

Drivers of intraspecific variation of plant functional traits,
plant performance and root exudates in German grasslands

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TABLE OF CONTENTS

Summary	4
Zusammenfassung	6
Chapter 1: General Introduction.....	8
Chapter 2: Drivers of intraspecific trait variation of grass and forb species in German meadows and pastures	18
Chapter 3: Predicting individual plant performance in grasslands	20
Chapter 4: Linking root exudates to functional plant traits in ten grassland species	22
Chapter 5: Synthesis	24
References.....	37
Danksagung	44
Appendix	45
Curriculum vitae	46
Eigenständigkeitserklärung.....	49

SUMMARY

Intraspecific variation of plant functional traits got rising attention in the last years of ecological research. It was often described that the variation between different species (interspecific) exceeds the variation within species (intraspecific). However, concerns about this assumption rose and a framework when and how to assess intraspecific variation in ecological research was established. At smaller scales and in grasslands it is not fully clear what drives intraspecific variation in functional traits, individual plant performance and root exudation patterns.

Therefore, I established an experiment in the German Biodiversity Exploratories to find the most important drivers of intraspecific variation. In each of the three regions 18 plots were set up in 2014 in which five individuals of 20 common grassland species, 10 forbs and 10 grasses, were planted as phytometers. After three months (in 2014) and one year (in 2015) after planting one individual per species per plot was harvested and plant functional traits, biomass (here used as performance) and polar metabolites derived from the primary metabolism exuded by the roots were measured. Furthermore, the cover of each species occurring in a 15 cm radius around each phytometer was assessed and functional traits and performance of the surrounding plants were measured. By that I was able to quantify the diversity of the local neighborhood. As the plots used in this thesis are agriculturally used, another important factor was land use intensity. Other environmental factors were climatic variables and soil conditions. These biotic and abiotic factors were used in different approaches to explain intraspecific variation in functional traits, performance and exudates.

Interspecific variation was higher than intraspecific variation in functional traits but lower in exudates across both growth forms (forbs and grasses). Forbs had higher interspecific variation than grasses in functional traits. Among the investigated predictors, abiotic conditions were most important for functional traits and exudates, while functional traits were most important for individual plant performance. Local neighborhood diversity as well as land use intensity were of minor importance for explaining intraspecific variation of all investigated variables.

This thesis wants to highlight the importance of integrating intraspecific variation in ecological studies and to encourage the conductance of interdisciplinary studies to further increase our knowledge of the drivers of intraspecific variation of plant properties and processes in the rhizosphere.

ZUSAMMENFASSUNG

Die intraspezifische Variation von Pflanzenmerkmalen gewann in den letzten Jahren der ökologischen Forschung zunehmend an Bedeutung. Es wurde oft beschrieben, dass die Variation zwischen verschiedenen Arten (interspezifisch) die Variation innerhalb der Arten (intraspezifisch) übersteigt. Allerdings entstanden Bedenken über diese Annahme und ein Rahmenkonzept, wann und wie man intraspezifische Unterschiede in der ökologischen Forschung berücksichtigen sollte, wurde entworfen. Für kleinere Maßstäbe (lokal, regional) und in Grünländern allgemein ist nicht vollständig geklärt, wodurch intraspezifische Unterschiede in funktionellen Merkmalen und der individuellen Performance bestimmt werden. Ein bisher eher unberücksichtigt gebliebener Faktor ist außerdem die Bestimmung der Variation von Wurzel-Exsudationsmustern.

Um die wichtigsten Einflussfaktoren für intraspezifische Variation zu finden, wurde ein Experiment in den deutschen Biodiversitäts-Exploratorien etabliert. In drei Regionen wurden je 18 Plots eingerichtet, in denen fünf Individuen von 20 häufigen Grünlandarten, 10 Kräuter und 10 Gräser, als Phytometer gepflanzt wurden. Nach drei Monaten und noch einmal ein Jahr nach der Pflanzung wurde ein Individuum pro Art pro Plot geerntet und funktionelle Pflanzenmerkmale, Biomasse (hier als Performance verwendet) sowie polare Metabolite aus dem Primärmetabolismus, die von den Wurzeln ausgeschieden (exsudiert) werden, wurden gemessen. Weiterhin wurde die Deckung jeder Art, die in einem Radius von 15 cm um jede Phytometer-Pflanze herum wächst, bestimmt sowie die funktionellen Merkmale und die Performance der umgebenden Pflanzen erfasst. Damit war es möglich die Artenzahl, Diversität und funktionelle Vielfalt der lokalen Nachbarschaft zu quantifizieren. Da die in dieser Arbeit verwendeten Flächen landwirtschaftlich genutzt werden, war ein weiterer wichtiger Faktor die Landnutzungsintensität. Weitere Umwelteinflüsse waren klimatische Variablen und Bodeneigenschaften. Diese biotischen und abiotischen Faktoren wurden in verschiedenen Ansätzen verwendet, um die intraspezifischen Variationen in funktionellen Merkmalen, Performance und Exsudatzusammensetzung zu erklären.

Über beide Wachstumsformen (Kräuter und Gräser) hinweg war die interspezifische Variation höher als die intraspezifische Variation der funktionellen

Merkmale, aber niedriger bei der Exsudatzusammensetzung. Kräuter hatten eine höhere interspezifische Variation als Gräser in funktionellen Merkmalen. Von allen untersuchten Prädiktoren waren die abiotischen Bedingungen für die funktionellen Merkmalen und die Exsudatzusammensetzung am wichtigsten, während funktionelle Merkmale für die individuelle Performance am wichtigsten waren. Die Diversität der lokalen Nachbarschaft sowie die Landnutzungsintensität waren von untergeordneter Bedeutung für die Erklärung der intraspezifischen Variation aller untersuchten Variablen.

Diese Arbeit möchte betonen, wie wichtig es ist, intraspezifische Variation in ökologische Studien zu integrieren und interdisziplinäre Studien durchzuführen, um die Auslöser der intraspezifischen Variation von Pflanzenmerkmalen sowie Vorgänge in der Rhizosphäre besser verstehen zu können.

CHAPTER 1

General Introduction

Plant functional traits and trait variation

Plant functional traits are used to describe physiological processes, life-history processes, fitness and performance of individual plants (Violle et al. 2007). There is a plethora of functional traits that is used in ecological research (Pérez-Harguindeguy et al. 2013). For many traits we know the exact function and the relationships between them. Pérez-Harguindeguy et al. (2013) established a new standardized protocol on how to measure plant traits and described the function of each. How traits are correlated was described in the leaf economics spectrum for leaf traits (Wright et al. 2004) and for the whole plant later by Freschet et al. (2010) who found evidence for a plant economics spectrum (Reich 2014). It is known that there is a trade-off between fast growing and slow growing species which is reflected by certain trait constellations. The most commonly used traits are specific leaf area (SLA), leaf, root or shoot dry matter content and tissue nitrogen and carbon content (Freschet et al. 2010; Pérez-Harguindeguy et al. 2013). For example, high SLA and leaf nitrogen content are often associated with a high relative growth rate and fast leaf turnover rate (Freschet et al. 2010; Pérez-Harguindeguy et al. 2013). On the contrary, high leaf dry matter content (LDMC) and leaf carbon content are indicators for slow growth, high leaf longevity and low leaf turnover rate (Freschet et al. 2010; Pérez-Harguindeguy et al. 2013). The same conclusions were drawn for roots by measuring root dry matter content as proxy for root tissue density (Birouste et al. 2014).

Not only the functions of traits but also their variation within species along environmental gradients is considerable (Albert et al. 2011; Jung et al. 2014). It was often stated that variation within species (intraspecific) is much smaller than variation between species (interspecific) (Garnier et al. 2001; Jung et al. 2010; Albert et al. 2011; Kazakou et al. 2014). Still, Jung et al. (2010) highlighted the importance of intraspecific trait variation for the detection of habitat filtering in grassland communities. However, Messier et al. (2010) found in a tropical rain forest intra- and interspecific variation in LDMC and LMA (leaf mass per area) were of equal magnitude. This pattern might not be consistent across several traits. For example, Al Haj Khaled et al. (2005) and Garnier et al. (2001) found that intraspecific variation in SLA was higher than in LDMC. Nevertheless, to my

knowledge there is no study so far that quantified intraspecific trait variation in grasslands along a gradient of land use intensity.

Although, many studies already investigated root traits (e.g. Aerts & Chapin 2000; Bausenwein et al. 2001; Chanteloup & Bonis 2013; Birouste et al. 2014), there are still substantial knowledge gaps (Bessler et al. 2009; Cadotte et al. 2009). Due to the difficulties in handling roots they are often neglected (Leuschner et al. 2013). However, they have a great importance for ecosystem functions as they can make up to 90 % of the net primary productivity in grasslands (Stanton 1988). Root traits that were investigated very frequently are specific root length, root tissue density, specific root area, root diameter, root N and C concentration, root P and lignin concentration and root dry matter content (Ryser & Lambers 1995; Ryser 1996; Jackson et al. 1997; Wahl & Ryser 2000; Roumet et al. 2006; Freschet et al. 2010; Chanteloup & Bonis 2013; Pérez-Harguindeguy et al. 2013; Birouste et al. 2014; Kong et al. 2015). Nevertheless, data about traits such as root nutrient concentrations (e.g. Ca, K and Mg) and root volume remain rare.

Root exudates

Other potential functional traits such as root exudates are rarely addressed. Root exudates are primary and secondary metabolites which are secreted by plant roots (Badri & Vivanco 2009; Faure et al. 2009). Root exudation is an active process and is associated with a high carbon cost for the plant (Badri & Vivanco 2009). The compounds that are exuded range from ions, inorganic acids, oxygen and water to costly intensive carbon compounds like amino acids, sugars, phenolics, proteins, lignins, flavonols and many others (Badri & Vivanco 2009; Faure et al. 2009). So far, these substances are only known from model plants, such as *Arabidopsis thaliana*, or from crop plants grown under controlled conditions. Nevertheless, exudates of 20 wild plant species were measured in a study of Tyler & Strom (1995), but also under controlled laboratory conditions. Some exudates are just waste products of the plants' metabolism, while others can have several functions such as lubrication, nutrient and water acquisition, plant defence or communication with soil organisms (Faure et al. 2009). However, the functions of

exudates are not well understood and only a few functions have been investigated yet. To my knowledge, there was no study so far that viewed root exudates from an ecological perspective and measured exudates on a variety of plant species under field conditions. Therefore, I had no clear expectation what kind of exudates were secreted by grass and forb species. However, I expected root exudate composition to differ between these two growth forms, as they are morphologically and functionally distinct, what should make it also possible to explain variation in exudate composition via plant functional traits. For example, traits describing root system architecture had previously been found to be closely linked to exudate composition (Badri & Vivanco 2009; Kuijken et al. 2015).

Environmental influences

The main abiotic factors influencing a trait's expression and resulting in intraspecific variation are soil properties and climatic conditions (Ordoñez et al. 2009; Moles et al. 2014; Rosbakh et al. 2015). Despite climate and soil conditions, one of the main environmental gradients in grasslands affecting species composition and ecosystem functions is land use intensity (Sala 2000; Poschlod et al. 2005; Laliberte et al. 2010). Increased land use intensity has been shown to negatively influence species richness and diversity of communities (Foley et al. 2005; Blüthgen et al. 2012; Allan et al. 2015). Often, land use is described by categorical variables (e.g. mown versus grazed), which have several limitations as they do not capture differences within these categories (Blüthgen et al. 2012). Therefore, some efforts had been made to capture the relative importance of human made land use intensity in one single variable (Blüthgen et al. 2012). For the German Biodiversity Exploratories Blüthgen et al. (2012) developed a quantitative index, that summarizes the frequency of mowing, grazing and fertilization. The authors showed that this land use intensity index (LUI) was a good predictor for nutrient concentrations of soil and aboveground biomass. In addition, they were able to show that single parts of the index such as fertilization intensity alone could not sufficiently explain nutrient concentrations of soil and aboveground biomass and thus highlighting the superiority of their index.

Grasslands and growth forms

In total, 26 % of global land area and 80 % of agriculturally used land consist of grasslands (meadows and pastures), which have a great importance for human wellbeing (Boval & Dixon 2012). They deliver many ecosystem services (Boval & Dixon 2012; Allan et al. 2015) and have a high biodiversity at a small spatial scale (Wilson et al. 2012). Grasslands inhabit two main growth forms: grasses (monocotyledons) and forbs (dicotyledons) (Box 1996). Regarding anatomical features, grasses have a secondary root system, and roots are adventitious while roots of forbs develop from the radicle (Strasburger 2002). Furthermore, grasses possess sclerenchymatic tissue to support stability whereas the here studied forbs only use turgor to stand upright (Strasburger 2002). Several studies found differences in trait values between these two growth forms (Craine et al. 2001; Tjoelker et al. 2005; Roumet et al. 2006; Salpagarova et al. 2014). For example, investigating 92 alpine species, Salpagarova et al. (2014) found higher carbon and nitrogen concentrations in fine roots of herbs compared to those of grasses. Craine et al. (2001) found that grasses had thin, dense leaves and thin roots whereas forbs were characterized by traits indicating thick, low-density leaves and thick roots. However, it was also pointed out that not all traits differ between grasses and forbs and that individuals of both growth forms can have traits indicating an acquisitive and conservative strategy (Grime et al. 1997; Craine et al. 2001). Moreover, the extent of inter- and intraspecific variation of the two growth forms is not fully clear. For example, Siebenkäs et al. (2015) found phenotypic plasticity, in response to different levels of light and soil nutrients, of grasses to be higher in aboveground traits but to be lower in belowground traits compared to forbs.

Diversity

Another potential factor influencing intraspecific variation is the biotic environment expressed as diversity. The diversity of a plant community can be quantified by several measures. The easiest and most widely used measure is species richness. It has been shown to be a good predictor for community productivity in several studies (Hector

1999; Balvanera et al. 2014; Fraser et al. 2015). However, many studies could not find such a general relationship (Hooper 1997; Balvanera et al. 2006) or found even negative effects of biodiversity (He et al. 2002). A possible explanation might be that species richness cannot be seen as a surrogate for functional richness (Díaz & Cabido 2001) and thus cannot capture all properties of a community. Therefore, species richness per se is no reliable predictor for productivity but rather the identity of species or number of functional groups (Hooper 1997, 1998; Balvanera et al. 2006). Hector et al. (2011) found that species richness and the community composition were of equal importance for predicting community productivity across several experiments in Europe. On the contrary, Cadotte et al. (2009) found the presence of legumes and phylogenetic diversity to be the best predictors for community productivity. They also stated that traits could be even better predictors. Therefore, better alternatives are community weighted means (CWM) and functional diversity (FD). Due to the existence of large trait databases, information about traits are not as hard to obtain as some decades ago. CWM are calculated by weighing the traits of all plants in a community by their relative abundance (Garnier et al. 2004) and thus reflect the most abundant trait values. On the contrary, FD describes the dissimilarity between traits among the species in a community and thus reflects the niche space that is occupied by the plants. Some effort had been made to find the optimal proxy for diversity. Comparing phylogenetic diversity, CWM and FD, Fu et al. (2014) found CWM to be the best predictor for community productivity. This was confirmed by a study of Kröber et al. (2015) for growth rates of trees in a subtropical forest. The authors found CWM to explain more variation in tree growth than FD. In a grazed wet grassland, Chanteloup & Bonis (2013) found the CWM of height, LDMC, SLA and specific root area to positively influence biomass production while CWM of root tissue density had a negative effect.

While CWM and FD are valuable for predicting productivity of the whole community, they are rarely used for individuals. The diversity at a smaller scale of the local neighbourhood can also have impacts on single individuals (von Oheimb et al. 2011). For example, Bittebiere & Mony (2014) found that species in a radius of 10 cm have an influence on traits such as LDMC, specific rhizome mass and height of the target individual. This influence was even present when neighbours were growing in a distance

of 20-25 cm. The identity of the neighbours was also important, as some species influenced LDMC of the target individual positively while the influence of others was negative. Furthermore, the abundance of the local neighbourhood explained 70 % of variation in LDMC (Bittebiere & Mony 2014). However, the influence of diversity on individual plant performance (expressed as biomass) has been rarely addressed.

Objectives

To summarize, many studies investigated the importance of functional traits for whole communities and factors influencing traits. Plant functional traits were widely used as predictors for community productivity in grasslands. However, it was unclear how especially belowground traits vary within species along environmental gradients. The aim of this thesis was to investigate which factors determine variation of functional plant traits of grassland plant species, with an emphasis on root traits and root exudates, and to use these traits to predict performance of single plants. In the thesis I tested the following hypotheses:

- 1) The intraspecific variation of traits can be explained by land use intensity, climate and soil conditions and local neighbourhood diversity. I expected the overall interspecific variation to be higher than intraspecific variation, whereas the intraspecific variation of grasses is expected to be higher than that of forbs. Furthermore, I expected differences in trait values between the two growth forms.
- 2) The individual plant performance can be predicted and its intraspecific variation explained by individual functional traits, environmental variables and the functional composition of the local neighbourhood.
- 3) Plant functional traits and performance variables are related to root exudates and root exudates differ between grass and forb species and are species-specific. Furthermore, variation in exudates can be explained by local neighbourhood diversity.

In an extensive phytometer approach (Clements & Goldsmith 1924; Dietrich et al. 2013), where 5400 plant individuals (Table 1) were planted into existing grassland communities, I tested the relationship between traits and their environment and root exudates. The

focus was especially on belowground traits, but also aboveground traits were measured. The grassland communities used in this thesis were part of the German Biodiversity Exploratories (Fischer et al. 2010). The Exploratories consist of three regions: Biosphere Reserve Schorfheide-Chorin in the north-east of Germany, National Park Hainich-Dün in the middle of Germany and Biosphere Reserve Schwäbische Alb in south-west of Germany (Fig. 1). Data from three months (**chapter 4**) and one year after planting (**chapter 2** and **3**) were used for the following chapters.

In **chapter 2** I present results of trait variation along environmental gradients. I tested how local neighbourhood diversity and land use intensity as well as climatic and edaphic conditions affect plant functional traits. Furthermore, I present the differences in intraspecific trait variation between grass and forb species. Land use intensity, climate and soil conditions as well as local neighbourhood diversity were used as predictors for plant functional traits (Fig. 2).

In **chapter 3** I describe the most important predictors for individual plant performance (Fig. 2). Four predictor groups were tested, which include community weighted means and functional diversity of the local neighbourhood, environmental conditions (land use intensity, climate and soil conditions) as well as the plant functional traits of the phytometers. Furthermore, I tested the influence of the best predictors on individual plant performance.

In **chapter 4** I compared root exudate composition of grass and forb species. I investigated whether exudate composition is species specific, differs between the two growth forms and is related to plant functional traits. The variation in root exudates is assessed by local neighbourhood diversity as well as the plant functional traits and performance of the phytometers (Fig. 2).

In Fig. 2 it is also illustrated on which levels each response and predictor variable was assessed. All response variables were measured on single individuals, while predictors were measured at the plot level (climate and soil conditions and land use intensity), at the local level (local neighbourhood diversity, 15 cm radius around each phytometer) and also at the individual level (functional traits and performance). The direction of the arrows illustrates the direction of the tested effect.



Fig. 1. Map of the locations of the three German Biodiversity Exploratories.

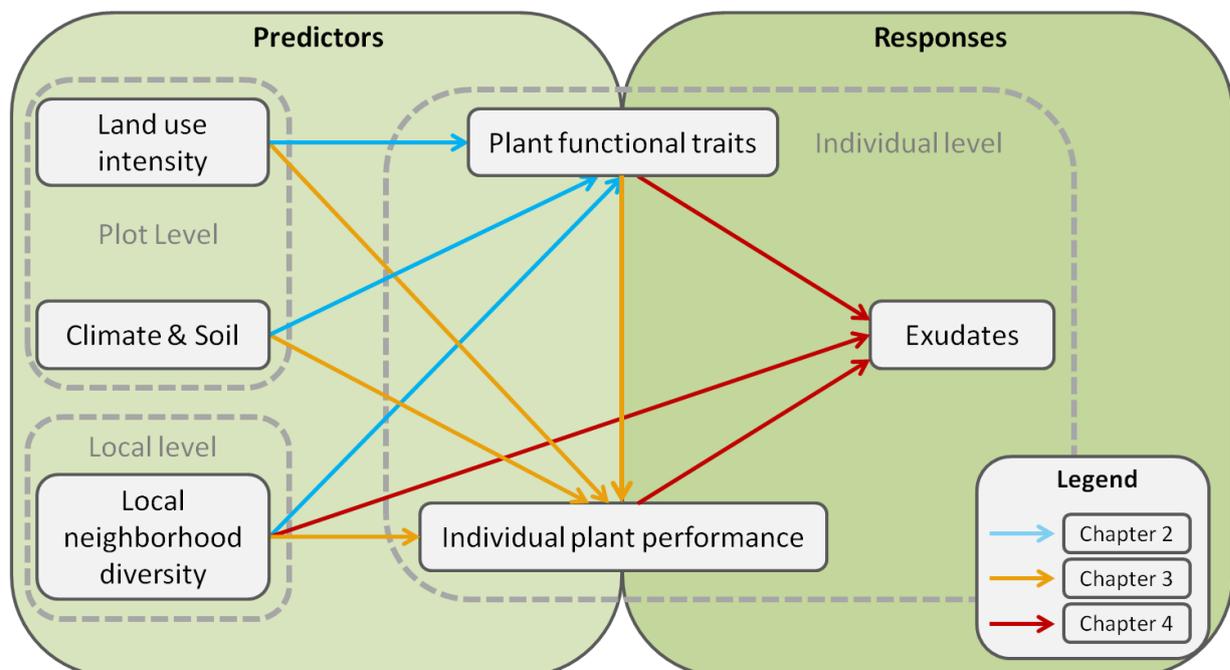


Fig. 2. Overview of predictors and responses of each chapter used to assess intraspecific variation with their different organizational levels (dashed, grey boxes).

Table 1. Summary of all planted phytometer species. All species were used to measure plant functional traits and plant performance. Species highlighted with grey background were used for exudate analyses.

Growth Form	Family	Species
Grass	<i>Poaceae</i>	<i>Alopecurus pratensis</i> L.
Grass	<i>Poaceae</i>	<i>Anthoxanthum odoratum</i> L.
Grass	<i>Poaceae</i>	<i>Arrhenatherum elatius</i> (L.) P.Beauv. ex J.Presl & C.Presl.
Grass	<i>Poaceae</i>	<i>Cynosurus cristatus</i> L.
Grass	<i>Poaceae</i>	<i>Dactylis glomerata</i> L.
Grass	<i>Poaceae</i>	<i>Festuca pratensis</i> Huds.
Grass	<i>Poaceae</i>	<i>Helictotrichon pubescens</i> (Huds.) Schult. & Schult.f.
Grass	<i>Poaceae</i>	<i>Lolium perenne</i> L.
Grass	<i>Poaceae</i>	<i>Poa pratensis</i> L.
Grass	<i>Poaceae</i>	<i>Poa trivialis</i> L.
Forb	<i>Asteraceae</i>	<i>Achillea millefolium</i> L.
Forb	<i>Asteraceae</i>	<i>Bellis perennis</i> L.
Forb	<i>Asteraceae</i>	<i>Centaurea jacea</i> L.
Forb	<i>Rubiaceae</i>	<i>Galium mollugo</i> L.
Forb	<i>Rubiaceae</i>	<i>Galium verum</i> L.
Forb	<i>Plantaginaceae</i>	<i>Plantago lanceolata</i> L.
Forb	<i>Ranunculaceae</i>	<i>Ranunculus acris</i> L.
Forb	<i>Ranunculaceae</i>	<i>Ranunculus bulbosus</i> L.
Forb	<i>Polygonaceae</i>	<i>Rumex acetosa</i> L.
Forb	<i>Plantaginaceae</i>	<i>Veronica chamaedrys</i> L.

CHAPTER 2

Drivers of intraspecific trait variation of grass and forb species in German meadows and pastures

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Abstract

Questions: To what extent is trait variation in grasses and forbs driven by land-use intensity, climate, soil conditions and plant diversity of the local neighbourhood? Do grass and forb species differ in the degree of intraspecific trait variation?

Location: Managed grasslands in three regions of Germany.

Methods: Using a phytometer approach, we raised 20 common European grassland species (ten forbs and ten grasses) and planted them into 54 plots of different land-use types (pasture, meadow, mown pasture). After 1 yr in the field, we measured above- and below-ground plant functional traits. Linear mixed effects models (LMEM) were used to identify the most powerful predictors for every trait. Variation partitioning was applied to assess the amount of inter- and intraspecific trait variation in grasses and forbs explained by environmental conditions (land-use intensity, climate and soil conditions) and plant species diversity of the local neighbourhood.

Results: For 12 out of the 14 traits studied, either land-use intensity or local neighbourhood diversity were predictors in the best LMEM. Land-use intensity had considerably stronger effects than neighbourhood diversity. Root dry matter content and root phosphorus concentration of forbs were more affected by landuse intensity than those of grasses. For almost all traits, intraspecific trait variation of grasses was much higher than that of forbs, while traits of forbs varied more among species. Overall, inter- and intraspecific variation was of the same magnitude.

Conclusion: The similar magnitude of intra- and interspecific trait variation suggests that both sources should be considered in grassland studies at a scale similar to that of our study. The high amount of intraspecific trait variation that was explained by environmental factors and local neighbourhood diversity clearly demonstrates the high potential of species to adjust to local conditions, which would be ignored when only considering species mean trait values.

Keywords: Biodiversity Exploratories; Grassland; Growth form; Intraspecific trait variation; Land-use intensity; Local neighbourhood; Phytometer; Plant functional traits; Root traits; Shannon Index; Trait adjustment

CHAPTER 3

Predicting individual plant performance in grasslands

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Abstract

Plant functional traits are widely used to predict community productivity. However, they are rarely used to predict individual plant performance in grasslands. To assess the relative importance of traits compared to environment, we planted seedlings of 20 common grassland species as phytometers into existing grassland communities varying in land-use intensity. After 1 year, we dug out the plants and assessed root, leaf, and aboveground biomass, to measure plant performance. Furthermore, we determined the functional traits of the phytometers and of all plants growing in their local neighborhood. Neighborhood impacts were analyzed by calculating communityweighted means (CWM) and functional diversity (FD) of every measured trait. We used model selection to identify the most important predictors of individual plant performance, which included phytometer traits, environmental conditions (climate, soil conditions, and land-use intensity), as well as CWM and FD of the local neighborhood. Using variance partitioning, we found that most variation in individual plant performance was explained by the traits of the individual phytometer plant, ranging between 19.30% and 44.73% for leaf and aboveground dry mass, respectively. Similarly, in a linear mixed effects model across all species, performance was best predicted by phytometer traits. Among all environmental variables, only including land-use intensity improved model quality. The models were also improved by functional characteristics of the local neighborhood, such as CWM of leaf dry matter content, root calcium concentration, and root mass per volume as well as FD of leaf potassium and root magnesium concentration and shoot dry matter content. However, their relative effect sizes were much lower than those of the phytometer traits. Our study clearly showed that under realistic field conditions, the performance of an individual plant can be predicted satisfyingly by its functional traits, presumably because traits also capture most of environmental and neighborhood conditions.

Keywords

Biodiversity Exploratories, community-weighted means, functional diversity, local neighborhood, phytometer, plant performance

CHAPTER 4

Linking root exudates to functional plant traits in ten grassland species

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Abstract

Primary and secondary metabolites exuded by plant roots have mainly been studied under laboratory conditions, while knowledge of root exudate patterns of plants growing in natural communities is very limited. Focusing on ten common European grassland plant species, we asked to which degree exuded metabolite compositions are specific to species or growth forms (forbs and grasses), depend on environments and local neighbourhoods, and reflect traditional plant functional traits. Root exudates were collected under field conditions and analysed using a non-targeted gas chromatography coupled mass spectrometry (GC-MS) approach. In total, we annotated 153 compounds, of which 36 were identified by structure and name as metabolites, mainly derived from the primary metabolism. Here we show by using variance partitioning, that the composition of exuded polar metabolites was mostly explained by plot identity, followed by plant species identity while plant species composition of the local neighbourhood played no role. Including traditional plant traits increased the total variance explained, while exclusively explained variance by traits was mostly brought about by total and root dry mass. Thereby, our study clearly demonstrated the feasibility of measuring exudates under non-sterile field conditions by mass spectrometry, what opens new avenues of research for functional plant ecology.

CHAPTER 5

Synthesis

General Discussion

In this thesis I focused on the drivers of intraspecific variation of plant functional traits, individual plant performance and root exudates. In a transplant experiment across three regions in Germany, including 20 grassland species I investigated the impacts of climatic and edaphic conditions as well as land use intensity and plant species diversity of the local neighbourhood on plant functional traits and individual plant performance (Fig. 2 in **chapter 1**). Furthermore, I used plant functional traits to predict individual plant performance and traits, performance variables and local neighbourhood diversity to explain variation in root exudate composition (not similar to the concentration of exuded substances).

The key results were:

- 1) Intraspecific variation of functional traits was best explained by climate and soil conditions, while land use intensity and local neighbourhood diversity were of minor importance. Forbs had higher interspecific variation than grasses. The two growth forms differed in 10 out of 14 functional traits.
- 2) Individual plant performance was best predicted by plant functional traits rather than by environmental variables or traits of the local neighbourhood. Furthermore, the intraspecific variation of performance was mainly explained by functional traits.
- 3) Only a small amount of variation in exudate composition was explained by growth form or species identity, phytometer traits or local neighbourhood diversity. The most important predictors for exudates were variables varying at the plot level such as climate and soil variables.

Is interspecific variation higher than intraspecific variation?

There is a tendency that interspecific variation is greater than intraspecific variation (Albert et al. 2011), with evidence found in several studies (Garnier et al. 2001; Jung et al. 2010; Kazakou et al. 2014). However, similar to this thesis other studies found no evidence for this assumption (Lecerf & Chauvet 2008; Messier et al. 2010). Although,

across both growth forms as in **chapter 4**, interspecific variation in plant functional traits was much higher than intraspecific variation (ITV), I was able to show in **chapter 2** that it is not generalizable across different growth forms. While forbs met the assumption by displaying higher interspecific than intraspecific variation in almost all functional traits studied, the opposite was true for grass species (Fig. 1). This is in line with the results of Siebenkäs et al. (2015) who found a higher plasticity of grass species compared to forbs. For this thesis, the observed pattern can be explained by their phylogenetic relatedness as they all belong to the family of Poaceae. Furthermore, grass species might be able to better cope with different environmental conditions due to higher phenotypic plasticity or a higher genetic variability, what might be one aspect of explaining their dominance in grasslands. In summary, ITV is considerable and should not be ignored in ecological studies (Albert et al. 2011; Lepš et al. 2011; Violle et al. 2012) as it affects many ecological processes such as community assembly (Jung et al. 2010). Furthermore, trait-based studies can benefit by considering ITV, because e.g. predictions or responses to environmental conditions can be stronger when including ITV (Albert et al. 2011; Lepš et al. 2011). However, to be included in further ecological studies, it was at first important to quantify the magnitude and drivers of ITV (Albert et al. 2011). In addition, the magnitude of ITV strongly depends on the habitat studied (Lepš et al. 2011), the trait and scale considered (Albert et al. 2011) and the length of the environmental gradient studied. Therefore, my thesis gives a basis for other ecological trait-based studies.

	more variation in forbs	more variation in grasses
interspecific	LDMC, SLA, LAR, RDMC, RSR, Rvol, RMC, RNC, RPC, RKC, RMgC, RCaC	RCC, RCNR
intraspecific	SLA, RPC	LAR, RDMC, RSR, Rvol, RMV, RCC, RNC, RCNR, RKC, RMgC, RCaC

Fig. 1. Summary of results of **chapter 2**. Boxes indicate which trait had a higher interspecific (yellow) or intraspecific (blue) variation in either forbs or grasses. For abbreviations of traits see Table 1 in **chapter 2**.

Intraspecific variation in exudate composition of polar metabolites derived from the primary metabolism was almost six times higher than interspecific variation across

both growth forms (Fig. 2d). As so far exudate compositions had only been investigated under lab conditions, the influence of realistic environmental conditions was a new step in this research area. However, it was already shown that under nutrient deficiency a higher amount of such exudates are released that enhance nutrient acquisition (reviewed in Badri & Vivanco 2009). For example, under P-deficiency certain legumes and trees exude more phenolic compounds than under optimal nutrient availability (Badri & Vivanco 2009). Furthermore, other factors like temperature, light and soil moisture can alter the exudation pattern (Badri & Vivanco 2009; Kuijken et al. 2015; van Dam & Bouwmeester 2016). Not only the amount of the exudates but also their composition can be influenced by environmental factors (Badri & Vivanco 2009). These studies were all conducted under controlled lab conditions and now the importance of environmental factors for exudation patterns could be confirmed by my results assessed under realistic field conditions. In my case the factor plot, which represents the variation of all environmental conditions, explained 15 % in polar metabolites (Fig. 2d). Therefore, the exudate composition represented a clear response to the environment. A higher species specificity and thereby higher interspecific variation might be visible in secondary metabolites, as they are specific for several functions such as plant-plant or plant-microbe interactions (van Dam & Bouwmeester 2016).

Environmental and biotic drivers of intraspecific trait variation

The drivers of intraspecific variation of performance, functional traits and exudates were determined in **chapters 2 to 4**.

Climate, soil conditions and land use intensity

In **chapter 2** I demonstrated that climate and soil conditions were the major source of intraspecific variation in plant functional traits, with explaining up to 18 % of variation across all traits in grass species (Fig. 2a-b). This might rely on the environmental gradient, along which the Exploratories were set up. Strong effects of climate and soil conditions have therefore been often found in studies using the Exploratory plots. (Blüthgen et al. 2012; Herold et al. 2014; Fiore-Donno et al. 2016). For example, Herold et al. (2014)

found that microbial biomass and community composition and enzyme activities were more affected by soil properties than by LUI. Although climate and soil were suitable for explaining intraspecific variation of functional traits, they could not very well explain variation in individual plant performance (**chapter 3** and Fig. 2c). In **chapter 3**, out of the 10 abiotic variables only land use intensity index (LUI) and relative humidity were important for root dry mass and aboveground biomass, respectively. The factor plot, which captures the climatic and edaphic conditions the phytometers' were exposed to, explained most intraspecific variation in root exudates (**chapter 4**; see also Fig. 2d) and increased the amount of intraspecific variation of plant functional traits (**chapter 2**). This means, that most variation occurred at the plot level. Still, in all three chapters, LUI was of minor importance for predicting the chosen responses. As stated above, the environmental conditions might be overruling the effects of LUI. Despite the high value of this index as highlighted by Blüthgen et al. (2012), the index bares some weaknesses. Although, I know the land use intensity of each plot caused by fertilization, grazing and mowing, I do not know the effects of this land use on a smaller scale, such as the exact amount of fertilizer provided for each individual, whether a cow or sheep defecated or rested on a plant, etcetera. I would therefore suggest making such kind of experiments (or repeat the experiment) under controlled conditions, such as to determine when grazers enter the pasture or the exact mowing date and fertilizer amount and type applied.

Local neighbourhood diversity

The low influence of the many diversity metrics, which describe the impact of the local neighbourhood, considered in **chapters 2-4** on intraspecific variation of traits, performance and exudates, was surprising. Many studies reported an effect of biodiversity on ecosystem functioning (Hector 1999; Balvanera et al. 2014; Fraser et al. 2015; Kröber et al. 2015). A possible explanation for the low importance of the local neighbourhood in my studies might be the short residence time of the phytometers as they were at maximum one year old. Ravenek et al. (2014) showed that effects of plant species richness on root productivity in the Jena Experiment occurred only four years after the establishment of the experiment. Some studies highlighted that diversity *per se*

cannot be able to predict such functions, as for example productivity, but rather the functional composition of a community (Cadotte et al. 2009; Fu et al. 2014; Kröber et al. 2015). However, when predicting productivity on the individual scale (performance) I found that only one community weighted mean (CWM) trait was a good predictor for root dry mass. Out of the 54 biotic variables describing the local plant neighbourhood, only CWM of root calcium concentration occurred in the best model of root dry mass but for no other performance variable (Tab. 1). The other performance traits were predominantly explained by functional traits of the phytometers. On the one hand, functional traits of the phytometers seem to already capture the environmental conditions of the plot. On the other hand, the link between performance and functional traits is close as both variables were assessed at the same plant.

Tab. 1. Summary of results of the model selection made in **chapter 3** with a full dataset.

	LAR	RCaC	RCC	RMV	RSR	RVol	SLA	LUI	rH_200	CWM	RCaC
DM roots	-	+	-					+			+
DM leaves	+			+	-	+	-				
DM above				+	-	+			+		
DM total				+	-	+					

A minus indicates a negative effect of the trait on the performance variable while a plus indicates a positive effect. DM = dry mass. All relationships have P -values < 0.01

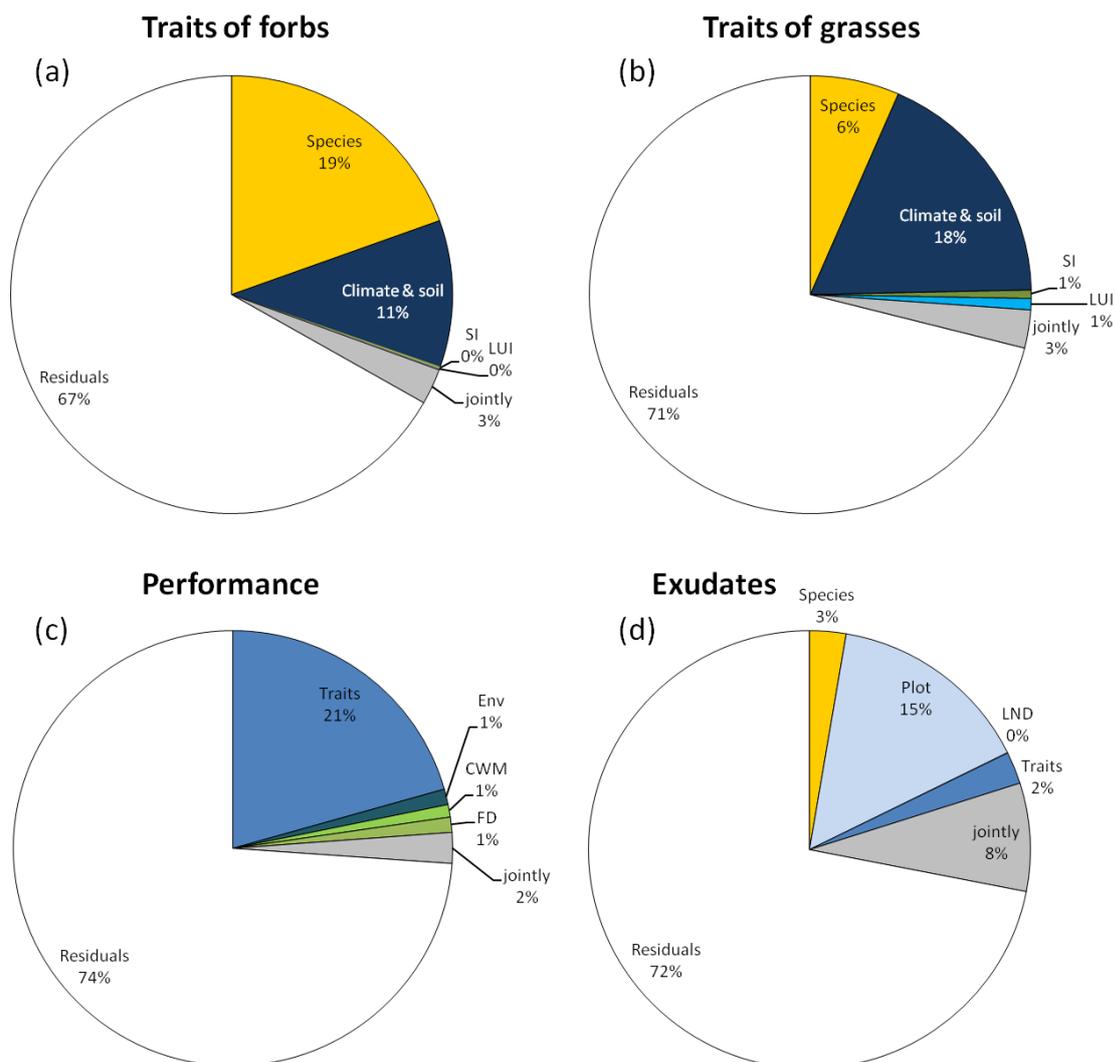


Fig. 2. Summary of variance partitioning results of all three chapters. The analyses were run with all traits as response matrix (a, b), all performance variables as response matrix (c) and all predictor variables used to explain variation in exudate composition (d) using the function `varpart` (package `vegan`). The factor “jointly” sums up all variances that are explained by two to four factors. Env = climate & soil and land use intensity index (LUI), CWM = community weighted mean traits, FD = functional diversity traits, LND = local neighbourhood diversity including species richness, Shannon diversity Index (SI), total cover and species composition of the local neighbourhood (obtained from the first four axes of a detrended correspondence analysis). The used factors were kept analogue to the three chapters. For example, the factor “Climate & soil” and “LUI” were used separately in (a) and (b) but were summarized to the factor “Env” in (c).

All processes in the rhizosphere, such as exudation, happen at a very small scale. As local neighbourhood diversity was assessed at a smaller scale than the other environmental variables, it was thought to have a higher impact on exudate composition than factors varying at the plot-level. This assumption did not meet the results of **chapter 4**. Accordingly, the low variance explained by local neighbourhood diversity in root exudates can be explained by their function. So far, in cooperation with Sophie Dietz of the Leibniz Institute for Plant Biochemistry Halle, only polar metabolites derived from the primary metabolism have been investigated, which are, in contrast to secondary metabolites, not primarily responsible for communication with other soil organisms (van Dam & Bouwmeester 2016). The interactions with other plants are mostly attributed to secondary metabolites, although the exact mechanisms are unclear as specific receptors for plant-plant communication haven't been identified yet (van Dam & Bouwmeester 2016). Therefore, effects of local neighbourhood diversity might only be visible in secondary metabolite composition.

Functional traits and performance as predictors

Plant functional traits were the best predictors in **chapter 3**, because they explained between 14 % and 61 % of variation and therefore captured the environmental and biotic conditions (not exceeding 5 % explained variation) and were a proxy for a plants' resource use strategy (Freschet et al. 2010). Therefore, the effects of the target individual's functional traits might be overruling the effects of the biotic neighbourhood or of abiotic site factors investigated in this study. Nevertheless, functional traits played an important role and their value in predicting performance should be highlighted. The role of traits and performance as predictors for exudate composition is discussed in a separate section.

Unexplained variation

Although, much variation was explained by abiotic and biotic conditions and species identity, a high amount of variation remained unexplained by the chosen factors (up to 74 % in performance, Fig. 2c). Stochastic events such as grazers trampling or defecating on single plants or other scientists disturbing the plot could explain trait variation. In

addition, other environmental variables at the plot level like inclination, slope and exposition or radiation (e.g. Kuijken et al. 2015; Siebenkäs et al. 2015) or ground temperature might further decrease the unexplained plot-level variation. Biotic conditions at the individual level such as the microbial community composition, herbivores, pathogens or endophytes could also explain more variation in trait values. As data on the mentioned factors were not available or are still to be quantified, these factors were not part of my analyses. All in all, these factors would only decrease the unexplained variation captured by plot identity. Nevertheless, some factors can't be controlled for and when working under realistic field conditions unexplained residual variation will always occur.

All in all, I can conclude that the expression of plant properties depends more on the environmental conditions varying at the plot level and in the case of plant performance on functional traits, rather than the identity of the target species or local neighbourhood.

Linking exudates to traits

It was expected that plant functional traits could explain variation in polar metabolite composition, because root system architecture had previously been found to be closely linked to exudate composition (Badri & Vivanco 2009; Kuijken et al. 2015). Root system architecture comprises of root length, root density, root branching and total root surface (Kuijken et al. 2015). Although, all functional traits and performance variables together did not explain much variation in exudates (2 %, Fig. 2d), the single trait that could explain a small amount of variation was root dry mass (1.58 %). However, as root dry mass could influence all variables of root system architecture, another explanation might be more convenient. It could point to the fact that exudate composition shifts with the age of the plant, because it was previously found that the exudate composition changes with a plants' developmental stage (Aulakh et al. 2001; Badri et al. 2013). Still, the amount of variation explained by this trait was small. Therefore, other factors such as microbial community or nutrient availability might be more important for root exudate composition than plant functional traits (Badri & Vivanco 2009; Kuijken et al. 2015).

Root exudates, especially secondary metabolites, hold the potential to be used as new functional traits or finger prints. Certain sets of metabolites might be specific for each plant species and could predict specific functions. However, lot of work has to be done to get to this point as the identification of substances and their functions takes much time and effort (Raguso et al. 2015). This thesis gives first insights into the topic.

Differences between growth forms - the plant economics spectrum

Grass and forb species in this thesis differed in several functional traits as well as in root exudates. In total, 10 out of 14 investigated functional traits differed between growth forms (Fig. 3). A conservative strategy of resource use was found for aboveground traits of grasses (high leaf dry matter content and low leaf area ratio) but for belowground traits of forbs (high root dry matter content and root mass per volume and low root volume) in **chapter 2** (Pérez-Harguindeguy et al. 2013). Therefore, both growth forms cannot *per se* be separated into different strategies.

Predominantly found in	Fast-growing → Acquisitive	Slow-growing → Conservative	Predominantly found in
forbs	LDMC ←————→ LAR		grasses
grasses	RVol ←————→ RDMC, RMV, RCC, RNC, RPC, RKC, RMgC		forbs

Fig. 3. Summary of results regarding the plant economics spectrum. Arrows indicate that these traits oppose in the two strategies. Based on the linear mixed effect models in **chapter 2** grasses and forb species could be attributed to the strategies. The full model contained one of the traits as response variable related to growth form (GF), land use intensity index (LUI) and Shannon Index of the diversity of the local neighbourhood (SI) as fixed factors as well as all possible interactions. Random factors were species, exploratory and plot nested in exploratory. *P*-value for RNC is < 0.1, for all other traits < 0.05 and can be found in **chapter 2**, Table 2. For abbreviations of traits see Table 1 in **chapter 2**.

In addition, not all traits of forbs indicated a conservative strategy. For example, the higher root nitrogen concentration compared to grasses is thought to increase nutrient acquisition in fine roots because of a higher respiration rate and metabolic activity (Roumet et al. 2016; Weemstra et al. 2016). Roumet et al. (2016) and Weemstra et al. (2016) only showed this for fine roots whereas in my study fine and thick roots were not distinguished. On the contrary, higher nutrient concentrations can be seen as conservative strategy. A high nutrient concentration in roots might be an indication for a storage root, which is a common characteristic in the investigated forb species due to their heterogeneous root system (Strasburger 2002). However, as the difference between grass and forbs in root N concentration was only marginally significant, this result needs to be approved by other studies. Furthermore, leaf phosphorus concentration also indicates an acquisitive strategy (Wright et al. 2004; Pérez-Harguindeguy et al. 2013), whereas root P concentration (RPC) belonged to neither of both strategies in a meta-analysis by Freschet et al. (2010), but RPC was higher in forb species (**chapter 2**).

In conclusion, not all questions in explaining resource use strategies are fully solved and both strategies might be present in both growth forms. Especially root nutrient concentrations have not been well investigated so far and should be included with other measurements such as root respiration, water and nutrient acquisition, root lifespan and root decomposability to identify their function along the root economics spectrum (RES) (Roumet et al. 2016). Similarly, if not considering the habitat conditions like nutrient availability, a clear separation in acquisitive and conservative strategy might not be possible (Pérez-Harguindeguy et al. 2013; Weemstra et al. 2016). Furthermore, Weemstra et al. (2016) argued that a RES might not be applicable for all traits as roots could have different functions along the acquisitive-conservative axis than leaves. For example, as SLA is directly linked to photosynthetic rate and leaf N concentration, it is also expected that specific root length has an analogous function in the RES (Weemstra et al. 2016). However, Weemstra et al. (2016) were not able to find such a clear evidence for the existence of a RES in their review. Furthermore, Kong et al. (2015) found evidence for the RES only for fine roots but not for thick roots.

Conclusion and future directions

My overarching hypotheses made in the introduction (Fig. 2 in **chapter 1**) have to be adjusted (Fig. 4). In Fig. 4 all relationships between the variables used in **chapters 2 to 4** were summarized using a partial least squares path model (PLSPM). It gives an overview about the strength of the correlations investigated in all chapters. In this now bigger model it still holds true that exudates and functional traits are mainly influenced by variables varying at the plot level especially climate and soil conditions as described in **chapters 2 and 4**. Land use intensity had the lowest influence on all three response variables. The effect of local neighbourhood diversity was highest on plant functional traits and of unexpected high magnitude (Fig. 4b). Among the properties of the phytometers, individual plant performance had the greatest impact on exudates similar to the variance partitioning in **chapter 4**. Similar to **chapter 3**, individual plant performance was best predicted by the phytometers' plant functional traits. All in all, the PLSPM perfectly reflected most of the results of **chapters 2 to 4**, although the goodness of fit of the models was relatively low. This model should be developed further with additional data such as microbial community, root and secondary metabolites, nematodes, mycorrhizal community, rhizosphere enzyme activity and endophytes, which were measured during this project but would have exceeded the scope of this thesis. Nevertheless, this thesis highlights the importance of plant functional traits and of including intraspecific variation in most measurable plant properties. The conducted experiment was very valuable as it reflects the natural conditions in grasslands and displays a basis for further research. In the next step more variables as described above can be included to further increase our knowledge about drivers of intraspecific variation and the complex processes in the rhizosphere.

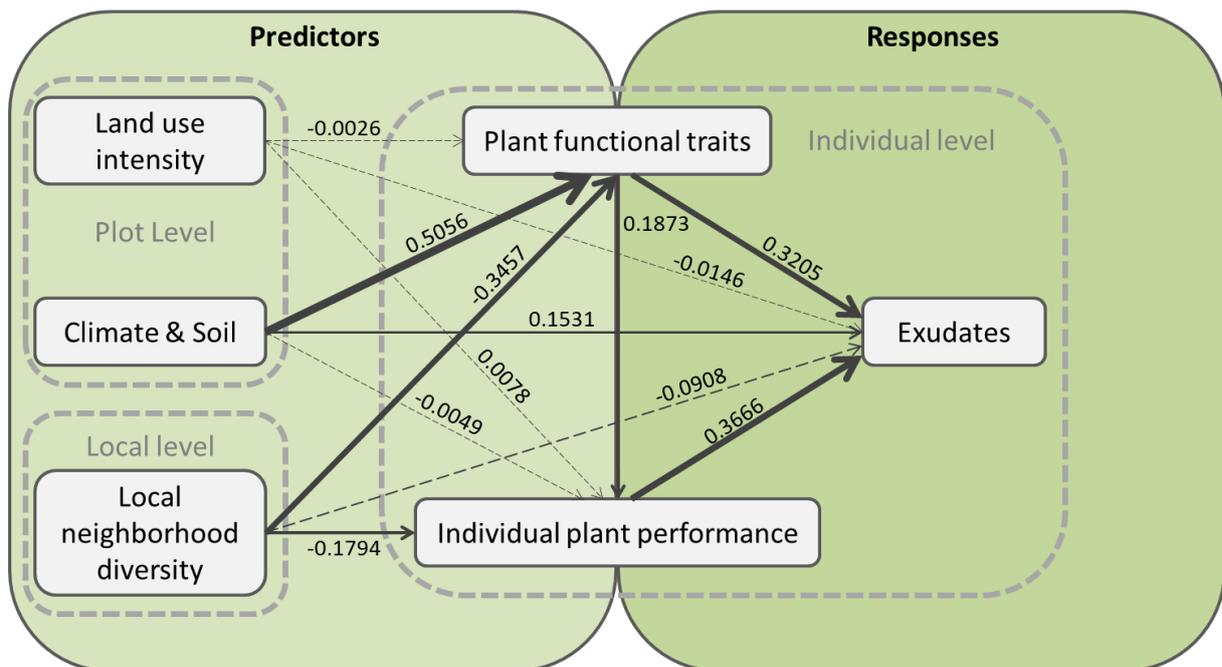


Fig. 4a. Illustration of the research questions tackled in this thesis. Numbers on the arrows show the estimates obtained from a partial least squares path model using the function `plspm` in R (package `plspm`; Sanchez 2013). Dashed lines indicate non significant and solid lines significant relationships. In this Figure only data from the harvest of 2014 was used. All variables used in the **chapters 2 to 4** (except CWM and FD values as they were assessed in 2015) were combined to the six displayed latent variables (white boxes). LDMC, RSR, RPC, RKC, and RMgC were excluded from the analysis as, according to the cross-loadings of the path model, they did not fit to the latent variable “Plant functional traits”. The thickness of arrows was scaled to the magnitude of the estimates. Goodness of fit = 0.219.

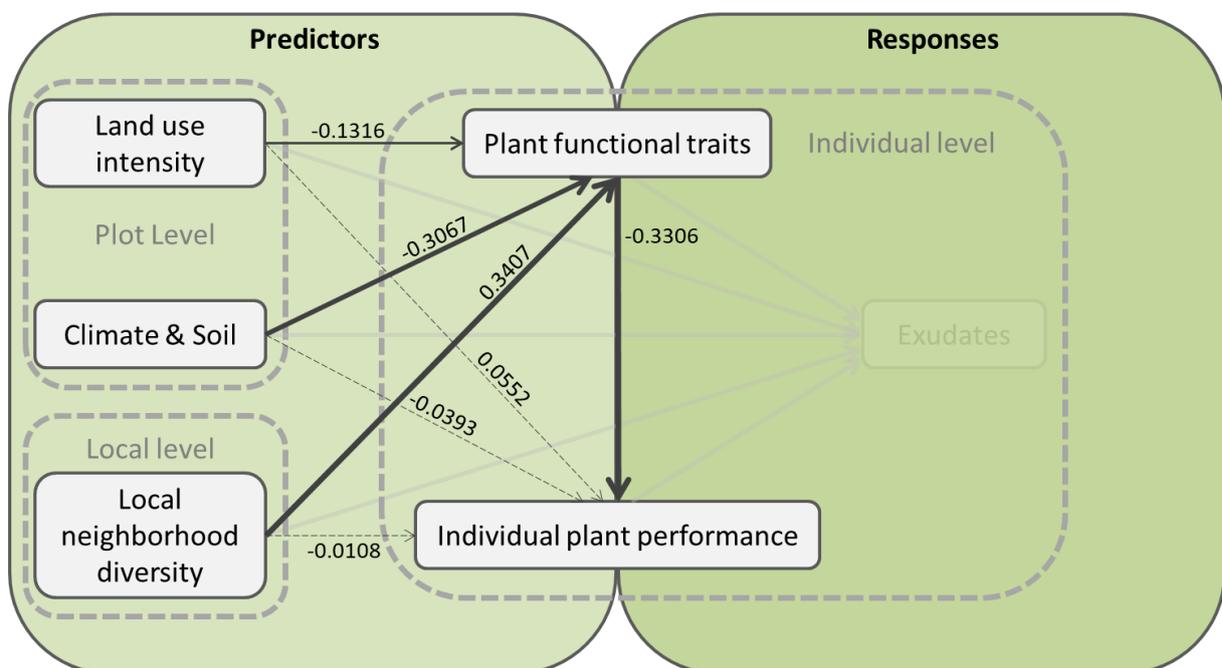


Fig. 4b. Illustration of the research questions tackled in this thesis. Numbers on the arrows show the estimates obtained from a partial least squares path model using the function `plspm` in R (package `plspm`; Sanchez 2013). Dashed lines indicate non significant and solid lines significant relationships. In this Figure only data from the harvest of 2015 was used. All variables used in the **chapters 2 and 3** were combined to the five displayed latent variables (boxes). RCNR, RCaC and RCC were excluded from the analysis as, according to the cross-loadings of the path model, they did not fit to the latent variable “Plant functional traits”. Exudates were not part of this model, as data from 2015 was not available. The thickness of arrows was scaled to the magnitude of the estimates. Goodness of fit = 0.216.

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APPENDIX

Curriculum vitae

Katharina Herz

Born 19 May 1989 in Lauchhammer, Germany

Nationality: German

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79252 Stegen

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Education

April 2014 – September 2017

PhD student at Martin-Luther-University Halle-Wittenberg (MLU), Institute of Biology / Geobotany and Botanical Garden.

Research topic: "Intraspecific variation of plant functional traits and root exudates in German meadows and pastures"

Funding: German Research Foundation (DFG)

Thesis advisor: Prof. Dr. H. Bruelheide (MLU)

October 2011 - November 2013

Master in Biology at Martin-Luther-University Halle-Wittenberg

Master thesis: „Invasive versus native seed heteromorphic annuals – which one performs better?“ (1.1, excellent)

Thesis advisors: Dr. S. Klotz and Prof. Dr. I. Hensen

September 2008 - September 2011

Bachelor in Biology at Martin-Luther-University Halle-Wittenberg

Bachelor thesis: „Auswirkungen eines Klimagradienten auf die Keimungseigenschaften der Nachkommen von Pflanzenarten unterschiedlichen Arealen“

Thesis advisor: Prof. Dr. H. Bruelheide

September 2001 - July 2008

Abitur at Freifrau-von-Löwendal-Gymnasium in Lauchhammer, Germany

Professional experience

December 2013 - April 2014

Student assistant, Helmholtz Centre for Environmental Research, Dr. S. Klotz (Writing a Review about the global distribution and characteristics of seed heteromorphic species)

November 2011 - January 2012	Student assistant, Institute for Geobotany and Botanical Garden, Prof. Dr. H. Bruelheide and Eva Breitschwerdt, project “biodiversity exploratories“
September 2010 - July 2011	Student assistant, Institute for Geobotany and Botanical Garden, Dr. U. Jandt (Digitalizing vegetation records for the German Vegetation Reference Database using the software Turboveg)

Teaching and supervision

September 2015 - July 2017	Carolin Graichen. Master Thesis: „Die Auswirkungen verschiedener Landnutzungsintensitäten auf die Merkmalszusammensetzung von Pflanzengesellschaften des Grünlands“. Main supervisor: Prof. Dr. H. Bruelheide
June 2016 - February 2017	Philipp Strohmeyer. Bachelor Thesis: “Auswirkung der Landnutzungsintensität auf Blattmerkmale von Grünlandarten“. Main supervisor: Prof. Dr. H. Bruelheide
September 2015 - January 2017	Robert Reuter. Master Thesis: „Auswirkung von Nachbarschaftseffekten auf oberirdische und unterirdische Merkmale und Produktivität von Gras- und Krautarten des Grünlandes“. Main supervisors: Dr. S. Haider, Prof. Dr. H. Bruelheide
November 2015 and November 2016	Teaching laboratory methods in the Bachelor course “Populations- und Standortökologie“

List of Publications

Rana, R., **Herz, K.**, Bruelheide, H., Dietz, S., Haider, S., Jandt, U., Pena, R. (2018): Leaf Attenuated Total Reflection Fourier Transform Infrared (ATR-FTIR) biochemical profile of grassland plant species related to land-use intensity. *Ecological Indicators* **84**, 803–810

Herz, K., Dietz, S., Haider, S., Jandt, U., Scheel, D., Bruelheide, H. (under Review): Linking root exudates to functional plant traits in ten grassland species. *Scientific Reports*

Herz, K., Dietz, S., Haider, S., Jandt, U., Scheel, D., Bruelheide, H. (2017): Predicting individual plant performance in grasslands. *Ecology and Evolution*, early view, DOI: 10.1002/ece3.3393

Herz, K., Dietz, S., Haider, S., Jandt, U., Scheel, D., Bruelheide, H. (2017): Drivers of intraspecific trait variation of grass and forb species in German meadows and pastures. *Journal of Vegetation Science* **28** (4), 705-716

Sendek, A., **Herz, K.**, Auge, H., Hensen, I., Klotz, S. (2015): Performance and responses to competition in two congeneric annual species: does seed heteromorphism matter? *Plant Biology (Stuttgart, Germany)* **17** (6), pp. 1203–1209.

Conference contributions

Herz K, Dietz S, Bruelheide H, Jandt U, Scheel D (2016): Linking root exudates to functional plant traits in natural grassland communities. 2nd Annual Conference of the German Centre for Integrative Biodiversity Research (iDiv); Leipzig, Germany. *Talk*

Herz K, Dietz S, Bruelheide H, Jandt U, Scheel D (2016): Linking root exudates to functional plant traits of ten grassland species in natural grassland communities. 46th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ); Marburg, Germany. *Talk*

Herz K, Dietz S, Bruelheide H, Jandt U, Scheel D (2016): BE LOW - Analysis of root traits and root exudates in grassland communities. 13th Assembly of the Biodiversity Exploratories; Wernigerode, Germany. *Poster*

Herz K, Dietz S, Bruelheide H, Jandt U, Scheel D (2015): Effects of biodiversity and land use on root traits and root exudates in grassland communities. Annual Conference of the German Centre for Integrative Biodiversity Research (iDiv); Leipzig, Germany. *Talk*

Herz K, Dietz S, Bruelheide H, Jandt U, Scheel D (2015): BE LOW - Analysis of root traits to test for environmental filtering and niche complementarity in grassland communities. 12th Assembly of the Biodiversity Exploratories; Wernigerode, Germany. *Talk*

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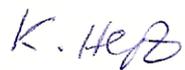
Eigenständigkeitserklärung

Hiermit erkläre ich an Eides statt, dass die Arbeit mit dem Titel „Drivers of intraspecific variation of plant functional traits, plant performance and root exudates in German grasslands“ bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Darüber hinaus erkläre ich, dass ich die vorliegende Arbeit eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), 14.06.2017



Katharina Herz