltration rate and the hydraulic roughness (i.e. the frictional resistance that vegetation creates when in contact with a water flow). As long as the hydraulic conductivity of the soil remains unsaturated, the soil infiltration rate, increased by the presence of vegetation, slows runoff generation (Styczen and Morgan 1995). However, once the soil reaches the saturated hydraulic conductivity, the main process inducing sediment retention and runoff velocity reduction is the hydraulic roughness created by the vegetation (Styczen and Morgan 1995), which also furthers infiltration (Dabney et al. 1995; Gilley et al. 2000; Dosskey et al. 2010). Indeed, the aboveground biomass of the herbaceous vegetation slows the velocity of the flow down which creates a backwater area in front of the vegetation. Then, the sediment retention occurs in the backwater area, as the sediment transport capacity of the flow is reduced (Hussein et al. 2007; Akram et al. 2014; Cantalice et al. 2015).

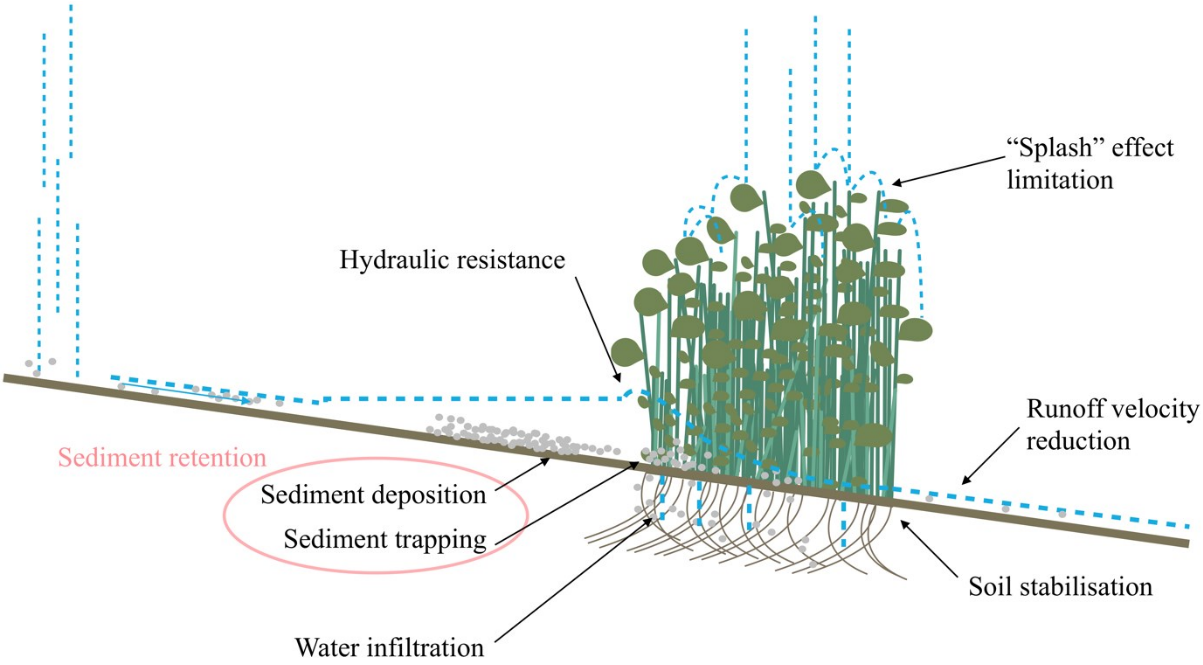

Figure 1. Effects of herbaceous vegetation on soil erosion processes.

Runoff and soil erosion are mainly reduced by the plant hydraulic roughness at the vegetation patch scale in agricultural catchments, distinctive to temperate oceanic climates, which are regularly affected by intense runoff and soil erosion episodes, due to the intensified tillage and cultivation of annual crops on sloping loamy soils (Styczen and Morgan 1995; Gobin et al. 2003; Boardman and Poesen 2006). The improvement of herbaceous vegetation efficiency for soil erosion mitigation requires a good understanding of the relationship between the plant functional traits, the infiltration rate and the hydraulic roughness. Functional traits are defined as 'morpho-physio-phenological traits which indirectly impact fitness via their effects on growth, reproduction and survival' (Violle et al. 2007). Trait-based ecology and agroecology allows characterising plant responses to environmental changes and their effects on ecosystem processes. Studying the linkages between plant functional traits and soil properties and processes constitutes an essential approach to understand ecosystem processes (e.g. hydrological processes) allowing to design new ecosystems offering the desired ecosystem services (Faucon et al. 2017). Functional diversity, defined as “the value, range, and relative abundance of plant functional traits in a given ecosystem” (Tilman 2001b; Díaz et al. 2007a), influences ecosystem processes and functioning, although its effects are controversial (Garnier et al. 2016). The “mass ratio hypothesis” stipulates that ecosystem properties are driven by the traits of the dominant species in the community (Grime 1998). Accordingly, ecosystem properties would be determined by the community-weighted mean trait values of the dominant species (Díaz et al. 2007b). On the other hand, ecosystem processes can also be driven by non-additive effects (i.e. complementarity or facilitation) among coexisting species with diverse trait values, which can be designated by functional diversity indices (e.g. functional divergence, distance between high abundant species and the centre of the functional space) (Díaz et al. 2007b; Mouillot et al. 2011; Garnier and Navas 2012). Given that functional diversity impacts various ecological processes and notably soil erosion (Erktan et al. 2013; Zhu et al. 2015; Garnier et al. 2016), the effects of plant functional diversity can be analysed to understand the potential impacts on hydraulic roughness and the resulting sediment retention.

This review synthesises recent advances and contemporary understanding on the effects of plant functional traits of herbaceous vegetation on runoff mitigation and sediment retention in agricultural catchments of temperate climates by reviewing (1) the effects of plant belowground functional traits on the infiltration capacity of vegetation, (2) the influence of plant aboveground functional types and traits on hydraulic roughness and sediment retention; (3) the contrasting effects of functional diversity on hydraulic roughness and sediment retention and (4) the applications of the trait-based approach for the design and management of herbaceous hedges for sediment retention and erosion control.

2. Effects of plant belowground functional traits on the infiltration capacity of herbaceous vegetation

Water infiltration in the soil is one of the main process influencing runoff generation (Morgan 2005). Within a vegetation patch (i.e. herbaceous hedge), the presence of roots increases the soil permeability by the creation of macropores, enhancing the water flow within the soil and thus, the infiltration capacity (Styczen and Morgan 1995; Gyssels et al. 2005; Dosskey et al. 2010; Ghestem et al. 2011). Dense fibrous root systems, with a root diameter smaller than 1mm, are positively correlated with the soil permeability (Li et al. 1992). The effects of the root channel diameter and the root channel area on the efficiency of the infiltration rates have also been emphasised (Wu et al. 2017). Studies focussing on the effects of vegetation on the infiltration capacity mostly investigate the effects of different functional types or species, rather than identifying the functional traits involved (Clark and Zipper 2016). Nonetheless, the infiltration capacity is influenced by the root biomass, the root weight density (i.e. the weight of living roots divided by the soil sample volume, expressed in kg.m^{-3}), the root length density and the root surface area density (Li et al. 2013; Liu et al. 2016; Wu et al. 2016). Once runoff has been generated, the infiltration is also furthered by the hydraulic roughness of the vegetation, especially by the slowing down of the flow and the creation of a backwater area. Indeed, the infiltration capacity is increased by the longer contact between the water and the surface in the backwater area (Gilley et al. 2000; Dosskey et al. 2010). The aboveground functional traits impacting hydraulic roughness would thus, indirectly, further infiltration capacity.

3. Effects of plant aboveground functional types and traits on hydraulic roughness and sediment retention

3.1. Effects of plant functional types

A plant functional type can be defined as a group of plant species sharing similar functioning at the organismic level, similar responses to environmental factors and/or similar roles in ecosystems (Lavorel and Garnier 2002). Developing herbaceous vegetation with relevant hydraulic roughness values requires the identification of the influencing functional types. By ensuring a homogeneous and dense cover to limit the presence of preferential flow paths within the vegetation, species presenting rhizomes or stolon can play a key role in hydraulic roughness and sediment retention. Indeed, rhizomes and stolon guarantee a lateral spreading growth pattern, with a maximum ground cover (100%), and a burying tolerance towards recurring sedimentation (Maun 1998). Perennial herbaceous species under the Raunkiaer's life-form categories "herbaceous chamaephytes", "hemicryptophytes" and "geophytes" provide an effective soil cover through all seasons by increasing hydraulic roughness compared to bare soils. Within these life-form categories, caespitose and non-caespitose types allow a constant ground cover with fresh or dry biomass in winter, when soil erosion is observed at its highest in temperate climates (Boardman and Poesen 2006). Species and herbaceous vegetation which are efficient against concentrated flows, present a higher vegetative height than the water maximal level found in the targeted areas (e.g. 20cm in north-west Europe). Vegetative height defined by the water maximal level constitutes a major trait to reduce runoff and increase sediment retention. Functional types involved in the increase of hydraulic roughness and sediment retention could constitute a set of criteria to select potential candidate species within a specific phyto-geographical area for soil erosion control (Figure 2A). Perspective is to define selection method to design efficient herbaceous vegetation.

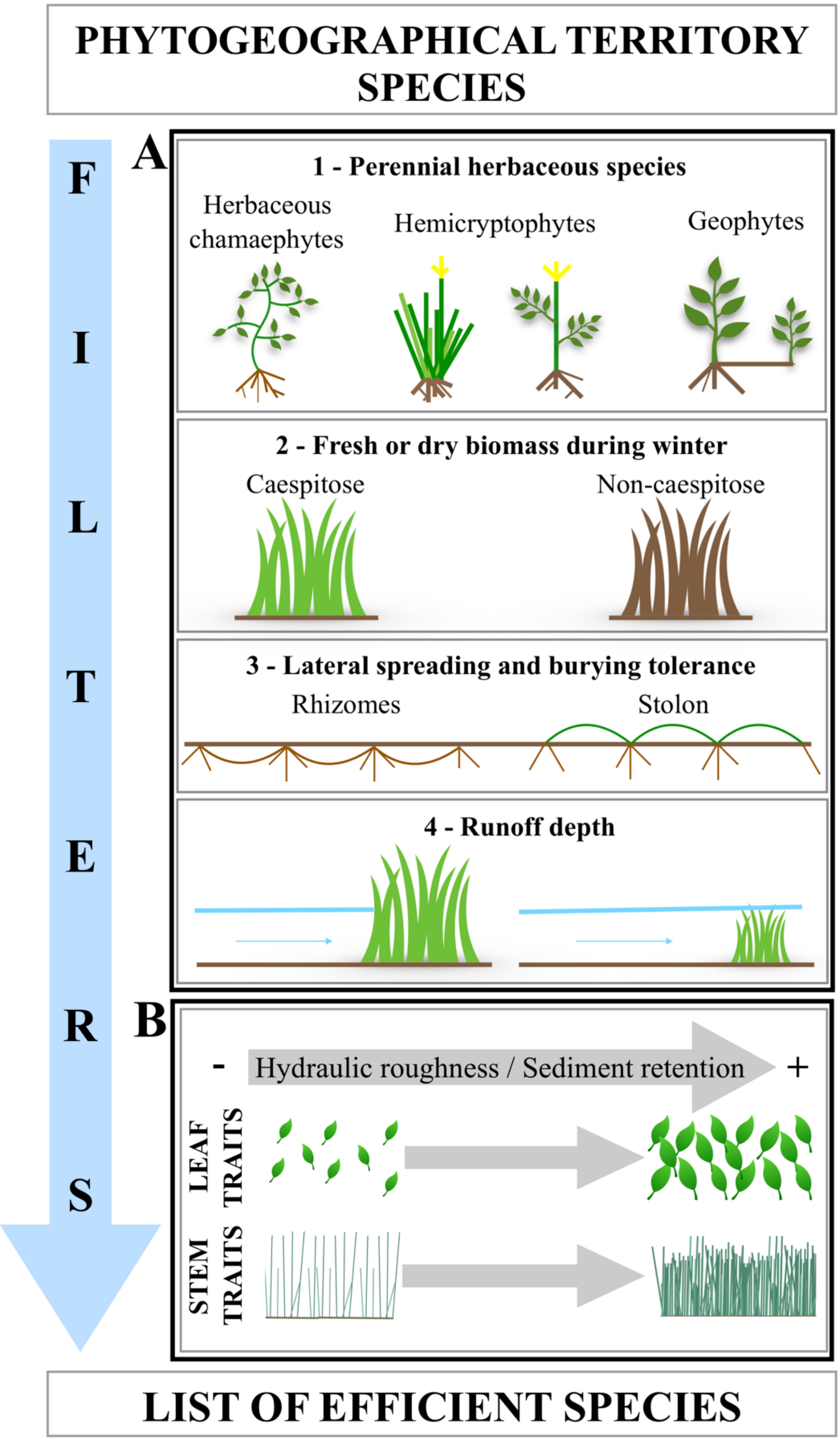

Figure 2. Functional types (A) and traits (B) involved in the increase of the hydraulic roughness and sediment retention in temperate climates to select efficient herbaceous vegetation.

3.2.Effects of leaf and stem functional traits

Most of the studies about vegetation impacts on soil erosion and sediment retention focus on the impacts of aboveground functional traits. Both stem and leaf traits have been identified for the past decades as efficient for triggering sediment retention (Figure 2B). The stem density and diameter are two of the main traits influencing sediment retention (Hayes et al. 1978; Temple 1982; Meyer et al. 1995; Bochet et al. 2000; Isselin-Nondedeu and Bédécarrats 2007; Morgan and Duzant 2008; Mekonnen et al. 2016). The efficiency of the stem density on runoff depends on the number of stems, the slope and the type of soil. Indeed, on 20% slopes of silty soils, vegetation with a stem density of 7500 stems.m^{-2} would reduce the flow velocity by 90.6%, while on a 10% slope 2500 stems.m^{-2} would reduce the velocity by 91.9% compare to bare soil (Morgan 2004). The stem stiffness have also been found to induce sediment retention (Meyer et al. 1995), although contrasting results are found in the literature (Burylo et al. 2012a). These contrasting results could be explained by the differences in the discharges used, as with higher discharges (from 11 to 43.7 l.s^{-1}.m^{-1}) an effect of the stem stiffness was found compared to smaller discharges (1.6 l.s^{-1}.m^{-1}). Considering the leaf traits, the leaf density, the leaf area and specific leaf area are involved in sediment retention (Graff et al. 2005; Burylo et al. 2012a; Lambrechts et al. 2014).

The effects of traits on the hydraulic roughness is a central process to understand the effects on sediment retention and the management of soil erosion in agricultural catchments. The traits influencing the hydraulic roughness were highlighted, as well as the most efficient combinations of these traits and their range of efficiency (Kervroëdan et al. 2018). The leaf area and density were the main traits involved in the hydraulic roughness increase. The effects of density-weighted traits (trait weighted by the trait's density) were also investigated to characterise the trait effects at the vegetation's (hedge's) level. This approach showed the effects of the density-weighted leaf area (i.e. leaf area x leaf density, in mm^2.dm^{-2}), the density-weighted stem diameter (i.e. stem diameter x stem density, in mm.dm^{-2}) and the density-weighted projected stem area (which represents the projected area towards the flow; stem projected area x stem density, in mm^2.dm^{-2}) for discharges from 2 to 11 L.s^{-1}.m^{-1}. Using generalised linear models, the most efficient combinations of traits and density-weighted traits were identified as: (1) the leaf area with the leaf density; (2) the density-weighted leaf area with the density-weighted stem diameter and (3) the density-weighted leaf area with the density-weighted projected stem area, also emphasing the indirect effect of the stem density.

The results also showed a changing response in the effects of the leaf density, the leaf area and the density-weighted specific leaf area towards different discharges which is consitent with the literature (Temple et al. 1987; Vieira and Dabney 2012). Indeed, the leaf density was efficient for important discharges (8 and 11 $L.s^{-1}.m^{-1}$) while the leaf area was efficient for small discharges (2 and 4 $L.s^{-1}.m^{-1}$) and the density-weighted specific leaf area was efficient from 4 to 11 $L.s^{-1}.m^{-1}$. The traits and density-weighted traits' range of efficiency were also determined, using a critical value of 0.004 $m.s^{-1}$ as a maximum threshold, which represents the critical value of the dissipated energy of the flow above which the soil is likely to erode in loamy soils found in the European loess belt (Govers 1990).

The knowledge of plant trait effects on runoff and sediment retention processes constitutes a new advancement into the modelling of vegetation effects for soil erosion and runoff mitigation, such as in VFSMOD (Vegetative Filter Strip Modelling System). This model evaluates the effects of vegetation on hydrology and sediment transport processes through vegetative filter strips. The model is physically-based and simulates sediment retention resulting of vegetation's hydraulic roughness (e.g. Manning index). Although this model is widely used, the characterisation of the vegetation's hydraulic roughness is based on a limited number of plant traits: stem density and height (Muñoz Carpena and Parsons 2014). Adding traits identified as efficient for hydraulic roughness in herbaceous hedges would increase the precision in modelling vegetative barriers efficiency and broaden the model's field of application. Therefore, improvements may apply to: (1) the estimation of sediment transport and retention capacities, (2) the application of the model for other vegetative objects than vegetative filter strips and (3) the design of herbaceous vegetation by creating efficient vegetation for hydraulic processes encountered in the implantation landscape. Perspective is to compare results obtained using the model with ones obtained by experimentation and identifying the main traits involved in hydraulic roughness and sediment retention.

4. Contrasting effects of the functional diversity in herbaceous vegetation on hydraulic roughness and sediment retention

For decades, studies highly focused on the effects of functional diversity on some main ecosystem processes, notably carbon cycles (Garnier et al. 2004; Zuo et al. 2016b; Cadotte

2017), but the functional diversity effects for a same process are found contrasting (Garnier et al. 2016; Mariotte et al. 2017; Faucon et al. 2017). These controversial results stress the need to widen the range of processes related to plant-soil interactions which could be affected by functional diversity.

The effects of functional diversity on runoff and soil erosion processes have not been thoroughly studied. Land restoration with monospecific vegetation may be inefficient in reducing soil erosion given as their simple canopy (Cao et al. 2009; Cao 2011). Hypothesis is that vegetation with high species diversity and functional diversity positively influence the hydraulic roughness and reduce soil erosion. Indeed, plants with wider stem diameters would support the stems and leaves of species with higher leaf area and density. The biomass productivity of herbaceous vegetation positively influences the hydraulic roughness and sediment retention (Podwojewski et al. 2011; Burylo et al. 2012a). Positive effects of the functional diversity on plant productivity would thus lead to an increase of the hydraulic roughness and the sediment retention. These positive effects could notably come from the belowground traits by inducing spatial niche differentiation by a diversification in the nutrients and water sources accessibility and acquisition in the soil profile (Tilman et al. 2014; Faucon et al. 2017). Only few studies have focussed on the functional diversity effects on soil erosion at the ecosystem level, with controversial results (Erktan et al. 2013; Zhu et al. 2015). In semi-arid grassland, the functional divergence explained up to 40% of the variation of the erosion rates, due to a greater niche differentiation within the tested communities (Zhu et al. 2015). However, when focusing on effects of functional types mixtures in Mediterranean mountainous ecosystems, no effect of the functional diversity on sediment retention was found, due to areas of least resistance to flow created by the shrubs and trees individuals (Erktan et al. 2013). Although the results found for these erosion processes are controversial, combining herbaceous species with efficient traits on the hydraulic roughness and sediment retention could lead to a better understanding of the functional diversity effect types on these processes (Figure 3). Perspective is to study a number of species combinations and a wide functional diversity gradient comprising traits involved in hydraulic roughness and sediment retention. This would allow to analyse these controversial findings and identify if they could be results of idiosyncratic effects of the traits, corresponding to contrasting effects of functional diversity influenced by species-traits and plant-soil interactions.

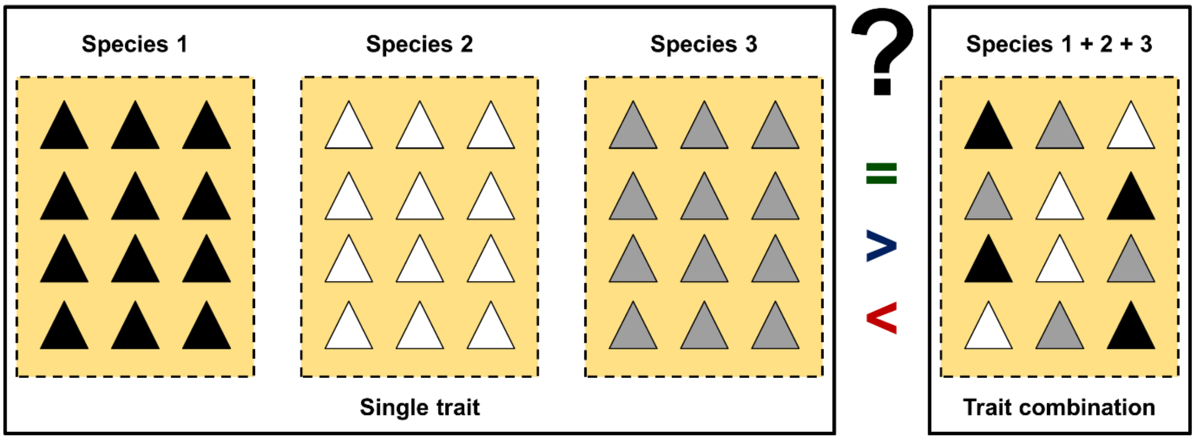

Figure 3. Hypothesis on the effects of plant functional diversity on the hydraulic roughness and sediment retention.

= Absence of functional diversity effect: the effect of the functional traits depends on the relative abundance or the contribution to the total biomass of dominant species.

> Negative effect of the functional diversity: the opposite processes of the ones that are positively affected (e.g. mobilisation/immobilisation, competition for light).

< Positive effect of the functional diversity: complementary resource use between the plant species or the canopy architecture would explain a positive effect of the functional diversity.

5. Applications to design and manage herbaceous hedges for sediment retention and erosion control

In agricultural areas, implanting vegetative barriers in the form of herbaceous hedges across the flow path would reduce sheet and concentrated erosion (Dabney et al. 1995). Herbaceous hedges are narrow strips of dense and stiff perennial vegetation and present a high efficiency on the reduction of soil erosion caused by concentrated flows (Dabney et al. 1995; Yuan et al. 2009). They are differentiated from vegetative filter strips by their width and functions, while herbaceous hedges are specially designed to further hydraulic roughness and sediment retention in concentrated flow paths, vegetative filter strips further infiltration and sediment retention on a wide area (> 5m width) under superficial and shallow flows and are useless under concentrated runoff events (Dillaha et al. 1989; Dabney et al. 1995).

5.1. Candidates plant species to design herbaceous hedges: the case of north-west Europe

The first challenge is to apply defined criteria to design the species composition of herbaceous hedges in different phyto-geographical territories. Taking north-west Europe, composed of 3,500 spermatophyte species (Lambinon et al. 2012), with the following criteria based from the functional types: (1) perennial herbaceous vegetation "herbaceous chamaephytes", "hemicryptophytes", "hemicryptophytes" and "geophytes" which present biomass in winter (caespitose or non-caespitose types) when soil erosion is observed at its highest in north-west Europe (Boardman and Poesen 2006); (2) the presence of rhizomes or stolon; (3) a minimum vegetative height equal or higher than 20 cm, being the maximal level of the water flows in the north-west European catchments; (4) a broad ecological niche for an implantation in several silty agricultural soils; and (5) non-weed species to avoid the spreading of the vegetation into the agricultural fields; only 76 candidate species potentially able to mitigate runoff and soil erosion are highlighted (Table 1) ((Villarroel 2015)). The characterisation of leaf and stem trait effects on the hydraulic roughness and sediment retention should be integrated into the selection criteria to narrow the list of efficient species, using the trait values' range of efficiency. Perspective is to select the candidate species regarding their stem and leaf traits using trait databases, which could be completed with applied traits such as the one influencing hydraulic roughness and sediment retention.

Table 1. The 76-candidate species list potentially able to mitigate soil erosion in the north-west European loess belt. The minimum vegetative heights are represented under the median value (Quartile 1; Quartile 4) of the data obtained from *(Hegi 1906; Mansion et al. 1989; Bugnon 1995; Rothmaler and Jäger 2009; Jauzein and Nawrot 2011; Lambinon et al. 2012; Université de Bourgogne (UFR Science de la vie) 2018).*

Family	Species name	Life form	Minimum vegetative height (cm)
Adoxaceae	*Sambucus ebulus L.*	Hemicryptophyte	55 (50; 80)
Apiaceae	*Anthriscus sylvestris (L.) Hoffmann*	Hemicryptophyte	45 (40; 80)
	Bupleurum falcatum L.	Hemicryptophyte	30 (20; 50)
	Heracleum sphondylium L.	Hemicryptophyte	50 (30; 50)
Asteraceae	*Achillea ptarmica L.*	Hemicryptophyte	20 (20; 30)
	Artemisia verlotiorum	Hemicryptophyte	70 (67.5; 150)
	Artemisia vulgaris L.	Hemicryptophyte	60 (52.5; 60)
	Aster laevis L.	Hemicryptophyte	60 (60; 60)
	Aster salignus Willd.	Hemicryptophyte	80 (72.5; 90)
	Eupatorium cannabinum L.	Hemicryptophyte	55 (50; 80)
	Hieracium piloselloides Vill.	Hemicryptophyte	20 (20; 20)
	Senecio jacobaea L.	Hemicryptophyte	30 (30; 40)
	Tanacetum corymbosum L.	Hemicryptophyte	30 (30; 50)
	Tanacetum parthenium L.	Hemicryptophyte	30 (30; 30)
	Tanacetum vulgare L.	Hemicryptophyte	55 (42.5; 60)
Caryophyllaceae	*Saponaria officinalis L.*	Hemicryptophyte	30 (30; 30)
Clusiaceae	*Hypericum perforatum L.*	Hemicryptophyte	27.5 (21.25; 30)
Cyperaceae	*Carex acutiformis Ehrh.*	Hemicryptophyte	50 (35; 50)
	Carex binervis Smith	Caespitose hemicryptophyte	30 (30; 30)
	Carex brizoides L.	Hemicryptophyte	25 (25; 30)
	Carex canescens L.	Hemicryptophyte	20 (20; 25)
	Carex otrubae Podp.	Hemicryptophyte	30 (30; 30)
	Carex diandra Schrank	Hemicryptophyte	20 (20; 30)
	Carex distans L.	Hemicryptophyte	22.5 (20; 30)
	Carex divulsa Stokes	Caespitose hemicryptophyte	20 (20; 30)
	Carex elongata L.	Caespitose hemicryptophyte	30 (30; 30)
	Carex flacca Schreb.	Hemicryptophyte	20 (10; 20)
	Carex flava L.	Hemicryptophyte	20 (20; 30)
	Carex paniculata L.	Caespitose hemicryptophyte	40 (40; 50)
	Carex pendula Huds.	Caespitose hemicryptophyte	50 (50; 60)
	Carex pilosa Scop.	Hemicryptophyte	20 (20; 30)
	Carex pseudocyperus L.	Caespitose hemicryptophyte	40 (40; 50)
	Carex remota Jusl. ex L.	Caespitose hemicryptophyte	30 (22.5; 30)

	Carex spicata Huds.	Caespitose hemicryptophyte	20 (10; 30)
	Carex strigosa Huds.	Caespitose hemicryptophyte	35 (22.5; 50)
	Carex sylvatica Huds.	Caespitose hemicryptophyte	20 (12.5; 30)
	Carex vulpina L.	Caespitose hemicryptophyte	30 (30; 40)
Lamiaceae	*Calamintha nepeta (L.) Savi*	Hemicryptophyte	30 (27.5; 30)
	Clinopodium vulgare L.	Hemicryptophyte	25 (20; 30)
	Mentha longifolia L.	Hemicryptophyte	40 (30; 50)
	Mentha spicata L.	Hemicryptophyte	35 (27.5; 50)
	Mentha suaveolens Ehrh.	Hemicryptophyte	25 (16.25; 40)
	Origanum vulgare L.	Chamaephyte; Hemicryptophyte	25 (20; 40)
Linaceae	*Linum perenne L.*	Hemicryptophyte	25 (22.5; 30)
Papaveraceae	*Meconopsis cambrica (L.) Vig.*	Hemicryptophyte	30 (25; 40)
Poaceae	*Agrostis gigantea*	Hemicryptophyte	30 (30; 40)
	Arrhenatherum elatius L.	Hemicryptophyte	60 (50; 70)
	Brachypodium pinnatum (L.) Beauv.	Hemicryptophyte	40 (32.5; 60)
	Brachypodium sylvaticum (Huds.) Beauv.	Hemicryptophyte	50 (50; 60)
	Bromus erectus Huds.	Hemicryptophyte	30 (30; 30)
	Bromus inermis Leyss.	Hemicryptophyte	30 (30; 50)
	Bromus ramosus Huds.	Hemicryptophyte	70 (45; 100)
	Calamagrostis arundinacea (L.) Roth	Caespitose hemicryptophyte	60 (60; 60)
	Calamagrostis epigejos (L.) Roth	Hemicryptophyte	60 (45; 60)
	Calamagrostis varia (Schrad.) Host	Hemicryptophyte	40 (40; 50)
	Calamagrostis villosa (Chaix ex Vill.) J.F. Gmel.	Hemicryptophyte	60 (45; 60)
	Cynosurus cristatus L.	Hemicryptophyte	20 (20; 30)
	Dactylis glomerata L.	Hemicryptophyte	20 (20; 50)
	Deschampsia cespitosa (L.) Beauv.	Hemicryptophyte	30 (30; 50)
	Deschampsia flexuosa (L.) Trin.	Caespitose hemicryptophyte	25 (20; 30)
	Festuca arundinacea Schreb.	Hemicryptophyte	60 (40; 70)
	Festuca gigantea (L.) Vill.	Hemicryptophyte	55 (50; 60)
	Festuca heteropachys (St-Yves) Patzke ex Auquier	Caespitose hemicryptophyte	27.5 (23.75; 40)
	Festuca heterophylla Lam.	Caespitose hemicryptophyte	40 (40; 60)
	Festuca longifolia Thuill.	Caespitose hemicryptophyte	20 (20; 30)
	Festuca marginata (Hack.) K. Richt.	Caespitose hemicryptophyte	20 (18.75; 20)
	Festuca polesica Zapal.	Caespitose hemicryptophyte	20 (20; 20)
	Festuca pratensis Huds.	Hemicryptophyte	30 (30; 40)
	Festuca rubra L.	Geophyte with rhizomes	30 (20; 40)

	Koeleria pyramidata (Lam.) Beauv.	Hemicryptophyte	20 (20; 45)
	Melica ciliata L.	Hemicryptophyte	22.5 (20; 30)
	Melica nutans L.	Hemicryptophyte	30 (22.5; 30)
	Melica uniflora Retz.	Hemicryptophyte	25 (20; 30)
	Milium effusum L.	Hemicryptophyte	55 (50; 80)
	Phalaris arundinacea L.	Hemicryptophyte	50 (50; 80)
Rosaceae	*Filipendula ulmaria (L.) Maxim.*	Rosette hemicryptophyte	50 (50; 100)

5.2.Monospecific or multi-specific herbaceous hedges?

Biodiversity is generally corresponding to a more ecologically stable system, as a stable and healthy system would be less vulnerable to abiotic and biotic stress (Tilman 1999). Therefore, practitioners may ask if it is better to use only one or a few species that can efficiently decrease runoff, increase sediment retention or mitigate soil erosion, or if a diverse range of species, sometimes less efficient, should be used. Investigating this problem, Erktan et al. (2013) showed that a morphological diversity of plant species used in vegetation barriers on bioengineering structures did not increase sediment retention in eroded marly gully floors in the French Southern Alps. However, a positive effect of the diversity of functional groups in vegetation communities on interrill erosion mitigation was found for Swiss alpine sites (Martin et al. 2010). A positive effect of plant diversity was also found on soil erosion resistance (Berendse et al. 2015).

Taking into account these controversial results, it can be suggested using only few species with the best traits involved in decreasing runoff, increasing sediment retention or mitigating soil erosion in a same herbaceous hedge (Rey and Labonne 2015), but to favour as far as possible species diversity to: 1/ enable reducing the risks of failure of vegetation systems in case of loss of a species on a site due to abiotic/biotic factors, as stated by Doak et al. (1998), and 2/ provide other ecosystem services (e.g. habitat creation, ecological connectivity enhancement, integrated pest control).

5.3. Management of herbaceous hedges to conserve their efficiency for sediment retention and erosion control

Once the herbaceous hedges are designed and implanted, definition of their management is essential to conserve or improve their efficiency on hydraulic roughness, sediment retention and erosion control. To do so, it is necessary to conserve initial vegetation structure, which has the best community-weighted traits involved in hydraulic roughness, by slowing down vegetation succession and notably shrub and tree colonisation. Vegetation cutting is thus recommended in order to limit the development of tree and shrub species within the hedge. The presence of ligneous species would limit the development of the herbaceous species by competing for the light and would then lead to the degradation of the herbaceous vegetation and thus, limit the effects on hydraulic roughness and sediment retention. The hedge's cutting should be performed every two/three year at the end of spring (circa end of June) in order to (1) allow the plants to grow back before the highest erosion events in winter and (2) limit the damages on the local fauna using the herbaceous hedges for nesting. The first 10 cm should be let in place to keep a reserve for the plant in case erosive events happen before the plant growth. Perspective is to test these management practices regarding the durability of the herbaceous hedge and its efficiency towards sediment retention.

5.4. Fom field to hillslope: location design and modelling of herbaceous hedges using trait-based approach

Numerous soil and landscape processes can control runoff sources and pathways, which result in a spatially heterogeneous runoff erosion distribution. Sediment control is site specific and thus requires specific studies to target the efficiency of the herbaceous hedges (Tomer et al. 2008; Mekonnen et al. 2015). The first criteria when designing herbaceous hedges is setting the expected levels of impacts, regarding the rainfall properties and the reduction of suspended sediment. As functional traits effects can change regarding the flow characteristics (i.e. discharges), it is important to implement the desired hedge's efficiency range depending on the flow discharges into its design (Kervroëdan et al. 2018). For recurrent processes (from twice to once a year), the vegetation composing the hedge should comprise dense stems with large diameters, as well as large leaf areas. For more stronger processes occurring less regularly (from once every two to five years), vegetation with dense leaves and stems, important leaf specific areas and large stem diameters should be considered for the design of herbaceous hedges.

The following factors should also be taken into account for design and modelling purposes (Dosskey et al. 2015; Carluer et al. 2017): (1) the specific catchment area (i.e. upslope area contributing to runoff generation); (2) the soil characteristics (e.g. texture); (3) the slope gradient and topographical features (e.g. thalwegs); (4) the crops and (5) the observed runoff pathways. These factors can be implemented in a scoping tool to help local planners to set-up the herbaceous hedges at the most efficient location (Tomer et al. 2008; Dosskey et al. 2011, 2015; Carluer et al. 2017). These tools often rely on the field scale model VFSMOD (Muñoz Carpena and Parsons 2014).

Two main approaches can be used to find out relevant placements of herbaceous hedges (Dosskey et al. 2011). The first approach assesses the capability of vegetated areas to reduce runoff and sediment transport through infiltration and sediment retention processes. This means using soil and slopes properties to determine the infiltration capacity of the vegetated area which allows to calculate indexes such as the 'Sediment Trapping Efficiency' of the herbaceous hedge (Dosskey et al. 2011). The second approach performs terrain analysis through GIS use, especially on elevation dataset (Digital Elevation Model), to predict runoff spatial patterns. The elevation dataset is processed to create flow direction and flow accumulation. The resulting data enables to map the hydrological network used by the runoff and to delineate the watersheds or specific catchment areas of previously selected places such as field limits or human infrastructures.

Existing models focus on vegetative filter strips, based on their specific design, to evaluate the vegetation efficiency towards sediment retention. Perspective is to examine the effects of herbaceous hedges on sediment retention *in situ*, to validate the modelling of their efficiency and design.

Conclusions

Pivotal knowledge review of the plant trait effects on hydraulic roughness and sediment retention has allowed to improve the understanding of vegetation's role on runoff and sediment transfer and the design of herbaceous hedges for erosion control. The challenge of designing vegetation structures for soil erosion and runoff mitigation is to include plant traits involved in the increase of hydraulic roughness and sediment retention into the modelling of vegetation effects by using existing models for soil erosion control. Perspective is to unravel contrasting functional diversity effects on runoff and sediment retention by studying a wide functional diversity gradient on this ecosystem process. Comparison of functional diversity effects among several processes and services should also be examined to design multifunctional ecosystems and specifically manage major ecosystem services in each territory.

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REFERENCES

Akram S, Yu B, Ghadiri H, et al (2014) The links between water profile, net deposition and erosion in the design and performance of stiff grass hedges. J Hydrol 510:472–479. doi: 10.1016/j.jhydrol.2014.01.001

Berendse F, van Ruijven J, Jongejans E, Keesstra S (2015) Loss of plant species diversity reduces soil erosion resistance. Ecosystems 18:881–888. doi: 10.1007/s10021-015-9869-6

Boardman J, Poesen J (eds) (2006) Soil Erosion in Europe. John Wiley & Sons, Ltd

Bochet E, Poesen J, Rubio JL (2000) Mound development as an interaction of individual plants with soil, water erosion and sedimentation processes on slopes. Earth Surf Process Landf 25:847–867

Bugnon F (1995) Nouvelle flore de Bourgogne, tome II : clés de détermination, Edition hors-série. Bulletin scientifique de Bourgogne, Dijon, France

Burylo M, Rey F, Bochet E, Dutoit T (2012) Plant functional traits and species ability for sediment retention during concentrated flow erosion. Plant Soil 353:135–144. doi: 10.1007/s11104-011-1017-2

Cadotte MW (2017) Functional traits explain ecosystem function through opposing mechanisms. Ecol Lett 20:989–996. doi: 10.1111/ele.12796

Cantalice JRB, Melo RO, Silva YJAB, et al (2015) Hydraulic roughness due to submerged, emergent and flexible natural vegetation in a semiarid alluvial channel. J Arid Environ 114:1–7. doi: 10.1016/j.jaridenv.2014.10.012

Cao L, **Zhang Y, Lu H, et al (2015)** Grass hedge effects on controlling soil loss from concentrated flow: A case study in the red soil region of China. Soil Tillage Res 148:97–105. doi: 10.1016/j.still.2014.12.009

Cao S (2011) Impact of China's Large-Scale Ecological Restoration Program on the Environment and Society in Arid and Semiarid Areas of China: Achievements, Problems, Synthesis, and Applications. Crit Rev Environ Sci Technol 41:317–335. doi: 10.1080/10643380902800034

Cao S, Chen L, Yu X (2009) Impact of China's Grain for Green Project on the landscape of vulnerable arid and semi-arid agricultural regions: a case study in northern Shaanxi Province. J Appl Ecol 46:536–543. doi: 10.1111/j.1365-2664.2008.01605.x

Carluer N, Lauvernet C, Noll D, Munoz-Carpena R (2017) Defining context-specific scenarios to design vegetated buffer zones that limit pesticide transfer via surface runoff. Sci Total Environ 575:701–712. doi: 10.1016/j.scitotenv.2016.09.105

Clark EV, Zipper CE (2016) Vegetation influences near-surface hydrological characteristics on a surface coal mine in eastern USA. CATENA 139:241–249. doi: 10.1016/j.catena.2016.01.004

Dabney SM, Meyer LD, Harmon WC, et al (1995) Depositional patterns of sediment trapped by grass hedges. Trans ASAE 38:1719–1729

De Baets S, Poesen J, Gyssels G, Knapen A (2006) Effects of grass roots on the erodibility of topsoils during concentrated flow. Geomorphology 76:54–67. doi: 10.1016/j.geomorph.2005.10.002

De Baets S, Poesen J, Reubens B, et al (2009) Methodological framework to select plant species for controlling rill and gully erosion: application to a Mediterranean ecosystem. Earth Surf Process Landf 34:1374–1392. doi: 10.1002/esp.1826

Díaz S, Lavorel S, Chapin FS, et al (2007a) Functional Diversity — at the Crossroads between Ecosystem Functioning and Environmental Filters. In: Canadell JG, Pataki DE, Pitelka LF (eds) Terrestrial Ecosystems in a Changing World. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 81–91

Díaz S, Lavorel S, de Bello F, et al (2007b) Incorporating plant functional diversity effects in ecosystem service assessments. Proc Natl Acad Sci 104:20684–20689. doi: 10.1073/pnas.0704716104

Dillaha TA, Reneau RB, Mostaghimi S, Lee D (1989) Vegetative filter strips for agricultural nonpoint source pollution control. Trans ASAE 32:513–0519

Doak DF, Bigger D, Harding EK, et al (1998) The Statistical Inevitability of Stability-Diversity Relationships in Community Ecology. Am Nat 151:264–276. doi: 10.1086/286117

Dosskey MG, Neelakantan S, Mueller TG, et al (2015) AgBufferBuilder: A geographic information system (GIS) tool for precision design and performance assessment of filter strips. J Soil Water Conserv 70:209–217. doi: 10.2489/jswc.70.4.209

Dosskey MG, Qiu Z, Helmers MJ, Eisenhauer DE (2011) Improved indexes for targeting placement of buffers of Hortonian runoff. J Soil Water Conserv 66:362–372. doi: 10.2489/jswc.66.6.362

Dosskey MG, Vidon P, Gurwick NP, et al (2010) The role of riparian vegetation in protecting and improving chemical water quality in streams. J Am Water Resour Assoc 1–18. doi: 10.1111/j.1752-1688.2010.00419.x

Erktan A, Cécillon L, Roose E, et al (2013) Morphological diversity of plant barriers does not increase sediment retention in eroded marly gullies under ecological restoration. Plant Soil 370:653–669. doi: 10.1007/s11104-013-1738-5

Evrard O, Nord G, Cerdan O, et al (2010) Modelling the impact of land use change and rainfall seasonality on sediment export from an agricultural catchment of the northwestern European loess belt. Agric Ecosyst Environ 138:83–94. doi: 10.1016/j.agee.2010.04.003

Faucon M-P, Houben D, Lambers H (2017) Plant functional traits: soil and ecosystem services. Trends Plant Sci 22:385–394. doi: 10.1016/j.tplants.2017.01.005

Garnier E, Cortez J, Billès G, et al (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology 85:2630–2637. doi: 10.1890/03-0799

Garnier E, Navas M-L (2012) A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. Agron Sustain Dev 32:365–399

Garnier E, Navas M-L, Grigulis K (2016) Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties. Oxford University Press

Ghestem M, Sidle RC, Stokes A (2011) The Influence of Plant Root Systems on Subsurface Flow: Implications for Slope Stability. BioScience 61:869–879. doi: 10.1525/bio.2011.61.11.6

Gilley JE, Eghball B, Kramer LA, Moorman TB (2000) Narrow grass hedge effects on runoff and soil loss. J Soil Water Conserv 55:190–196

Gobin A, Govers G, Jones R, et al (2003) Assessment and reporting on soil erosion: Background and workshop report. European Environment Agency, Copenhagen

Govers G (1990) Empirical relationships for the transport capacity of overland flow. Int Assoc Hydrol Sci 189:45–63

Graff CD, Sadeghi AM, Lowrance RR, Williams RG (2005) Quantifying the sensitivity of the riparian ecosystem management model (REMM) to changes in climate and buffer characteristics common to conservation practices. Trans ASAE 48:1377–1387

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910. doi: 10.1046/j.1365-2745.1998.00306.x

Gyssels G, Poesen J, Bochet E, Li Y (2005) Impact of plant roots on the resistance of soils to erosion by water: A review. Prog Phys Geogr 29:189–217. doi: 10.1191/0309133305pp443ra

Haan CT, Barfield BJ, Hayes JC (1994) Design Hydrology and Sedimentology for Small Catchments. Academic Press

Hayes JC, Barfield BJ, Barnhisel RI (1984) Performance of grass filters under laboratory and field conditions. Trans ASAE 27:1321–1331

Hayes JC, Barfield BJ, Barnhisel RI (1978) Evaluation of grass characteristics related to sediment filtration. ASAE 78–2513:21

Hegi G (1906) Illustrierte Flora von Mitteleuropa. Band I - VI, 1st edn. Lehmanns Verlag München, Munich, Germany

Hussein J, Yu B, Ghadiri H, Rose C (2007) Prediction of surface flow hydrology and sediment retention upslope of a vetiver buffer strip. J Hydrol 338:261–272

Isselin-Nondedeu F, Bédécarrats A (2007) Influence of alpine plants growing on steep slopes on sediment trapping and transport by runoff. Catena 71:330–339. doi: 10.1016/j.catena.2007.02.001

Jauzein P, Nawrot O (2011) Flore d'Ile-de-France. QUAE, Versailles, France

Kervroëdan L, Armand R, Saunier M, et al (2018) Plant functional trait effects on runoff to design herbaceous hedges for soil erosion control. Ecol Eng 118:143–151. doi: 10.1016/j.ecoleng.2018.04.024

Lambinon J, Delvosalle L, Duvigneaud J (2012) Nouvelle flore de la Belgique, du G.-D. de Luxembourg, du nord de la France et des régions voisines, 6th edn.

Lambrechts T, François S, Lutts S, et al (2014) Impact of plant growth and morphology and of sediment concentration on sediment retention efficiency of vegetative filter strips: Flume experiments and VFSMOD modeling. J Hydrol 511:800–810. doi: 10.1016/j.jhydrol.2014.02.030

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Funct Ecol 16:545–556

Le Bissonnais Y, Lecomte V, Cerdan O (2004) Grass strip effects on runoff and soil loss. Agronomie 24:129–136

Li J, He B, Chen Y (2013) Root features of typical herb plants for hillslope protection and their effects on soil infiltration. Acta Ecol Sin 33:1535–1544. doi: 10.5846/stxb201205170737

Li Y, Xu XQ, Zhu XM, Tian JY (1992) Effectiveness of plant roots on increasing the soil permeability on the Loess Plateau. Chin Sci Bull 37:1735–1738

Liu Y-J, Hu J-M, Wang T-W, et al (2016) Effects of vegetation cover and road-concentrated flow on hillslope erosion in rainfall and scouring simulation tests in the Three Gorges Reservoir Area, China. CATENA 136:108–117. doi: 10.1016/j.catena.2015.06.006

Ludwig JA, Wilcox BP, Breshears DD, et al (2005) Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. Ecology 86:288–297. doi: 10.1890/03-0569

Mansion D, Dume G, Rameau JC (1989) Flore Forestière Française : Guide Ecologique Illustré. Institut pour le développement forestier, Paris

Mariotte P, Mehrabi Z, Bezemer TM, et al (2017) Plant–Soil Feedback: Bridging Natural and Agricultural Sciences. Trends Ecol Evol

Martin C, Pohl M, Alewell C, et al (2010) Interrill erosion at disturbed alpine sites: Effects of plant functional diversity and vegetation cover. Basic Appl Ecol 11:619–626. doi: 10.1016/j.baae.2010.04.006

Maun MA (1998) Adaptations of plants to burial in coastal sand dunes. 76:26

Mekonnen M, Keesstra SD, Ritsema CJ, et al (2016) Sediment trapping with indigenous grass species showing differences in plant traits in northwest Ethiopia. Catena 147:755–763. doi: 10.1016/j.catena.2016.08.036

Mekonnen M, Keesstra SD, Stroosnijder L, et al (2015) Soil Conservation Through

Sediment Trapping: A Review. Land Degrad Dev 26:544–556. doi: 10.1002/ldr.2308

Meyer LD, Dabney SM, Harmon WC (1995) Sediment-trapping effectiveness of stiff-grass hedges. Am Soc Agric Eng 38:809–815

Morgan RPC (2009) Soil Erosion and Conservation. John Wiley & Sons

Morgan RPC (2004) Vegetative-Based Technologies for Erosion Control. In: Stokes A, Spanos I, Norris JE, Cammeraat E (eds) Eco- and Ground Bio-Engineering: The Use of Vegetation to Improve Slope Stability. Springer, Dordrecht, The Netherlands, pp 265–272

Morgan RPC (2005) Soil Erosion and Conservation, 3rd ed. Blackwell Pub, Malden, MA

Morgan RPC, Duzant JH (2008) Modified MMF (Morgan–Morgan–Finney) model for evaluating effects of crops and vegetation cover on soil erosion. Earth Surf Process Landf 33:90–106. doi: 10.1002/esp.1530

Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional Structure of Biological Communities Predicts Ecosystem Multifunctionality. PLoS ONE 6:e17476. doi: 10.1371/journal.pone.0017476

Muñoz Carpena R, Parsons JE (2014) VFSMOD - Vegetative filter strips modelling system. University of Florida

Podwojewski P, Janeau JL, Grellier S, et al (2011) Influence of grass soil cover on water runoff and soil detachment under rainfall simulation in a sub-humid South African degraded rangeland. Earth Surf Process Landf 36:911–922. doi: 10.1002/esp.2121

Poesen J (2018) Soil erosion in the Anthropocene: Research needs. Earth Surf Process Landf 43:64–84. doi: 10.1002/esp.4250

Rey F, Labonne S (2015) Resprout and survival of willow (*Salix*) cuttings on bioengineering structures in actively eroding gullies in marls in a mountainous Mediterranean climate: A large-scale experiment in the Francon catchment (southern Alps, France). Environ Manage 56:971–983. doi: 10.1007/s00267-015-0542-9

Rothmaler W, Jäger EJ (2009) Rothmaler - Exkursionsflora von Deutschland. Bd. 3: Gefäßpflanzen: Atlasband, 11th edn. Sperktrum Akademischer Verlag, Berlin, Germany

Stokes A (ed) (2007) Eco- and ground bio-engineering: the use of vegetation to improve slope stability: proceedings of the First International Conference on Eco-Engineering, 13-17 September 2004. Springer, Dordrecht

Stokes A, Douglas GB, Fourcaud T, et al (2014) Ecological mitigation of hillslope instability: ten key issues facing researchers and practitioners. Plant Soil 377:1–23. doi: 10.1007/s11104-014-2044-6

Styczen ME, Morgan RPC (1995) Engineering properties of vegetation. In: Morgan RPC, Rickson RJ (eds) Slope Stabilization and Erosion Control: A Bioengineering Approach. E & FN SPON, London, pp 4–60

Temple DM (1982) Flow Retardance of Submerged Grass Channel Linings. Trans ASAE 25:1300–1303. doi: 10.13031/2013.33717

Temple DM, Robinson KM, Ahring RM, Davis AG (1987) Stability Design of Grass-Lined Open Channels. U.S. Department of Agriculture, Washington, D.C.

Tilman D (2001) Functional Diversity. In: Levin SA (ed) Encyclopedia of Biodiversity. Elsevier, New York, pp 109–120

Tilman D (1999) The ecological consequences of changes in biodiversity: A search for general principles. Ecology 80:1455–1474. doi: 10.1890/0012-9658(1999)080[1455:TECOCI]2.0.CO;2

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and Ecosystem Functioning. Annu Rev Ecol Evol Syst 45:471–493. doi: 10.1146/annurev-ecolsys-120213-091917

Tomer MD, Dosskey MG, Burkart MR, et al (2008) Methods to prioritize placement of riparian buffers for improved water quality. Agroforest Syst 10 P

Université de Bourgogne (UFR Science de la vie) (2018) Nouvelle Flore de Bourgogne - Tome II Clés de détermination. In: Flore Bourgogne. http://serres.u-bourgogne.fr/flore/rubrique.php3?id_rubrique=1. Accessed 26 Mar 2018

Vieira DAN, Dabney SM (2012) Two-dimensional flow patterns near contour grass hedges. Hydrol Process 26:2225–2234. doi: 10.1002/hyp.8262

Villarroel B (2015) Influence des traits morphologiques des végétaux herbacés sur l'érosion et le ruissellement des sols cultivés du nord-ouest de l'Europe. MSc Thesis, AgoParisTech

Violle C, Navas M-L, Vile D, et al (2007) Let the concept of trait be functional! Oikos 116:882–892. doi: 10.1111/j.2007.0030-1299.15559.x

Wu G-L, Liu Y, Yang Z, et al (2017) Root channels to indicate the increase in soil matrix water infiltration capacity of arid reclaimed mine soils. J Hydrol 546:133–139. doi: 10.1016/j.jhydrol.2016.12.047

Wu G-L, Yang Z, Cui Z, et al (2016) Mixed artificial grasslands with more roots improved mine soil infiltration capacity. J Hydrol 535:54–60. doi: 10.1016/j.jhydrol.2016.01.059

Yuan Y, Bingner RL, Locke MA (2009) A Review of effectiveness of vegetative buffers on sediment trapping in agricultural areas. Ecohydrology 2:321–336. doi: 10.1002/eco.82

Zhu H, Fu B, Wang S, et al (2015) Reducing soil erosion by improving community functional diversity in semi-arid grasslands. J Appl Ecol 52:1063–1072. doi: 10.1111/1365-2664.12442

Zuo X, Zhang J, Lv P, et al (2016) Plant functional diversity mediates the effects of vegetation and soil properties on community-level plant nitrogen use in the restoration of semiarid sandy grassland. Ecol Indic 64:272–280. doi: 10.1016/j.ecolind.2016.01.012

RESUME ETENDU

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Effets des traits et de la diversité fonctionnelle des plantes sur le ruissellement et la rétention des sédiments

Application pour le contrôle de l'érosion des sols dans les bassins versants agricoles tempérés

Léa KERVROËDAN

Directeur de thèse :

Dr. Michel-Pierre FAUCON (AGHYLE, UniLaSalle)

Co-directeur de thèse :

Dr. Romain ARMAND (AGHYLE, UniLaSalle)

Introduction

Rôles de l'écologie fonctionnelle dans les processus écosystémiques sol-plantes

L'écologie fonctionnelle végétale se focalise sur la compréhension des processus écosystémiques et des dynamiques des communautés face à des facteurs environnementaux afin de caractériser les relations entre plantes et processus écosystémiques. Les processus écosystémiques sont influencés par les caractéristiques des plantes, appelées « traits fonctionnels[1] », plutôt que par les espèces présentes dans la communauté ou leurs nombres. L'approche par les traits fonctionnels permet de prédire la réponse adaptative des communautés aux variations environnementales (notamment des conditions édaphiques) et aux effets des changements environnementaux sur l'écosystème. Les relations entre traits fonctionnels et propriétés du sol sont donc des outils majeurs pour caractériser les effets des communautés végétales sur les processus écosystémiques. Toutefois, la caractérisation des effets de la diversité fonctionnelle[2] sur ces processus permet la compréhension de la complexité de ces communautés et de leurs effets. La diversité fonctionnelle caractérise la variation du degré de fonctions à différents niveaux spatiaux et temporels de l'organisation de l'organisme au système. La structure des communautés végétales et leurs effets sur les processus écosystémiques suivent deux hypothèses non-exclusives : (1) les propriétés écosystémiques dépendent des traits de une ou des espèces dominante(s) dans la communauté et sont représentées par les moyennes des traits pondérées à la communauté (hypothèse de dominance) ; et (2) les propriétés écosystémiques sont influencées par la diversité de traits qui composent la communauté, amenant à une complémentarité dans l'utilisation des ressources, et sont représentées par des indices de diversité fonctionnelle. Un grand nombre de processus sol-plante ont été étudiés afin de comprendre les effets des traits fonctionnels et de la diversité fonctionnelle et des résultats discordants ont été trouvés. Cependant, les effets des traits et de la diversité fonctionnelle sur les propriétés physiques du sol liées au processus d'érosion des sols, processus majeur de dégradation des sols, ont été peu étudiés ; malgré le rôle clé des communautés végétales dans le contrôle du ruissellement et de l'érosion.

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[1] « Caractéristique morphologique, phénologique ou physiologique mesurable à l'échelle de l'individu (de la cellule à l'organisme entier) sans référence à l'environnement ou tout autre niveau d'organisation » (Violle et al. 2007).

[2] « la valeur, la gamme et l'abondance relative des traits fonctionnels dans un écosystème donné » (Díaz et al. 2007a).

Effets des traits fonctionnels sur l'érosion des sols par le ruissellement

L'érosion des sols, fréquemment observée dans les zones tropicales, méditerranéennes et tempérées, est le processus principal menant à la dégradation les sols. Elle est accentuée par des facteurs anthropiques, en particulier les pratiques agricoles. La dégradation des sols par l'érosion hydrique entraîne des effets à long terme sur la fertilité et la productivité des sols, mais aussi des dommages environnementaux plus importants (par le ruissellement et le transport des sédiments). L'érosion hydrique est composée de deux étapes : (1) le détachement des particules de sol et (2) le transport des sédiments ; toutes deux influencées par les traits fonctionnels des plantes. Suivant la forme des écoulements de ruissellement et de leur concentration en sédiments, trois principaux types d'érosion sont identifiés : (1) l'érosion diffuse ; (2) l'érosion concentrée ; et (3) l'érosion torrentielle. Les taux d'érosion sont influencés par la combinaison d'un certain nombre de paramètres : (1) les états de surface du sol ; (2) la topographie ; (3) la couverture végétale et l'utilisation des sols ; et (4) le climat. La présence de végétation, par effets des traits aériens et souterrains des plantes, offre une protection contre les mécanismes impliqués dans la partition infiltration/ruissellement (pré-génération du ruissellement) et dans les processus d'érosion diffuse et concentrée. En effet, les traits fonctionnels dans les communautés herbacées vont induire : (1) l'interception des gouttes de pluie ; (2) l'infiltration des eaux de ruissellement ; (3) une résistance mécanique plus élevée et la stabilisation du sol face aux forces d'arrachement du ruissellement ; et (4) une résistance hydraulique contre l'énergie des écoulements.

La nécessité de développer l'ingénierie écologique basée sur les traits fonctionnels de communautés herbacées pour lutter contre l'érosion des sols

L'utilisation de mesures basées sur les traits fonctionnels de végétations herbacées, en suivant le principe de l'ingénierie écologique[3], constitue une solution pour réduire l'érosion diffuse et concentrée au sein des bassins versants agricoles. Il est établi que l'implantation de zones tampons et/ou de barrières végétales dans le thalweg réduit efficacement l'érosion du sol. Parmi les objets utilisés pour contrôler le ruissellement et l'érosion des sols, deux types sont mis en évidence : (1) ceux composés principalement de matières mortes (*i.e.,* fascines) et (2) ceux composés de matières vivantes comportant un certain nombre de traits limitant le ruissellement et l'érosion (*i.e.,* bandes enherbées, haies herbacées). Parmi ces objets, la forte efficacité des

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[3] « La conception d'écosystèmes durables intégrant la société humaine à son environnement naturel dans l'intérêt des deux » (Mitsch and Jørgensen 2003).

haies herbacées a été reconnue pour des épisodes de ruissellement et d'érosion diffus et concentrés. Afin de créer des haies herbacées efficaces pour réduire le ruissellement et l'érosion des sols, une bonne compréhension de la relation entre les traits fonctionnels et la rugosité hydraulique[4], processus principal de réduction à l'échelle de la végétation, est nécessaire. La plupart des études sur les impacts de la végétation sur l'érosion des sols se sont concentrées sur les impacts des traits fonctionnels aériens sur la rétention des sédiments. La rugosité hydraulique étant le principal processus induisant la rétention des sédiments, les traits fonctionnels impactant la rétention des sédiments devraient avoir une influence directe sur la rugosité hydraulique. Cependant, la relation entre traits fonctionnels et rugosité hydraulique a besoin d'être clairement identifiée. Ainsi, parmi les traits influençant la rétention des sédiments, certains sont trouvés négativement associés, sous-entendant que l'utilisation d'une combinaison de traits contrastés et efficaces aurait un meilleur effet sur la rugosité hydraulique et la rétention des sédiments. Seules deux études ont étudié les effets de la diversité fonctionnelle sur l'érosion des sols et ont trouvé des résultats contradictoires ; ce qui souligne le besoin d'identifier les effets de la diversité fonctionnelle sur les processus de ruissellement et d'érosion pour comprendre comment les communautés végétales affectent ces processus.

Objectifs

Ce travail de thèse vise à approfondir les connaissances concernant les effets des traits fonctionnels des plantes sur les processus de ruissellement concentré et de rétention des sédiments, ainsi qu'à comprendre les effets de la diversité fonctionnelle sur ces processus afin de concevoir des haies herbacées pour réduire les impacts de l'érosion dans les bassins versants européens limoneux. Cette thèse est composée de trois chapitres correspondant aux objectifs principaux de l'étude. Dans un premier temps, le Chapitre 1 a pour objectifs (1) d'identifier les traits influençant la rugosité hydraulique des ruissellements concentrés caractéristiques des bassins versants agricoles du nord-ouest de l'Europe ; et (2) d'étudier les effets de ces écoulements concentrés sur la relation entre les traits et la rugosité hydraulique, par l'utilisation de plusieurs débits. Le Chapitre 2 vise à comprendre si l'effet de complémentarité de traits contrastés dans une communauté végétale entraîne une meilleure efficacité sur l'augmentation de la rugosité hydraulique et la rétention des sédiments grâce à une meilleure utilisation des ressources et de l'espace. Enfin, le Chapitre 3 a pour objectif d'améliorer la compréhension des

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[4] Résistance au frottement due au contact du ruissellement avec la végétation.

effets de la diversité fonctionnelle sur la rugosité hydraulique et de déterminer si ces effets sont induits par une dominance ou un effet additif des caractères dans la communauté.

Approche méthodologique

Les réponses des traits aux processus de ruissellement et d'érosion des sols dépendent du contexte et des processus intervenant dans le territoire phytogéographique d'étude, ce qui montre la nécessité de sélectionner une aire phytogéographique. La présente étude est focalisée sur les processus observés dans la ceinture limoneuse européenne, où l'érosion des sols induit une dégradation des sols majeure depuis, notamment, le remembrement des parcelles agricoles et la disparition des objets linéaires dans les bassins versants (haies arbustives et arborescentes, chemins enherbés, *etc.*).

Sélection des espèces candidates basée sur les types fonctionnels

La sélection des espèces potentiellement candidates pour concevoir une végétation efficace afin d'augmenter la rugosité hydraulique et la rétention des sédiments a nécessité l'identification des types fonctionnels influents et de critères sélectifs : catégories de forme de vie, la persistance de la biomasse pendant l'hiver, le recouvrement du sol, la résistance à l'enfouissement, la hauteur végétative minimale ; ainsi que l'amplitude écologique et le non-envahissement des parcelles sont pris en compte. Considérant le nord-ouest de l'Europe comme zone d'étude phytogéographique, les critères de sélection ont été appliqués aux 3 500 espèces indigènes de spermaphytes dont ce territoire est composé, en prenant en compte les débits moyens retrouvés dans ce territoire, et 76 espèces potentiellement candidates ont été mises en évidence.

Caractérisation de la rugosité hydraulique des végétations herbacées

La rugosité hydraulique est le processus principal favorisant la réduction de la vitesse de ruissellement et la rétention des sédiments dans les patchs de végétation herbacée. Dans les expérimentations faites tout au long de ce travail de thèse, l'écoulement concentré a été recréé à l'aide d'un simulateur de ruissellement (Figure 1), qui a permis de mesurer les hauteurs d'eau devant les végétations testées. Le simulateur comprend trois parties principales : deux canaux Venturi avec des sondes de débit placées aux deux extrémités du canal principal. Pour les expérimentations dans les chapitres 1 et 3, le canal principal mesurait 4 m de long sur 0,60 m de large et les placettes de végétation, 0,30 m de long sur 0,60 m de large ; alors que canal principal des expérimentations du chapitre 2 mesurait 4 m de long sur 0,90 m de large, avec des placettes de végétations de 1 m de long sur 0,90 m de large. Tout le système était entièrement imperméabilisé afin d'éviter toute perte d'eau par infiltration. Les hauteurs d'eau étaient mesurées grâce à des entretoises placées tout le long du canal principal. Ces hauteurs d'eau ont permis la caractérisation de la rugosité hydraulique associée à chaque placette de végétation. L'indice utilisé dans ce travail de thèse était le « *unit stream power*[5] », produit de la pente et de la vitesse moyenne de l'écoulement.

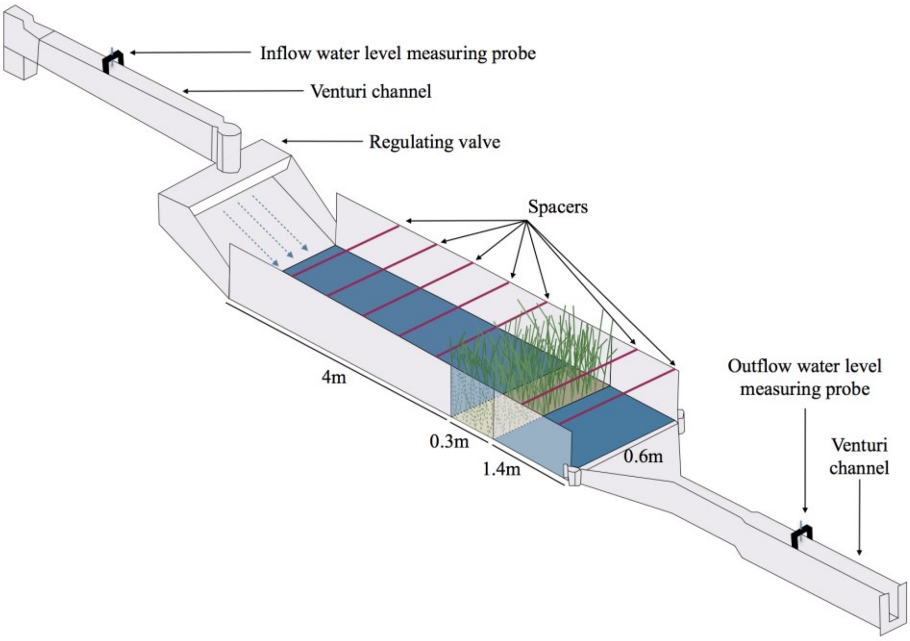

Figure 1. Simulateur de ruissellement

Chapitre 1 : Effets des traits fonctionnels sur le ruissellement pour concevoir des haies herbacées contrôlant l'érosion des sols

Dans la ceinture limoneuse européenne, la végétation contrôle le ruissellement et l'érosion concentrés en augmentant la rugosité hydraulique et la rétention des sédiments. Afin de comprendre les mécanismes de contrôle du ruissellement et de l'érosion par les plantes sur la vitesse des écoulements de ruissellement, les études sont généralement basées sur une caractérisation taxonomique et ne tiennent pas compte des effets des traits fonctionnels. Cette

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[5] « Dissipation d'énergie par unité de temps et par unité de poids de l'écoulement » (Govers 1992).

étude s'intéresse aux effets des traits fonctionnels aériens des plantes composant des haies herbacées sur la rugosité hydraulique. Huit traits fonctionnels aériens (densité de feuilles, surface foliaire, surface foliaire spécifique, densité de tiges, surface projetée des tiges, diamètre des tiges, rigidité des tiges et taux de matière sèche des tiges) ont été mesurés sur quatorze espèces de plantes vivaces indigènes (cespiteuse ou comprenant de la biomasse sèche en hiver) du nord-ouest de l'Europe présentant une grande variabilité morphologique. Pour chaque trait, une pondération a été effectuée en utilisant les densités de tiges ou de feuilles. Les effets des traits fonctionnels et des traits pondérés ont été examinés à l'aide d'un simulateur de ruissellement, pour quatre débits (2 ; 4 ; 8 et 11 $L.s^{-1}.m^{-1}$). La densité et la surface de feuilles, ainsi que la surface pondérée des tiges, la surface pondérée des feuilles, le diamètre pondéré des tiges et la surface spécifique pondérée des feuilles étaient corrélés positivement avec la rugosité hydraulique (Figure 2). Les modèles linéaires généralisés ont défini les meilleures combinaisons de traits simples et de traits pondérés : (1) la densité foliaire et la surface foliaire ; (2) la surface foliaire pondérée et la surface pondérée des tiges ; et (3) la surface foliaire pondérée et le diamètre pondéré des tiges. De plus, les effets de la densité de feuilles, de la surface foliaire et de la surface foliaire spécifique pondérée variaient en fonction du débit. Cette étude est l'une des premières caractérisations des effets des traits aériens sur la rugosité hydraulique et souligne qu'une végétation ayant une densité, un diamètre et une surface foliaire importants joue un rôle conséquent dans la réduction de l'érosion des sols. La sélection des espèces végétales peut dériver de ces effets des traits pour concevoir des haies herbacées afin de minimiser l'érosion des sols.

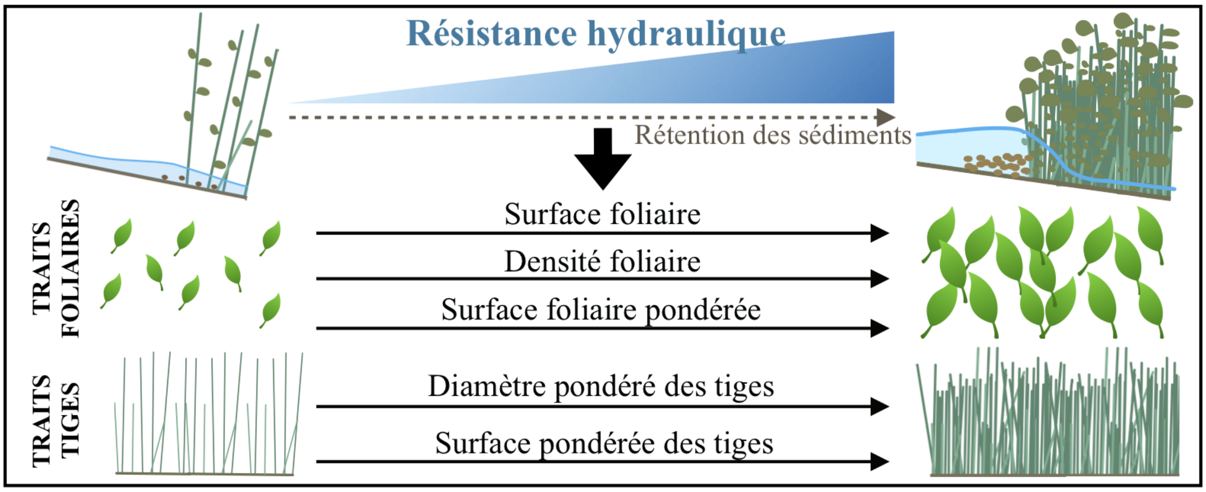

Figure 2. Récapitulatif des résultats obtenus sur la caractérisation des effets des traits aériens sur la rugosité hydraulique.

Chapitre 2 : Effets de la diversité en espèces de végétations herbacées sur le ruissellement et la rétention des sédiments

La diversité des espèces végétales a un impact sur les processus écosystémiques intégrant les interactions sol-plantes. Cependant, les effets de la diversité sur les processus associés au ruissellement et à l'érosion des sols ne sont pas complètement compris. Les végétations herbacées contrôlent le ruissellement et l'érosion concentrés dans le Nord-Ouest de l'Europe par l'augmentation de la rugosité hydraulique, qui entraîne la rétention des sédiments en diminuant la vitesse des écoulements. La rugosité hydraulique est influencée par la biomasse aérienne végétale, ainsi que les traits fonctionnels aériens (i.e., diamètre des tiges, densité de tiges, surface et densité foliaires). L'hypothèse était que la complémentarité des traits conduirait à une utilisation plus optimale de l'espace, favorisant la productivité de la biomasse aérienne et présentant donc une rugosité hydraulique et une rétention des sédiments plus importantes. Des simulations de ruissellement ont été effectuées en apportant des sédiments au flux, sur trois communautés mono-spécifiques et une multi-spécifique composées d'espèces indigènes du Nord-Ouest de l'Europe avec des traits contrastés favorisant la rugosité hydraulique et la rétention des sédiments. Les résultats ont mis en évidence des effets de non-complémentarité sur la rugosité hydraulique et la rétention des sédiments (Figure 3). Cette non-complémentarité était générée par des effets dominants de la densité de feuilles et de la surface foliaire pondérée dans les communautés multi-spécifiques. Cette absence d'effets de complémentarité sur la rugosité hydraulique et la rétention des sédiments s'expliquerait par la non-augmentation de la productivité de biomasse aérienne avec la diversité en espèces. Cette absence d'effets de complémentarité sur la rugosité hydraulique et la rétention des sédiments constitue une nouvelle avancée dans la caractérisation des effets de la diversité sur les processus de ruissellement et d'érosion des sols sous les climats tempérés.

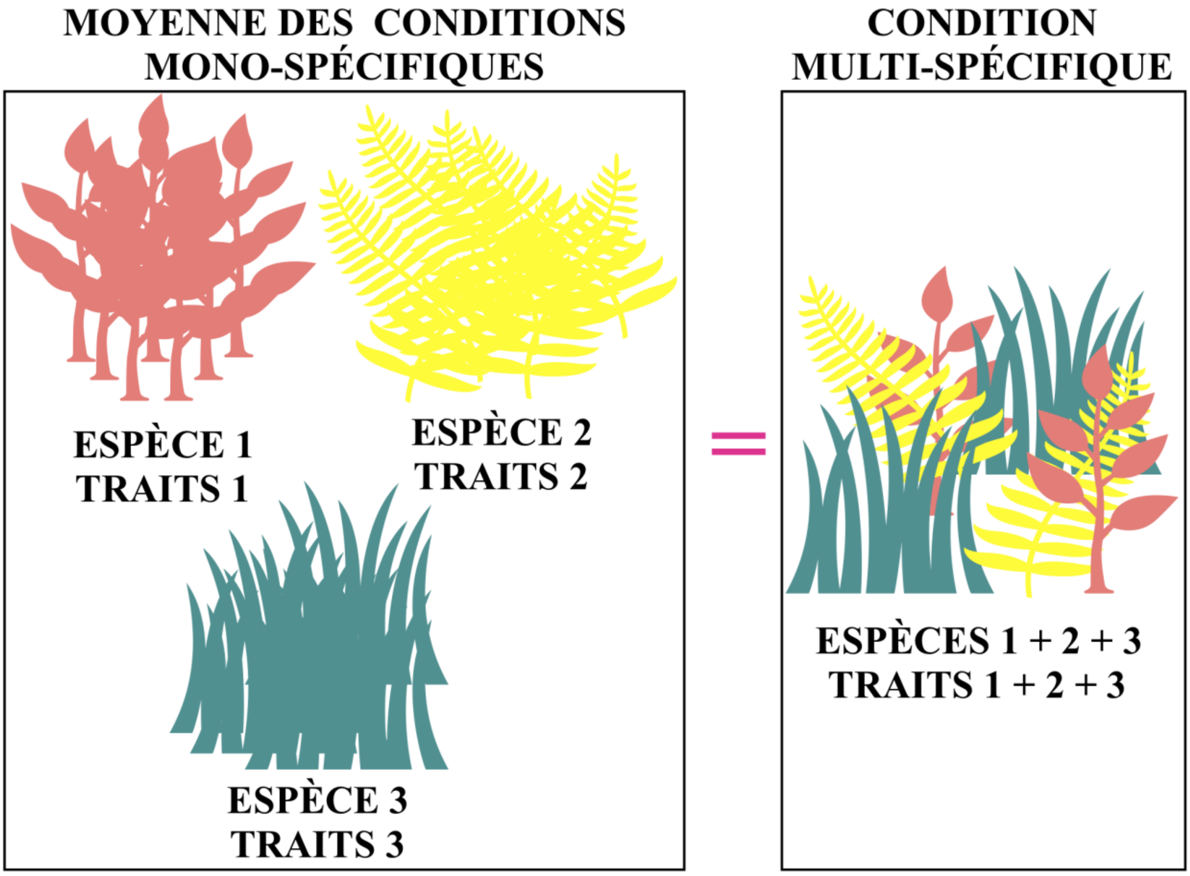

Figure 3. Récapitulatif des résultats obtenus sur le*s* effets de la diversité en espèces sur la rugosité hydraulique et la rétention des sédiments

Chapitre 3 : Effets de la diversité fonctionnelle sur le ruissellement en vue de concevoir des haies herbacées efficaces dans la rétention de sédiments

Les effets de la diversité fonctionnelle sur les processus écosystémiques tels que le ruissellement et l'érosion des sols, principaux processus de dégradation des sols, ne sont pas encore totalement compris. Les végétations avec une forte densité de tige et de larges diamètres de tiges (tous deux corrélés négativement), ainsi que d'importantes surfaces foliaires et densités de feuilles (toutes deux corrélées négativement), ont un impact sur la rugosité hydraulique. L'hypothèse était qu'une communauté végétale présentant une structure fonctionnelle composée de ces traits corrélés négativement, montrerait des effets positifs de la diversité fonctionnelle sur la rugosité hydraulique et la rétention des sédiments. Des simulations de ruissellement ont été effectuées sur quatre communautés mono-spécifiques et deux communautés multi-spécifiques composées d'espèces végétales indigènes au Nord-Ouest de l'Europe, présentant six traits fonctionnels aériens contrastés impliqués dans l'augmentation de la rugosité hydraulique. Les résultats ont montré les effets de traits dominants dans les communautés multi-spécifiques sur la rugosité hydraulique, identifiés comme étant la densité foliaire pondérée à la communauté (Figure 4). L'effet non-additif de la diversité fonctionnelle sur la rugosité hydraulique pourrait s'expliquer par l'absence d'augmentation de productivité de biomasse aérienne dans les communautés végétales présentant une diversité fonctionnelle importante. Il est soutenu que les effets de la diversité fonctionnelle sur la rugosité hydraulique et la productivité de biomasse pourraient changer en raison d'effets idiosyncratiques des traits. Ces effets non-additifs de la diversité fonctionnelle sur la rugosité hydraulique constituent une nouvelle avancée dans la compréhension des effets de l'assemblage des traits végétaux sur les processus de ruissellement et d'érosion des sols.

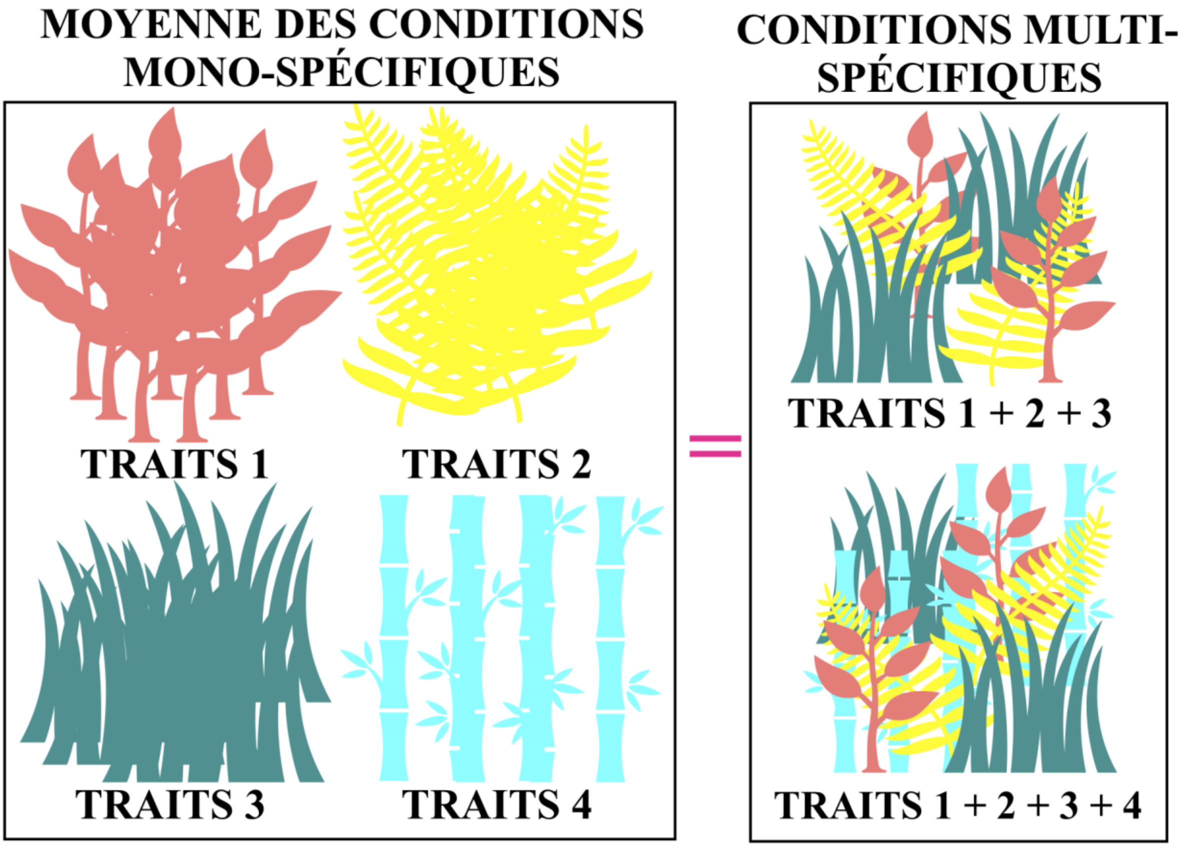

Figure 4. Récapitulatif des résultats obtenus sur les effets de la diversité fonctionnelle sur la rugosité hydraulique

Discussion générale et perspectives

Variations des effets des traits fonctionnels sur la rugosité hydraulique et la rétention des sédiments

L'analyse des effets des traits fonctionnels contrastés de 14 espèces a permis de constituer une base de référence pour l'identification des traits liés à une forte rugosité hydraulique. Focaliser l'analyse sur la rugosité hydraulique plutôt que sur le détachement du sol ou la rétention des sédiments, comme la plupart des études l'ont fait, a permis de caractériser les effets des traits sur la composante hydraulique de l'érosion des sols. Des huit traits originellement mesurés, seulement deux ont montré un impact sur la rugosité hydraulique : la surface foliaire et la densité de feuilles. Contrairement à la littérature, la densité de tiges n'a pas montré d'effet direct sur la rugosité hydraulique, sûrement dû à la présence d'espèces dicotylédones, mais un effet indirect. En effet, le principal apport de cette étude a été la caractérisation de traits pondérés (à la densité de feuilles ou de tiges) et de déterminer leurs effets sur la rugosité hydraulique. De plus, les combinaisons de traits et traits pondérés les plus efficaces pour augmenter la rugosité hydraulique ont été identifiées : (1) la surface foliaire avec la densité de feuilles ; (2) la surface foliaire pondérée avec le diamètre pondéré des tiges ; et (3) la surface foliaire pondérée avec la surface pondérée des tiges. La compréhension et la caractérisation des effets des traits sur la rugosité hydraulique et la rétention des sédiments peuvent être appliquées dans (1) la sélection des espèces herbacées candidates liées à un territoire phytogéographique spécifique ; et (2) les modèles d'érosion existants évaluant les effets de la végétation sur le ruissellement et l'érosion des sols.

- Prise en compte des effets des traits dans la sélection d'espèces potentiellement candidates

La première implication de la caractérisation des effets des traits sur la rugosité hydraulique est la sélection des espèces candidates qui seraient efficaces pour la zone phyto-géographique de l'implantation. Comme les effets des traits fonctionnels peuvent changer en ce qui concerne les caractéristiques d'écoulement (i.e. débits), il est important d'intégrer la gamme d'efficacité du trait souhaité en fonction des débits d'écoulement dans la sélection. Les résultats obtenus dans cette étude permettent de comprendre les différentes réponses des traits en fonction du débit et correspondent ainsi à une première étape de la caractérisation des relations entre traits et débits sous des climats tempérés. Conformément à l'approche des types fonctionnels pour les filtres sélectifs appliqués aux espèces spermaphytes indigènes du Nord-Ouest de l'Europe, 76 espèces potentiellement candidates ont été mises en évidence. La valeur seuil à partir de laquelle il y a un effet significatif sur la rugosité hydraulique a été déterminée, pour chaque trait et trait pondéré, en utilisant la valeur critique du *« unit stream power »* de 0,004 m.s^{-1}. Ces valeurs seuil des traits et traits pondérés ont été appliquées pour identifier les espèces les plus efficaces dans l'augmentation de la rugosité hydraulique pour la zone phytogéographique du Nord-Ouest de l'Europe.

- **Prise en compte des effets des traits dans la modélisation des effets de la végétation sur le ruissellement et l'érosion des sols**

La deuxième implication de l'identification des traits impliqués dans la rugosité hydraulique et la rétention des sédiments est leur intégration dans la modélisation des effets de la végétation sur le ruissellement et l'érosion des sols. Cette intégration des effets des traits permet (1) de comprendre les effets de la végétation sur la rugosité hydraulique et la rétention des sédiments de l'échelle locale vers celle du paysage ; et (2) d'évaluer ces effets par rapport aux autres composantes affectant le ruissellement et l'érosion des sols. La comparaison des résultats obtenus dans le chapitre 2 a été faite avec ceux obtenus par le modèle VFS-MOD, largement utilisé et choisi pour son efficacité reconnue dans l'évaluation des effets de la végétation sur les processus de ruissellement et d'érosion. L'analyse comparative a montré une faible précision du modèle. Cette imprécision était liée à la combinaison de paramètres hydrauliques et liés à la végétation, du fait que le modèle est conçu pour recréer des écoulements superficiels et ne tient pas compte des événements concentrés sur de petites zones de ruissellement et de végétation. Caractériser les écoulements concentrés dans le modèle, au travers de dimensions applicables de la zone de ruissellement et de la largeur de la végétation, pourrait élargir ses possibilités d'utilisation. L'intégration des traits et traits pondérés de la végétation donnerait une description plus précise de la communauté végétale et de ses effets sur la rugosité hydraulique.

Effets de la diversité fonctionnelle et spécifique sur la rugosité hydraulique et la rétention des sédiments

La diversité en espèces végétales et la diversité fonctionnelle affectent la rugosité hydraulique et la rétention des sédiments, même si les résultats n'ont pas validé les hypothèses de recherche. À la différence de l'effet de complémentarité des traits attendu sur la rugosité hydraulique et la rétention des sédiments, un effet dominant des traits a été trouvé ainsi que des effets non-additifs de la diversité fonctionnelle, en utilisant un gradient de structures fonctionnelles. Dans l'ensemble, les effets dominants étaient générés par les traits de feuilles dans les deux expériences : densité de feuilles, surface foliaire pondérée (chapitre 2) et densité de feuilles (chapitre 3). L'absence d'impact du gradient de ruissellement (débits utilisés variant de 2 à 11 $L.s^{-1}.m^{-1}$) sur les effets de la diversité fonctionnelle suggère que les effets non-additifs doivent être liés aux traits et à la productivité de biomasse des communautés testées. Les résultats ont souligné l'effet dominant d'espèces graminées (présentant une forte densité de longues feuilles) dans une communauté multi-spécifique, également mis en évidence dans la littérature, et un effet limitant des espèces dicotylédones présentant une faible densité foliaire à l'échelle de la végétation. L'absence d'effet de la diversité fonctionnelle sur la productivité de biomasse aérienne suggère également que l'utilisation de l'espace par les communautés testées était non-optimale, ce qui aurait pu entraîner les effets non-additifs de la diversité fonctionnelle sur la rugosité hydraulique et la rétention des sédiments. Poursuivre la présente étude en intégrant un gradient de combinaisons de traits plus large et une variation de l'abondance des traits dans la communauté approfondirait les connaissances sur les effets de la diversité fonctionnelle de la végétation herbacée sur les processus de contrôle du ruissellement et de l'érosion des sols.

Apports de l'approche des traits fonctionnels dans la conception de haies herbacées

- Du site au paysage : détermination de l'emplacement des haies herbacées par l'approche des traits

L'implantation de haies herbacées dans les bassins versants agricoles, perpendiculairement à l'écoulement, réduit l'érosion diffuse et concentrée. De nombreux processus liés au sol et au paysage peuvent contrôler les sources et les voies de ruissellement, ce qui se traduit par une répartition hétérogène de l'érosion par le ruissellement dans le paysage. Les principales composantes dans la conception des haies herbacées sont la détermination des niveaux d'impact attendus concernant la fréquence de l'épisode pluvieux et la réduction des sédiments en suspension dans les flux de ruissellement. Après avoir sélectionné les espèces composant les haies herbacées, la conception et la localisation de celles-ci doivent prendre en compte : (1) la surface spécifique du bassin versant ; (2) les caractéristiques du sol ; (3) les pentes et les caractéristiques topographiques ; (4) les cultures ; et (5) les voies de ruissellement observées. La localisation des haies herbacées peut également être déterminée par une analyse de terrain avec un outil de SIG afin de prédire les configurations spatiales des écoulements.

- Haies herbacées mono-spécifiques ou multi-spécifiques ?

La plupart des études faites sur les haies herbacées se sont focalisées sur des haies mono-spécifiques et n'ont pas étudié les effets de haies herbacées multi-spécifiques. La biodiversité correspond généralement à un système plus stable sur le plan écologique, ce qui le rendrait moins vulnérable aux stress abiotiques et biotiques. Les effets de la diversité fonctionnelle au sein des haies herbacées sont controversés, mais ne montrent pas d'interactions négatives avec l'efficacité des haies sur la réduction de l'érosion. Favoriser la diversité en espèces et la diversité fonctionnelle dans les haies herbacées pourrait permettre de (1) réduire les risques de défaillance de ces systèmes végétaux en cas de perte d'une espèce en raison de facteurs abiotiques ou biotiques, et (2) fournir d'autres services écosystémiques, tels que la création d'habitats à l'échelle locale et la restauration de réseaux écologiques à l'échelle du paysage.

Expliquer les effets contrastés de la diversité fonctionnelle sur les processus sol-plantes : perspective de méta-analyse

Bien que des résultats contrastés sur les effets de la diversité fonctionnelle aient été trouvés pour un certain nombre de processus sol-plantes, aucune analyse n'a été faite pour expliquer les facteurs qui ont conduit à ces résultats controversés. Une perspective intéressante serait d'effectuer une méta-analyse centrée sur les effets contrastés de la diversité fonctionnelle sur les processus plante-sol et comment ils peuvent être expliqués. Les effets de la diversité fonctionnelle sur les processus écosystémiques peuvent être influencés par des effets idiosyncratiques[6] des traits, tels que les interactions espèces-traits et sol-plantes et pourraient être liés à l'abondance de traits particuliers dans la communauté. Cette méta-analyse permettrait de cerner les effets discordants de la diversité fonctionnelle sur les processus sol-plante et de mettre en évidence les facteurs écologiques potentiels expliquant les effets idiosyncratiques des traits influençant les effets de la diversité fonctionnelle. Il est supposé que (1) la combinaison des traits dans la communauté joue un rôle majeur sur les effets de la diversité fonctionnelle sur les processus écosystémiques ; et que (2) la compréhension des différents paramètres influençant la diversité fonctionnelle permettrait de prédire les effets de la diversité fonctionnelle sur les principaux processus écosystémiques.

REFERENCES

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[6] Effets discordants de la diversité fonctionnelle, influencés par des facteurs abiotiques et biotiques.

Díaz S, Lavorel S, Chapin FS, et al (2007) Functional Diversity — at the Crossroads between Ecosystem Functioning and Environmental Filters. In: Canadell JG, Pataki DE, Pitelka LF (eds) Terrestrial Ecosystems in a Changing World. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 81–91

Govers G (1992) Relationship between discharge, velocity and flow area for rills eroding loose, non-layered materials. Earth surface processes and landforms 17:515–528

Loreau M (2000) Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91:3–17. doi: 10.1034/j.1600-0706.2000.910101.x

Mitsch WJ, Jørgensen SE (2003) Ecological engineering: A field whose time has come. Ecological Engineering 20:363–377. doi: 10.1016/j.ecoleng.2003.05.001

Violle C, Navas M-L, Vile D, et al (2007) Let the concept of trait be functional! Oikos 116:882–892. doi: 10.1111/j.2007.0030-1299.15559.x

PLANT TRAITS AND FUNCTIONAL DIVERSITY EFFECTS ON RUNOFF AND SEDIMENT RETENTION

Application to soil erosion control in temperate agricultural catchments

Plant-soil processes are driven and influenced by plant functional traits in vegetation communities. Concentrated runoff and erosion constitute the main cause of soil degradation and can be managed by herbaceous vegetation creating hydraulic roughness that induces flow velocity reduction and sediment retention. Using plant trait-based approach, unlike taxonomical approach, allows to understand and characterise the direct effects of the vegetation on runoff and sediment retention. This research project aims to deepen the knowledge regarding the effects of (i) plant functional traits (chapter 1), (ii) traits' complementarity (chapter 2) and (iii) functional diversity (chapter 3) on concentrated runoff and sediment retention processes, in order to evaluate the efficiency and design of herbaceous hedges to reduce the impacts of soil erosion in loamy European agricultural catchments. The identification of the main efficient traits and traits' combinations towards hydraulic roughness increase (stem density, diameter, leaf area and density) highlighted negatively correlated traits, suggesting that a trade-off could be reached within a plant species assemblage through a complementarity effect of the traits. However, non-additive effects of plant species diversity and functional diversity were found, both driven by dominant traits in the community. These dominant effects of the traits could be explained by idiosyncratic effects of the traits influencing the aboveground biomass productivity in plant communities. The effects of traits and functional diversity on the hydraulic roughness and sediment retention constitute a new advance in the understanding of plant trait assemblage on runoff and soil erosion processes and a baseline for the design and modelling of herbaceous hedges for runoff and erosion control.

***Key words**: Functional ecology, Concentrated soil erosion, Plant-runoff interactions, Ecological engineering, Herbaceous hedges, Aboveground plant traits, Hydraulic roughness, Dominance and complementarity hypotheses*.

EFFETS DES TRAITS ET DE LA DIVERSITE FONCTIONNELLE DES PLANTES SUR LE RUISSELLEMENT ET LA RETENTION DES SEDIMENTS

Application pour le contrôle de l'érosion des sols dans les bassins versants agricoles tempérés

Au sein des communautés végétales, les traits fonctionnels dirigent et influencent les processus sol-plantes. Le ruissellement et l'érosion concentrés, causes principales de la dégradation des sols, peuvent être contrôlés par des végétations herbacées qui créent une rugosité hydraulique induisant la réduction de la vitesse des flux de ruissellement et la rétention des sédiments. L'approche des traits, plutôt que taxonomique, permet de comprendre et caractériser les effets directs de la végétation sur le ruissellement et la rétention des sédiments. Ce projet de recherche vise à approfondir les connaissances vis-à-vis des effets (i) des traits fonctionnels (Chapitre 1), (ii) de la complémentarité des traits (Chapitre 2), et (iii) de la diversité fonctionnelle (Chapitre 3) sur les écoulements concentrés et la rétention des sédiments afin d'évaluer l'efficacité et le design de haies herbacées pour réduire les impacts de l'érosion des sols dans les bassins versants limoneux d'Europe. Parmi les combinaisons de traits principaux identifiées comme augmentant la rugosité hydraulique (densité et diamètre des tiges, et densité et surface foliaire), certains traits sont négativement corrélés. Un meilleur effet pourrait donc être atteint au sein d'assemblage d'espèces par un effet complémentaire des traits. Cependant, des effets non-additifs des diversités en espèces et fonctionnelle ont été trouvés, chacun généré par un effet dominant des traits dans les communautés testées. Ces effets dominants pourraient être expliqués par des effets idiosyncratiques des traits influençant la productivité en biomasse. Ces effets des traits et de la diversité fonctionnelle sur la rugosité hydraulique et la rétention des sédiments constituent une nouvelle avancée dans la compréhension des effets de l'assemblage des traits sur les processus d'écoulement et d'érosion des sols ainsi qu'une base pour le design et la modélisation des haies herbacées pour le contrôle du ruissellement et de l'érosion.

***Mots clés** : Écologie fonctionnelle, Érosion concentrée, Interactions plantes-ruissellement, Ingénierie écologique, Haies herbacées, Traits végétaux aériens, Rugosité hydraulique, Hypothèses dominance et complémentarité*.