

ANU LEPIK

Plant competitive behaviour:
relationships with functional traits
and soil processes



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with functional traits and soil processes



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Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in plant ecology at the University of Tartu on August 29, 2019 by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu

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Commencement: Room 218, 40 Lai Street, Tartu, on December 12, 2019, at 10.15

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu

ISSN 1024-6479
ISBN 978-9949-03-236-5 (print)
ISBN 978-9949-03-237-2 (pdf)

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University of Tartu Press
www.tyk.ee

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by Roman numerals:

- I Semchenko, M., Lepik, A., Abakumova, M., & Zobel, K (2018) Different sets of belowground traits predict the ability of plant species to suppress and tolerate their competitors. *Plant and Soil*, 424(1–2), 157–169.
- II Lepik, A., Abakumova, M., Davison, J., Zobel, K. & Semchenko, M. (2019). Spatial mapping of root systems reveals inefficient soil exploration and a lack of territoriality in temperate grassland plants. *Manuscript in preparation*
- III Lepik, A., Abakumova, M., Zobel, K., & Semchenko, M. (2012). Kin recognition is density-dependent and uncommon among temperate grassland plants. *Functional Ecology*, 26(5), 1214–1220.
- IV Semchenko, M., Saar, S., & Lepik, A. (2017). Intraspecific genetic diversity modulates plant-soil feedback and nutrient cycling. *New Phytologist*, 216(1), 90–98.

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The author's contribution to the papers:

Was responsible for ***, contributed substantially **, contributed *

	I	II	III	IV
Designing the experiments				**
Data collection	**	**	***	***
Analyzing the results	**		**	*
Manuscript preparation	**	***	***	*

1. INTRODUCTION

Due to their sessile lifestyle, plants cannot choose their neighbours and plant individuals are strongly influenced by the surrounding vegetation (Turkington & Harper 1979; Aarssen & Turkington 1985; Ehlers & Thompson 2004; Fridley et al. 2007). Neighbouring plants may belong to the same species and be more or less genetically related (distantly related individuals, siblings or the same clone), or they may belong to a different species. Plant genotypes and species can vary in their resource needs and competitive ability affecting the chances that neighbouring genotypes and species can stably co-exist in the same community (Lavorel & Garnier 2002; Fridley et al. 2007; de Bello et al. 2010; Genung et al. 2012; Götzenberger et al. 2012). Easily measured morphological characteristics have been widely used in studies of plant community assembly as proxies of plant function and resource niches (Lavorel & Garnier 2002; de Bello et al. 2010; Götzenberger et al. 2012). However, the mechanistic links between measurable phenotypic traits and plant resource niches and competitive strategies are still poorly described, particularly for belowground traits. Furthermore, some species are phenotypically plastic and able to modify their traits depending on the genetic identity of their neighbours (Murphy & Dudley 2009; Biernaskie 2011; Dudley et al. 2013; Mercer & Eppley 2014). Phenotypic plasticity as a function of neighbour identity can modify competitive outcomes and have cascading effects on ecosystem processes, such as nutrient cycling (Schweitzer et al. 2005a), but empirical evidence for such effects is limited.

The principle of limiting similarity predicts stronger competition between species with similar trait values and it has therefore been suggested that only species with sufficiently different trait values can stably co-exist (MacArthur & Levins 1967; Chesson 2000). However, to promote co-existence, differences in traits have to reflect differences in plant resource niches. Many plant traits do not satisfy this assumption and instead reflect plants' competitive ability. Individual's success in competition can be achieved in two principal ways (Goldberg 1996). Firstly, plants can display an ability to suppress their neighbouring plants by taking resources up quicker than their competitors, resulting in negative impacts on their neighbours; this kind of behaviour is called competitive effect. Secondly, plants can have a good ability to tolerate competition from neighbouring individuals and maintain growth and reproduction despite lower resource availability due to uptake by neighbours; such ability is known as competitive response (Goldberg & Barton 1992; Goldberg 1996; Keddy et al. 1998). These two aspects of competitive ability are not mutually exclusive, but may have different implications for plant resource use efficiency and species co-existence (Aschehoug et al. 2016; Hart et al. 2018).

Plant size and resource assimilation rate have been considered as key plant traits that ensure competitive success (Goldberg 1996; Keddy et al. 2002). These traits are closely associated with competitive effects allowing plants with large individual size and fast growth rates to effectively suppress their neighbours.

Growing taller than neighbours and investing in light capture by producing large leaves with high specific leaf area and high nitrogen content have been shown to give plants an advantage in competition for light (Goldberg & Landa 1991; Kunstler et al. 2012; Herben & Goldberg 2014; Fort et al. 2014; Kraft et al. 2015; Bennett et al. 2016). These traits have been primarily linked with competitive effect ability, while traits relating to competitive response ability have been more difficult to identify. This remains to be a major knowledge gap in our understanding of plant competition, particularly in the light of recent theoretical advances demonstrating that the ability to tolerate competition from conspecific and heterospecific neighbours is key to competitive success (Hart et al. 2018).

It has been proposed that belowground traits are more likely to allow niche differentiation among species and explain variation in competitive response ability (Cahill Jr et al. 2005; Wang et al. 2010). The advantage of large individual size may be important aboveground as competition for light is strongly size-asymmetric, with a small difference in plant size conferring a large advantage in the suppression of neighbours (Weiner 1990). Competition for belowground resources is mostly symmetric, meaning that the success in competition is proportional to plant size (Casper & Jackson 1997; Cahill & Casper 2000). Plants also rely on roots for a wider range of resources, such as space, water, nitrogen, phosphorus and other macro- and micronutrients, and engage in complex microbial interactions (Casper & Jackson 1997; Kaye & Hart 1997; Cahill & Casper 2000). Plants may secure these different resources in many different ways and may be less reliant on large size for competitive success belowground. Therefore, it has been predicted that root traits might be better at predicting plants' tolerance towards neighbours than aboveground traits (Lauchlan et al. 1998; Schwinning & Weiner 1998; Cahill & Casper 2000; Belter & Cahill Jr. 2015). However, due to difficulties in obtaining belowground data, research on plant functional traits has primarily focused on aboveground characteristics and the knowledge of belowground traits and their contribution to competitive effect and response is limited. It has been shown that species with larger root systems – either greater biomass allocation to roots or higher specific root lengths – can be superior in competition (Wang et al. 2010; Ravenek et al. 2016). Rooting depth has been considered a major axis of niche differentiation among plants (Parrish & Bazzaz 1976; Berendse 1982). However, in recent years, this hypothesis was not supported and it was found that rooting depth may be more closely related to competitive ability rather than niche differentiation (Mommer et al. 2010; Kraft et al. 2015; Hoekstra et al. 2015). Instead, simultaneous differences in multiple traits, such as specific root length in combination with aboveground traits, have been found to promote niche differentiation and species co-existence in annual plant communities (Kraft et al. 2015; Bennett et al. 2016).

Beyond morphological root traits and rooting depth, the distribution of roots at small spatial scales may also significantly modify competitive interactions and the efficiency of resource uptake. However, due to methodological difficulties of characterising root spatial distributions, fine-scale rooting patterns

have rarely been quantified and related to competitive outcomes (Mahall & Callaway 1992; Semchenko, et al. 2007a). Plant root systems are often extensive, comprising kilometres of root length and thousands of root tips. As all roots originate from a single rooting point (except for clonal plants, which may have multiple rooting points), plant root behaviour (defined as morphological or physiological responses to external events; Silvertown & Gordon 1989) could be analogous to that of eusocial central-place foragers such as bees and ants. In this case, root tips are alike to closely related individuals serving the purpose of foraging and delivering resources to a central “nest-site” – the rooting point connected to aboveground tissues. Root spatial distributions are expected to follow the ideal free distribution in the absence of competitors, minimising intraplant competition and maximising resource uptake efficiency (McNickle & Brown 2014). It has been shown that plants indeed invest root biomass into different soil patches in proportion to available resources (Robinson 1994; Hodge 2004). However, we still lack detailed measurements to determine whether plants attain an ideal free distribution at the scale of individual roots. Given that all roots are physically connected to each other and originate from a single rooting point, the spatial positioning of roots is likely to deviate from ideal free distribution and roots of the same plant are aggregated at small spatial scales, restricting the maximum efficiency with which plants can forage for resources (Robinson et al. 2003). However, plant species vary widely in root branching frequency and angles, creating a diversity of potential root spatial patterns as well as associated root construction costs (Lynch 1995; Rubio 2001; Mommer et al. 2010; Postma & Lynch 2012). For example, some species adopt the herringbone root branching pattern, which is characterised by high uptake efficiency but high construction costs. On the other hand, dichotomous root systems are cheaper to construct but offer low uptake efficiency (Fitter et al. 1991; Fitter & Stickland 1991; Dunbabin et al. 2004). How root architecture and associated spatial distributions relate to previously described plant growth strategies, and what are the consequences for plant interactions within and between species, is still poorly understood.

While plants have a limited ability to move and choose their neighbours, plants are able to exhibit high phenotypic plasticity in their traits when faced with competition for limiting resources. In limited light conditions plants are able to increase allocation to shoots, produce larger leaves and elongate stems and petioles (Weiher et al. 1999; Loehle 2000; Westoby et al. 2002); in conditions of nutrient limitation, on the other hand, plants invest more in root growth (Gersani et al. 2001; O’Brien et al. 2005). Such behaviour enhances the acquisition of limiting resources, but in situations where most individuals adopt the same behavioural pattern, the overall efficiency of resource acquisition may be reduced and each plant individual has a lower reproductive output than would be possible if plants restrained their allocation to resource-acquisitive organs. This phenomenon of individuals overexploiting a common resource due to collectively acting according only to their self-interest is called the tragedy of the commons (Hardin 1968) and it has been observed both in belowground

(Dudley & File, 2007; Falik, Reides, Gersani, & Novoplansky, 2003; Gersani et al., 2001; Gruntman & Novoplansky, 2004; but see Hess & De Kroon, 2007; Semchenko et al. 2007b) and above-ground competition (Anten 2002; Falster & Westoby 2003). Excessive allocation to resource-acquisitive organs at the expense of reproductive output is an evolutionary stable strategy when competing plants are unrelated to each other (Gersani et al. 2001). However, the situation changes when neighbouring plants are genetically closely related: by limiting their investment to root and shoot growth, plants can increase their fitness directly by allowing more resources to be invested into reproduction and as well as indirectly by reducing the competitive suppression of genetically related neighbours (Kelly 1996; Holzapfel & Alpert 2003; Semchenko et al. 2007a; Dudley & File 2007). The probability of having closely related neighbours depends on life-history traits, such as self-fertilization, barochory or clonal propagation (Turkington & Harper 1979; Cheplick 1992). When the probability to grow next to a closely related individual is sufficiently high, plants can benefit from neighbour recognition ability and adopting a cooperative behaviour towards close relatives (Hamilton 1964; Waldman 1988; Dudley & File 2007).

The ability to recognize genetically related plants and change root/shoot allocation to reduce competition with siblings has been shown in a few studies (Dudley & File 2007; Biedrzycki et al. 2010; Bhatt et al. 2011; Biernaskie 2011). Also, some plant species showed greater seed germination and seedling survival (Willson et al. 1987), higher flowering probability (Tonsor 1989) and greater allocation to reproduction when grown with siblings, suggesting that plant responses may have been shaped by kin selection (Donohue 2004; Biernaskie 2011). However, according to niche partitioning theory, closely related plants are expected to have more similar resource niches and experience stronger competition compared to genetically diverse groups (MacArthur & Levins 1967; Silvertown 2004). In support of niche theory, some studies have shown that plants exhibit lower shoot mass and lower reproductive output when grown with siblings compared to non-siblings (Escarre et al. 1994; Cheplick & Kane 2004). It is not yet possible to draw conclusions about how widely kin recognition is spread in natural plant communities, as usually only a single plant species is examined per study and a very limited set of traits is measured. Moreover, competition between plants is density-dependent and kin recognition may not be expressed equally at all neighbour densities but may depend to the severity of resource limitation and the relative costs and benefits of co-operative behaviour towards related individuals. Most of the studies on kin recognition have used a fixed neighbour density and the density-dependence of plant behaviour towards related neighbours remains unknown.

While plant behavioural responses to kin can have immediate consequences for plant fitness, associated morphological changes in plant traits may also influence ecosystem processes such as carbon and nitrogen cycling. Plant species diversity has been shown to play a significant role in regulating ecosystem functioning (Knops et al. 2002; Steinbeiss et al. 2008; Cong et al. 2014). Moreover, there is increasing evidence that intraspecific genetic diversity plays

an important role in species co-existence (Booth & Grime 2003; Whitlock 2014; Schoeb et al. 2015), increasing primary production (Crutsinger et al. 2006), enhancing litter decomposition (Schweitzer et al. 2005b) and increasing resistance to herbivores and pathogens (Zhu et al. 2000; Parker et al. 2010; Tooker & Frank 2012; Barton et al. 2015). In low diversity situations, plants possibly experience increased pathogen pressure and herbivore damage (Mitchell et al. 2002; Lau et al. 2008; Schnitzer et al. 2011). The mechanisms by which intraspecific genetic diversity can affect ecosystem functioning are still quite poorly understood. It has been shown that more diverse plant litter decomposes faster than expected (Schweitzer et al. 2005b; Wang et al. 2014) and it could be explained by providing a more complete range of substrates to a more diverse set of decomposers. Kin recognition and associated changes in the quantity and quality of litter could be an unexplored mechanism by which genetic diversity of co-existing plants could affect ecosystem processes. It has been shown that plants can produce roots with lower specific root length when subjected to cues of sibling as compared with non-sibling presence (Semchenko et al. 2014). Such changes in plant tissue properties can in turn influence microbial activity and composition, affecting soil functioning and feeding back to plant nutrition and fitness (known as plant-soil feedback; Bray, Kitajima, & Mack, 2012; Madritch & Lindroth, 2011; Whitham et al., 2006).

This thesis explores the variation in competitive ability and niche differentiation among common grassland species (I), the relationship between below-ground traits and spatial root distributions (II), and examines the prevalence of kin recognition among grassland species (III) and its consequences for soil processes (IV). To address these themes, we performed a series of common garden experiments where a range of grassland species were grown in competition with other species and conspecifics of different genetic identity and diversity. Plants were also subjected to soil previously occupied by plant groups of siblings or genetically diverse plants to examine the effects of kin and nonkin interactions on soil processes. The objectives of these studies were:

- 1) to determine which belowground traits enhance species' ability to suppress and tolerate neighbours and which traits or combinations of traits allow niche differentiation among common temperate grassland species;
- 2) to examine the efficiency of root spatial positioning across a range of grassland species in different neighbour density and identity settings;
- 3) to integrate root spatial patterns with previously measured size and morphological traits;
- 4) to determine if kin recognition is a widespread phenomenon, rather than an exception, in temperate grassland communities;
- 5) to determine how kin recognition responses are modified by the density of neighbouring individuals;
- 6) to identify the consequences of kin recognition for nutrient cycling in the soil and feedbacks between plants and soil biota.

2. MATERIALS AND METHODS

2.1. Plant competitive and kin recognition ability, root spatial distribution (Papers I, II, III)

To examine the variation in competitive and kin recognition ability, and determine root spatial patterns, across a range of grassland species, seeds were collected from seven grassland communities. All seeds were air-dried and stored at 4 °C until the experiments began. We selected twenty-six species as focal species for the interspecific competition experiment across all seven grassland communities (I). We selected one of the seven calcareous grasslands (58°38'31"N, 23°30'55"E) and corresponding eight focal species from the competition experiment (I) for the root spatial distribution study (II). Eight plant species for the kin recognition experiment (III) were collected from a floodplain meadow in Estonia (58°25'32"N; 26°30'40"E). The seeds were germinated on moist sand in a greenhouse and transplanted into pots filled with a mixture of soil from a horticultural supplier, sand and limestone powder. We prepared the soil mixtures differently, depending on the study site, trying to match the N content and pH of natural soil at the site of seed origin as closely as possible (Semchenko et al. 2013). Also, natural soil from the study site was added to the mixture to provide plants with “native” soil biota.

In the competition and root spatial distribution experiment (I, II), we planted a focal plant at the centre of each pot and a different number (0, 1, 2, 3, 4, 6 or 8) of conspecific or heterospecific neighbours from a single species in a circle surrounding the focal plant. Each combination was replicated twice (i.e. 28 pots per focal species). In the assessment of species competitive ability (I), only pots with heterospecific neighbours were used (i.e. 14 pots per focal species). In the root spatial distribution study (II), both species monocultures and mixtures were analysed. Pots were placed in a common garden and their position was randomised twice during the experiment.

Plant density and relatedness were used as treatments in the kin recognition experiment (III). We grew focal plants at two densities (2 or 14 plants per pot) together with either seedlings originating from the same mother plant (probably half-siblings) or a mixture of randomly selected seedlings from different mother plants (non-siblings).

Plants were harvested after 11–14 (I), 14 (II) or 10 (III) weeks of growth. In the competitive ability and root spatial distribution studies (I and II), above-ground biomass was removed and dried it at 70 °C for 48 h. In the kin recognition experiment (III), two fully expanded and healthy leaves were selected to measure leaf area, then dried and weighed to calculate specific leaf area (SLA). To provide an estimate of leaf elongation, mean leaf length was calculated using five fully expanded and healthy leaves. Petiole length was used as an estimate of leaf elongation in *Medicago lupulina* and *Trifolium repens*, because these

species have horizontally oriented leaf laminae. Plant shoots were oven-dried at 75 °C for 48 h and vegetative parts were weighed separately.

To assess root densities and spatial distributions, soil from each pot was frozen at -18 °C and subsequently sliced horizontally at depths of 5 cm and 10 cm below the soil surface. The surface of the soil was lightly cleared with water to expose root intersections and the defrosted surface was scanned. To estimate root density in the competition experiment (I), the number of root intersections was recorded in 19 sampling plots (Fig. 1). In the spatial root distribution study (II), the location of all visible root intersections within the central area of the scanned image ($2/3$ of the pot radius), were recorded (Fig. 1). In the hetero-specific treatment, examined species had different root colours, allowing the distinction between the roots belonging to focal and neighbouring species. In the conspecific treatment, focal and neighbouring plant roots were not distinguished. In the kin recognition experiment (III), the number of root intersections was recorded in 16 sampling plots distributed across the soil scans in a hexagonal pattern (Fig. 2).

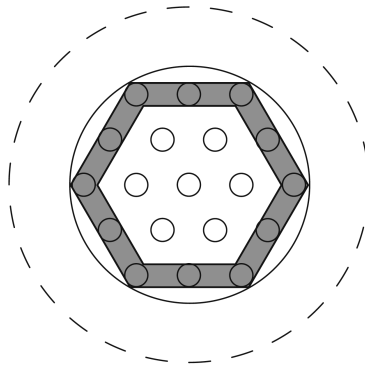


Figure 1. Root intersections visible on the scanned image of soil surface were recorded within 19 sampling plots (each 1 cm²) distributed in a hexagonal pattern across the central area of the pot (I) or all roots were recorded in the central area (II). Horizontal root system spread was calculated as the number of root tips located in the outer hexagon (grey area) divided by the total number of root tips recorded in the outer and inner hexagons. Pot outline is shown with the dashed line (redrawn from Fig. S1 in Paper I).

In the competition experiment (I), the scanned images were used to calculate the horizontal spread of root systems (number of root intersections at the periphery of the pot at 5 cm depth divided by the total number of root intersections at 5 cm soil depth, Fig. 1) and the vertical distribution of the root system (number of root intersections at 5 cm soil depth divided by the total number of focal root intersections recorded at 5 cm and 10 cm soil depth). In the root spatial distribution study (II), the coordinates of each root intersection were recorded using ArcGIS software (version 10.0, ESRI, Aylesbury, UK). In the kin

recognition experiment (III), we calculated root density based on the number of root intersections at 5cm depth.

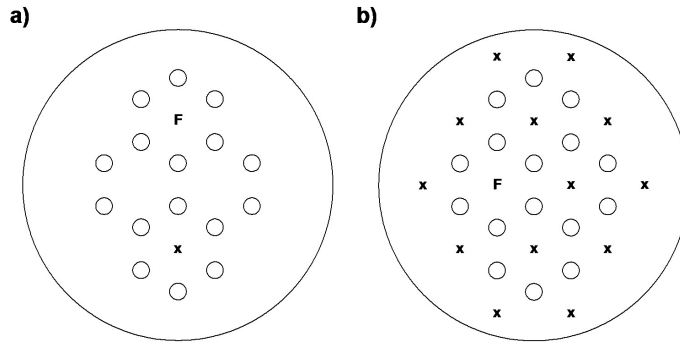


Figure 2. Planting patterns used in a) low density and b) high density treatments. “F” signifies the position of the focal plant and crosses represent positions of neighbour plants. Distance between plants was 10 cm in the low density pots and 5 cm in the high density pots. Circles represent the positions of 16 sampling plots (area 1 cm²) that were used for assessing root density on scanned soil images (redrawn from Fig. S1 in Paper III).

For the competition and root spatial distribution studies (I, II), to measure different root traits, we carefully washed out roots of focal and neighbouring plants from the top 5 cm soil layer and separated them. We selected two representative root axes with associated higher order laterals from each focal plant and its neighbours for morphological analysis. We scanned plant roots and calculated root length, volume, number of root tips and mean root diameter. Scanned roots and the rest of the roots and aboveground biomass were dried 70 °C for 48 h and weighed separately. SRL (ratio of root length and root dry mass), root tissue density (ratio of dry root mass and root volume), and branching frequency (number of root tips per unit of root length) were calculated.

Statistical analysis

In Paper I, to understand how much the focal plant loses in growth with increasing neighbour density, we calculated *growth response to competition* (GRC) as the slope of the regression between ln-transformed aboveground biomass of the focal plant and neighbour density (Figure 3). GRC was also calculated using root biomass. As root biomass showed very similar results, we used in further analysis slope values based on aboveground biomass. The more negative is the value of GRC, the stronger is the competitive suppression of the focal plant.

To examine how root vertical distribution and morphology were modified in focal species in *response to neighbour density*, linear models were constructed

with root traits as response variables and neighbour density as an explanatory variable. Directional plasticity was calculated as the slope of the linear relationship between neighbour density and ln-transformed root traits. The magnitude of plasticity was calculated as the absolute value of directional plasticity. Linear models were used to examine the role of root trait plasticity in *competitive ability*. Growth response to competition (GRC) was included in the models as the response variable and the plasticity of each trait as explanatory variables.

Values of seven belowground traits were calculated for each focal and neighbour species (mean horizontal spread, ln-transformed root mass, mean root vertical distribution, ln-transformed SRL, root diameter, root tissue density and root branching frequency across all neighbour densities). To estimate the maximum growth potential of these plants under the experimental conditions, root horizontal spread and root biomass were calculated for plants grown in the absence of competition.

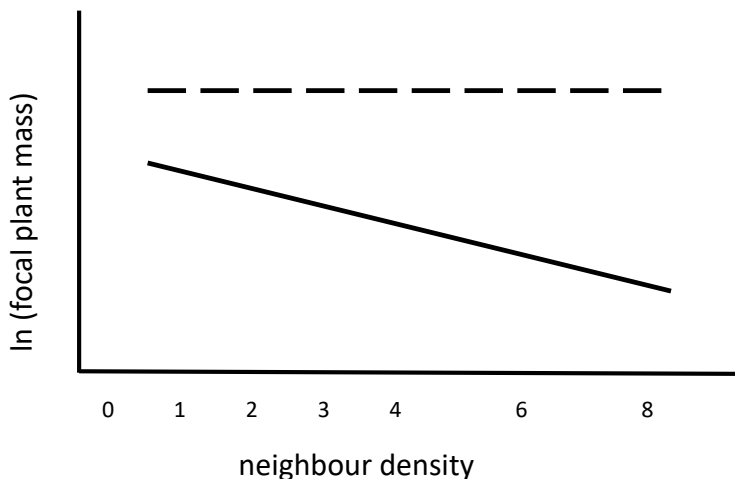


Figure 3. Growth response to competition was calculated as the slope of the regression between ln-transformed aboveground biomass of the focal plant and neighbour density. The more negative is the slope, the stronger is the competitive suppression of the focal plant. The dashed line illustrates no competitive suppression and the solid line illustrates strong competitive suppression.

To examine the effects of focal and neighbouring species' traits on *growth response to competition* (GRC), linear models were used with GRC as a response variable and either a) the mean trait value of the focal species and the mean trait value of the neighbouring species or b) the mean Euclidean distance between the focal and neighbouring species' trait values as explanatory variables. The first model tests the significance of focal and neighbouring species' root traits in explaining competitive suppression of focal plant species. The second model tests whether differences in root traits result in niche

differentiation (less severe competition occurring when there are greater distances between the focal and neighbouring species' trait values). Euclidean distances between the trait values of focal and neighbour species were calculated for each belowground trait separately as well as in a two- to seven-dimensional trait space. Model fit was assessed using Akaike Information Criterion (AIC).

In Paper II, root spatial aggregation was calculated at three spatial scales ($t = 2$ mm, $t = 1$ cm and $t = 2.85$ cm) for each pot and soil depth using the L function:

$$L(t) = \sqrt{\frac{K(t)}{\pi}} - t,$$

where $K(t)$ is the expected number of additional points (represented by root intersections in this study) within a distance t of an arbitrary point within the study area, divided by the overall density of the points and corrected for edge effects; Ripley 1976; Rowlingson & Diggle 1993). The study area was defined as the minimum convex polygon incorporating all root records within a given pot. L functions were calculated using *splanx* package in R (Rowlingson & Diggle 2017).

To assess how the roots of two species in mixture were positioned, we calculated the *bivariate L function* (L_{bv}), where bivariate K function – the expected number of roots belonging to species 1 within a distance t of an arbitrary root belonging to species 2 – is divided by the overall root density of species 1 and corrected for edge effects. The value of the $L(t)$ function is zero if roots of two species are distributed randomly. If the value is negative, then plant roots are segregated and if positive, then roots of one species aggregate towards other species' roots. Only root records in the area where root systems of the two species overlapped was used in calculations. L_{bv} was calculated at three spatial scales ($t = 2$ mm, $t = 1$ cm and $t = 2.85$ cm).

To estimate *home range size* (area, which is occupied by plant roots), two characteristics were calculated: minimum convex polygon range (MCP; the total area where roots are expanded) and the core area (defined as the 50% kernel area based on the bivariate normal kernel method (Worton 1989). Ranges were calculated using package *adehabitatHR* in R (Calenge 2006). In species mixtures, *home range overlap* was described using three parameters: the overlap between focal and neighbour species MCP ranges, core areas and total kernel volumes (the latter expressed as a proportion).

We used *linear mixed models* to estimate the effect of focal species identity (fixed factor eight species), neighbour density (fixed factor, continuous variable) and soil depth (fixed factor, two levels) on root spatial patterns. In all models, pot identity was included as a random factor and response variables were: (a) L function in species monocultures and in mixtures; (b) the differences between the observed L function and expected L function, based on monoculture

data; (c) bivariate L function; (d) MCP range of the focal plant; (e) core area of the focal plant; (f) MCP range overlap; (g) core area overlap; (h) kernel volume overlap between focal and neighbour plants. For a–c, separate models were performed for each spatial scale.

To examine relationships between root spatial patterns and plant traits, we used root trait data from Paper I. Focal species trait means were calculated as predicted values at the medium neighbour density (four neighbours) using a linear model with neighbour density as a continuous predictor and root trait as a response variable. Absolute differences between focal and neighbour trait values were calculated in species mixtures. Pearson's correlations between trait means and L functions at each spatial scale were examined in species monocultures. In the species mixtures, correlations between trait means and range size (MCP and core), and L functions, of the focal plant were calculated. Correlations between absolute trait differences between the two species in the mixture, home range overlap (MCP, core and kernel volume) and bivariate L functions were studied.

In Paper III, linear mixed models were constructed with neighbour density and genetic relatedness as fixed, explanatory factors, the family line of the focal plant as a random factor and plant traits as response variables. To assess size-independent changes in morphology and biomass allocation in response to the treatments, inflorescence mass, leaf length, SLA and root density were used as explanatory variables, with dry shoot mass included in the models as a covariate to eliminate plant size effects. All traits were ln-transformed before analysis.

2.2. Plant-soil feedback and nutrient cycling experiment (Paper IV)

To investigate the consequences of kin interactions for root litter decomposition and negative feedback between plants and soil biota, we designed an experiment with two phases: a) soil conditioning phase (to expose the soil to groups of siblings or genetically diverse groups); b) feedback phase (to study the influence of soil legacy on root litter decomposition and plant growth).

a) Soil conditioning phase

Seeds from multiple mother plants of *Deschampsia cespitosa* were collected from a floodplain meadow in Estonia (58°25'32"N; 26°30'40"E). We grew plants as sibling groups (using offspring from a single mother plant) or diverse groups (using offspring of multiple mother plants from the same population). Pots were filled with a mixture of fine sand, soil from a horticultural supplier and natural soil from the study site. In the control treatment, the same soil mixture was used but no seedlings were planted. Pots were placed in a glass-house, sown with seeds, and three weeks later seedlings were thinned to 15 plants per pot.

After three months of growth, shoots were cut at soil level and soil and roots were homogenised. To test the effects of soil microbes, soil was split into two parts, one part was sterilised by gamma radiation (dose 15KGy) and the other remained unsterilized. Soil from each sibling group was kept separately to maintain genetic relatedness between plants in the conditioning and feedback stages. Roots were separated from the soil, dried and root carbon and nitrogen content determined using a CN elemental analyser (Elementar vario EL cube; Elementar Analysensysteme GmbH, Langenselbold, Germany). Soil pH_{KCl} and N (Kjeldahl method) available P, K and organic matter content were also determined according to methods described in Moore and Chapman (1986).

b) Feedback phase

Seeds from the same mother plants were germinated and six seedlings from each mother plant were transplanted into pots (single plant per pot) using a factorial design, combining three soil conditioning treatments (conditioned by siblings, by a diverse group or control with no plants) and two sterilization treatments (sterilized or unsterilized). Each treatment combination was represented with 10 replicates resulting in 60 pots in total. Conditioned soil included dead roots to allow for root litter decomposition during the feedback stage.

The length of the longest leaf was recorded after two week of growth to estimate initial seedling growth. Plants were harvested after 58 days of growth. Roots were washed out and separated into roots belonging to the focal plants (roots from the focal plants that were attached to the shoots) and dead roots that were left undecomposed in the conditioned soil. An adventitious root branch with all attached higher order branches was selected and scanned. We calculated specific root length (SRL) for all plants using the dry mass of scanned root sample and total root length. Plant material was dried at 70 °C for 48 h and weighed separately. Root samples were analysed for C and N content.

c) Statistical analyses

In the soil conditioning phase, linear fixed effects models were used to assess the effects of conditioning treatment on root C and N content and C:N ratio and also to estimate the effect of soil conditioning and sterilization on soil pH, N, P, K and organic matter content at the end of the conditioning phase.

In the feedback phase, linear mixed models were used to estimate the effects of soil conditioning and sterilization on each of the following response variables: the proportion of root litter remaining undecomposed after 58 days of incubation, seedling length at two weeks, total dry mass, root:shoot biomass ratio, specific root length, C and N content and C:N ratio of focal plant roots and shoots. Data were log-transformed before analysis and mother plant lineage was included in the analyses as a random factor.

To assess the effect of soil biota associated with plants on plant growth and C and N content, the soil feedback index was calculated as $\ln(T_{\text{treat}} / T_{\text{control}})$, where T_{treat} is the trait mean for plants in each conditioning \times sterilization treatment combination (conditioned by siblings or non-siblings, sterile or unsterilized) and T_{control} is the trait mean for plants grown in the corresponding control soil (no plants in the conditioning stage, sterile or unsterilized soil).

In all experiments, roots, leaves and defrosted soil surface were scanned using scanner Epson Perfection V700 (Long Beach, CA, USA), and leaf area and root morphological parameters were measured using scanned images and the program WinRhizo 2008a (Regent Instruments Inc., Quebec, Canada). The program UTHSCSA Image Tool v3.0 was used to measure leaf length. All analyses were performed using R 2.11.1 (R Development Core Team 2010, in III) and R v.3.3.2 (R Core Team, 2016, in I, II, IV). Linear mixed models were fitted with the R package lme4 (Bates et al. 2015).

3. RESULTS

3.1. Traits underlying the ability of plants to suppress and tolerate their neighbours

Plant root traits were significantly affected by the density of neighbouring plants, but changes in root traits varied widely between plant species. Some species showed an increase in trait values with increasing neighbour density while other species showed a decrease in values of the same trait. Focal plants were more suppressed by neighbouring plants that had a larger root system (larger root mass and/or wider root system horizontal spread; Table 1 and Fig. 4 c–d). On the other hand, root mass and horizontal spread of the focal plant did not significantly affect the ability of the focal plant to withstand competition from neighbours (Table 1 and Fig. 1 a–b).

Table 1. Summary of the multiple regression models examining the relationship between growth response to competition (response variable) and mean trait values of the focal and neighbour species (explanatory variables). Model coefficients, standard errors and statistical significance (NS – $P > 0.01$; \$ – $P < 0.1$; * – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$) are presented. Negative coefficients mean greater competitive suppression with increasing trait value. Phyl. Signal denotes likelihood ratio test comparing models with and without phylogenetic correlation structure. N – number of species (Paper I).

Trait	Focal's trait	Neighbour's trait	Phyl.signal	N
Root mass (g)	–0.02(0.02) NS	–0.06(0.01) ***	NS	22
Horizontal spread	0.001(0.07) NS	–0.22(0.06) **	**	26
Vertical distribution	–0.52(0.16) **	0.06(0.19) NS	NS	18
SRL (cm/mg)	–0.07(0.04) \$	–0.01(0.03) NS	NS	22
Diameter (mm)	0.13(0.08) NS	–0.06(0.07) NS	NS	22
Tissue density (g/cm ³)	0.04(0.05) NS	0.12(0.05) *	NS	22
Branching frequency(1/cm)	–0.08(0.03) *	0.08(0.08) NS	NS	22

Species with deeper root systems, lower SRL and less branched roots were better at tolerating interspecific competition (Table 1 and Fig. 5a–b, c–d, i–j), but these traits did not affect the ability of plants to suppress neighbours. Root tissue density, on the other hand, had no significant impact on the competitive response of focal plants but affected the competitive effect of neighbours: root tissue density did not affect the ability of focal plants to withstand competition but neighbouring species with a lower root tissue density had a more suppressive effect on the growth of focal plants. When pot volume and soil N content were included in the model as covariates, the relationship between plant trait values and plant growth response to competition did not change significantly.

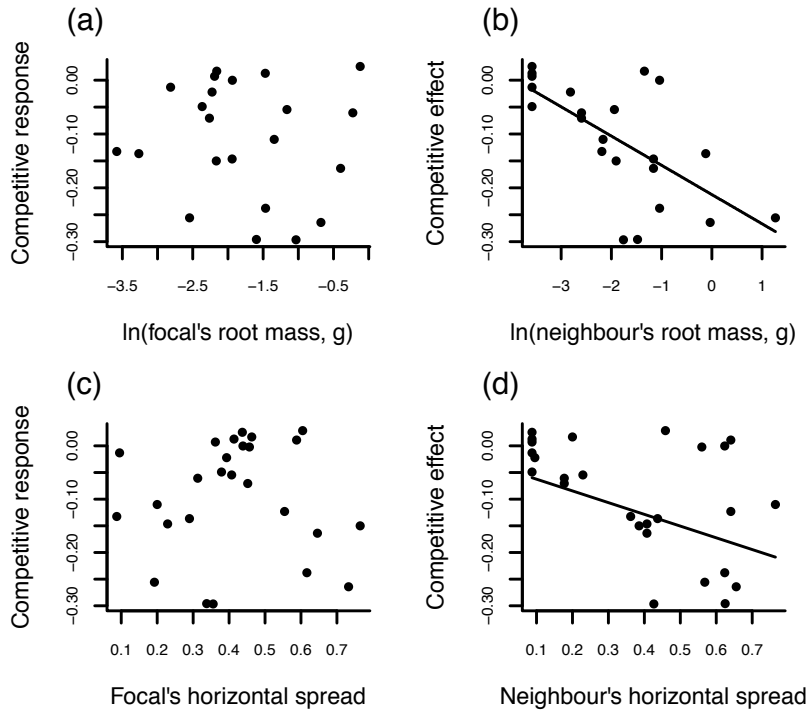


Figure 4. Interspecific relationships between the growth response of focal species to competition and a) root mass of focal species; b) root horizontal spread of focal species; c) root mass of neighbour species; and d) root horizontal spread of neighbour species. The y-axis shows the slope of the relationship between focal plant mass and neighbour density, with more negative values indicating stronger growth suppression by neighbours. Horizontal spread was measured as the proportion of total root tips located at the periphery of the pots at 5cm soil depth. All root traits were measured on plants grown in the absence of competition to estimate their growth potential. Solid lines show regression lines of relationships that were significant at $P < 0.05$ (Paper I).

Species with deeper root systems, lower SRL and less branched roots were better at tolerating interspecific competition (Table 1 and Fig. 5a–b, c–d, i–j), but these traits did not affect the ability of plants to suppress neighbours. Root tissue density, on the other hand, had no significant impact on the competitive response of focal plants but affected the competitive effect of neighbours. Root tissue density did not affect the ability of focal plants to withstand competition but neighbouring species with a lower root tissue density had a more suppressive effect on the growth of focal plants. When pot volume and soil N content were included in the model as covariates, the relationship between plant trait values and plant growth response to competition did not change significantly.

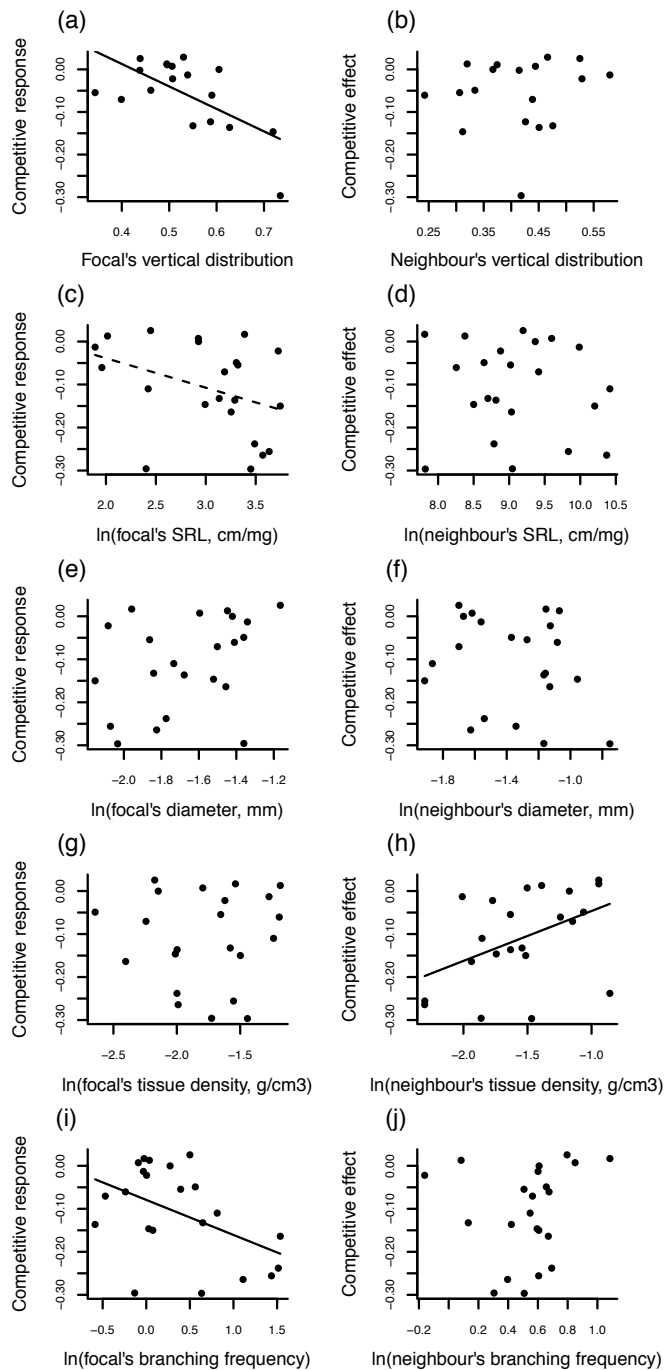


Figure 5. Interspecific relationship between the growth response of focal species to competition and (a–b) root vertical distribution; (c–d) SRL (specific root length); (e–f) diameter; (g–h) tissue density and (i–j) branching frequency. Relationships with trait values of focal and neighbour species are shown in the left-hand and right-hand column, respectively. The y-axis shows the slope of the relationship between focal plant mass and neighbour density, with more negative values indicating stronger growth suppression by neighbours. Root vertical distribution was measured as the proportion of root tips located at 5cm soil depth out of the total located at 5 cm and 10 cm depths. Solid and dashed lines indicate relationships that were significant at $P < 0.05$ or $P < 0.1$, respectively (Paper I).

Differences in root vertical distribution significantly affected growth response to competition, but in the opposite direction to that predicted by niche theory: focal species were least suppressed by their neighbours when the vertical distributions of focal and neighbours' root systems were more similar (Table 3). Similarly, the relationships between growth response to competition and trait distances were only negative when trait distances were calculated in multi-dimensional space: competitive suppression was weaker for species pairs with more similar trait combinations (Table 4).

Table 3. Summary of the models examining the relationship between growth response to competition (response variable) and trait distance between the focal and neighbour species (explanatory variable). Model coefficients, standard errors and statistical significance (NS – $P > 0.05$; * – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$) are presented. Negative coefficients indicate greater competitive suppression with increasing trait distance. Phyl. signal denotes likelihood ratio test comparing models with and without phylogenetic correlation structure. N – number of species (Paper I).

Trait	Trait distance	Phyl. Signal	N
Root mass (g)	0.02(0.02) NS	NS	22
Horizontal spread	0.14(0.13) NS	*	26
Vertical distribution	-0.42(0.17) *	NS	18
SRL (cm/mg)	-0.01(0.03) NS	NS	22
Diameter (mm)	-0.07(0.08) NS	NS	22
Tissue density (g/cm ³)	0.09(0.05) NS	NS	22
Branching frequency(1/cm)	0.01(0.09) NS	NS	22

Table 4. Summary of the models examining the relationship between growth response to competition and Euclidean distance between trait values of the focal and neighbour species. The distance was calculated based on seven root traits in one- to seven-dimensional space (i.e. 127 models in total). The analysis was performed on 14 focal species for which all of the seven root traits were measured. The best model based on Akaike Information Criterion (AIC) and the models with AIC less than 10 units different from the best fitting model are presented. For each model, the number and list of traits used to calculate the distance and slope of the relationship (negative slope meaning greater competitive suppression in species pairs with more dissimilar trait values) are shown. Hor_spread – horizontal spread; vert_dist – vertical distribution; SRL – specific root length; branch_freq – branching frequency. ** – $P < 0.01$; *** – $P < 0.001$ (S3 in Paper I).

No.	Trait list traits	Slope	P	R^2	AIC
4	Vert_dist, SRL, diameter, branch_freq	-0.124	***	0.73	-41.8
5	Hor_spread, vert_dist, SRL, diameter, branch_freq	-0.127	***	0.72	-41.7
3	SRL, diameter, branch_freq	-0.122	***	0.71	-41.1
4	Hor_spread, vert_dist, SRL, branch_freq	-0.136	***	0.71	-40.9
4	Hor_spread, SRL, diameter, branch_freq	-0.125	***	0.71	-40.9
3	Vert_dist, SRL, branch_freq	-0.129	***	0.7	-40.7
3	Hor_spread, SRL, branch_freq	-0.133	***	0.69	-40.2
2	SRL, branch_freq	-0.126	***	0.69	-40.0
2	Vert_dist, SRL	-0.105	***	0.62	-37.3
3	Vert_dist, SRL, diameter	-0.099	***	0.62	-37.3
3	Hor_spread, vert_dist, SRL	-0.111	***	0.62	-37.3
4	Hor_spread, vert_dist, SRL, diameter	-0.102	***	0.62	-37.2
2	SRL, diameter	-0.097	***	0.61	-36.8
1	SRL	-0.102	**	0.61	-36.8
2	Hor_spread, SRL	-0.109	**	0.6	-36.6
3	Hor_spread, SRL, diameter	-0.101	**	0.6	-36.6
5	Vert_dist, SRL, diameter, tissue_density, branch_freq	-0.119	**	0.55	-34.8
6	Hor_spread, vert_dist, SRL, diameter, tissue_density, branch_freq	-0.121	**	0.54	-34.6
4	SRL, diameter, tissue_density, branch_freq	-0.117	**	0.53	-34.3
5	Hor_spread, SRL, diameter, tissue_density, branch_freq	-0.118	**	0.52	-34.1
4	Vert_dist, SRL, tissue_density, branch_freq	-0.122	**	0.49	-33.1
5	Hor_spread, vert_dist, SRL, tissue_density, branch_freq	-0.124	**	0.48	-32.9
2	Vert_dist, diameter	-0.177	**	0.47	-32.6
3	SRL, tissue_density, branch_freq	-0.119	**	0.47	-32.6
4	Hor_spread, SRL, tissue_density, branch_freq	-0.121	**	0.46	-32.4
3	Hor_spread, vert_dist, diameter	-0.195	**	0.45	-32.1
4	Vert_dist, SRL, diameter, tissue_density	-0.092	**	0.45	-32
5	Hor_spread, vert_dist, SRL, diameter, tissue_density	-0.094	**	0.44	-31.9

3.2. Root spatial distribution

The pattern of root spatial distribution in monocultures was significantly affected by species identity, soil depth and neighbour density (Table 5). At the scale of 2 mm and 1 cm, roots were strongly aggregated (Fig. 6a–d) with the exception of *Lotus coniculatus*, whose roots were randomly distributed. At the largest spatial scale (2.85 cm), most of the plant species showed random root distribution (Fig. 6 e–f); only roots of *Filipendula vulgaris*, *Pimpinella saxifraga* and *Sesleria caerulea* remained still aggregated. Plant root aggregation generally declined with neighbour density (Table 5).

In species mixtures, root spatial aggregation varied among species combinations (Table 5, Fig 7). At the 2 mm spatial scale, roots of *F. vulgaris*, *L. corniculatus* and *P.officinatum* (growing with *S. caerulea*) were significantly more aggregated than expected based on monocultures, while the mixture of *Pimpinella saxifraga* with *S. caerulea* showed lower root aggregation than expected based on monocultures (Fig 7a–d). With increasing soil depth in mixtures of *F. vulgaris* and *Galium verum* (growing with *S. caerulea*), root aggregation deviated more than would be expected based on monoculture data (Table 5, Fig. 7a–b). At the largest spatial scale, all species showed aggregation levels similar to those expected based on monoculture data, though *V. vulgaris* and *L. corniculatus* tended to aggregate less than expected (Fig. 7e–f).

Root spatial aggregation was negatively correlated with aboveground productivity and positively with root tissue density in species monocultures (Fig 8a–b). Focal plant roots were less aggregated in species mixtures if the focal plant attained high shoot and root biomass and high root density (Fig 8c). Minimum convex polygon (MCP) range overlap was positively related to the absolute difference in root tissue density and negatively related to the absolute difference in root branching frequency between focal and neighbour plants (Fig. 8d–e). Range volume overlap and 50% kernel overlap were positively correlated with the absolute difference between biomass of focal and neighbour plants (Fig. 8f).

Table 5. Results of linear mixed models examining the effects of species or species pair identity, neighbour density and soil depth on root aggregation (L-function) in species monocultures, the difference between observed and expected root aggregation patterns in species mixtures (based on L-functions, $L_{\text{obs}}-L_{\text{exp}}$) and interspecific root aggregation in the area of home range overlap in species mixtures (bivariate L-function). Root aggregation patterns were examined at three spatial scales (2 mm, 1 cm, 2.85 cm). F-values and their significance are shown. \$ $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. df – degrees of freedom. Residual degrees of freedom were 93 for species monoculture models and approximately 73 for species mixture models (based on Kenward-Roger approximations) (Paper II).

	Monoculture L-function			$L_{\text{obs}}-L_{\text{exp}}$ in mixtures			Bivariate L-function			
	df	2mm	1cm	2.85cm	2mm	1 cm	2.85cm	2mm	1cm	2.85cm
Species (S)	7	23.2 ***	19.1 ***	7.8 ***	31.2 ***	21.9 ***	2.2 *	0.93	0.76	1.1
Neighbour density (N)	1	28.9 ***	36.2 ***	18.4 ***	1.2	3.9	4.0 *	0.09	0.11	1.4
Depth (D)	1	2.3	9.2 **	1.6	7.7 **	4.5 *	0.04	1.6	0.62	0.91
S:N	7	2.4 *	2.3 *	7.2 ***	1.0	0.97	1.5	0.52	0.40	1.8 \$
S:D	7	15.0 ***	4.8 ***	3.8 **	2.4 *	3.7 **	1.0	2.8 *	3.2 **	2.1 *
N:D	1	0.11	2.9 \$	13.3 ***	1.1	4.9 *	11.3 **	1.7	0.21	<0.01
S:N:D	7	2.8 *	1.5	1.3	1.8	1.5	1.3	1.5	2.4 *	1.2

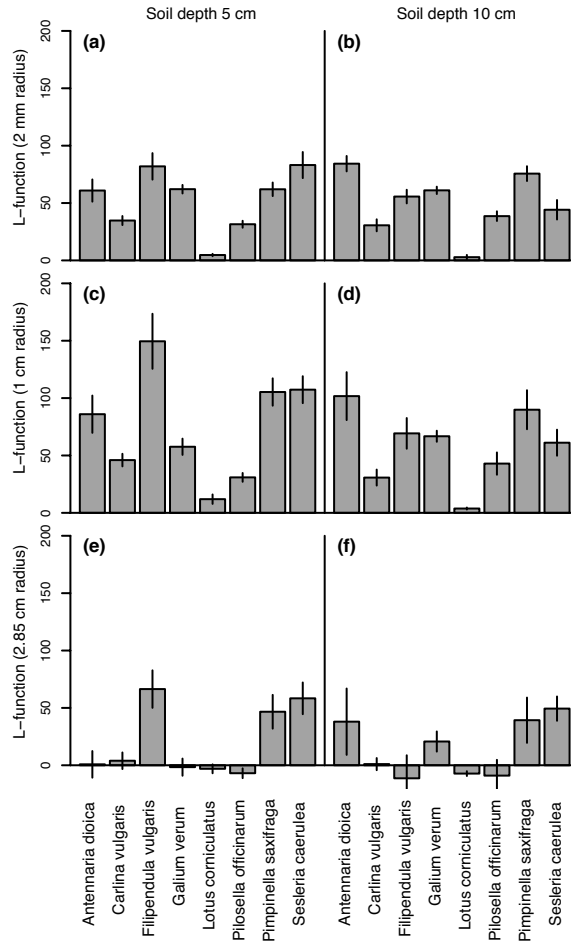


Figure 6. Root spatial aggregation (L-function) in eight species monocultures at two soil depths (5 cm and 10 cm) and three spatial scales (2 mm, 1 cm, 2.85 cm). Predicted means \pm SE at the density of four neighbours are shown (Paper II).

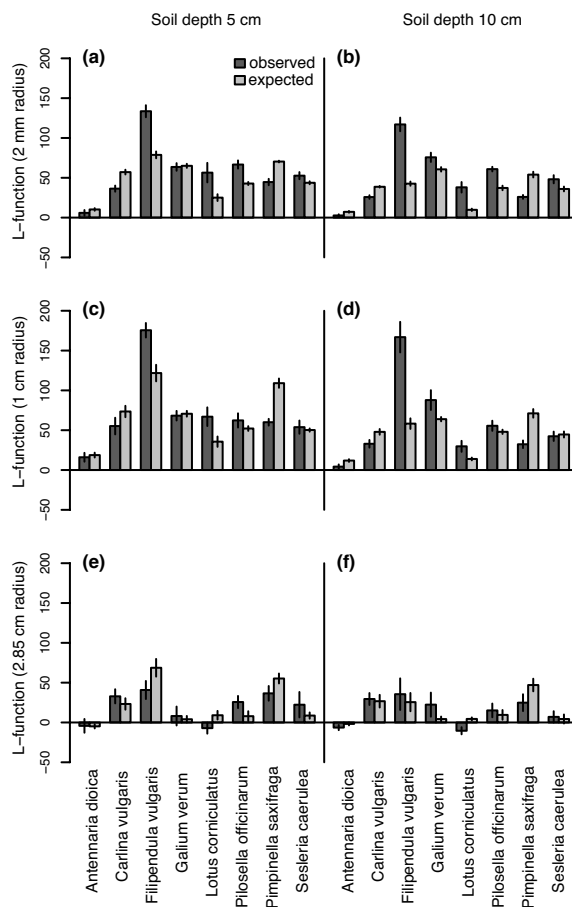


Figure 7. Observed and expected root spatial aggregation (L-function) in eight species mixtures at two soil depths (5 cm and 10cm) and three spatial scales (2mm, 1cm, 2.85cm). Means \pm SE at the density of four neighbours are shown. Expected values were calculated based on root spatial data in monocultures of the two species comprising the mixture. The names of the focal species are shown; see Table 1 for the names of the neighbour species (Paper II).

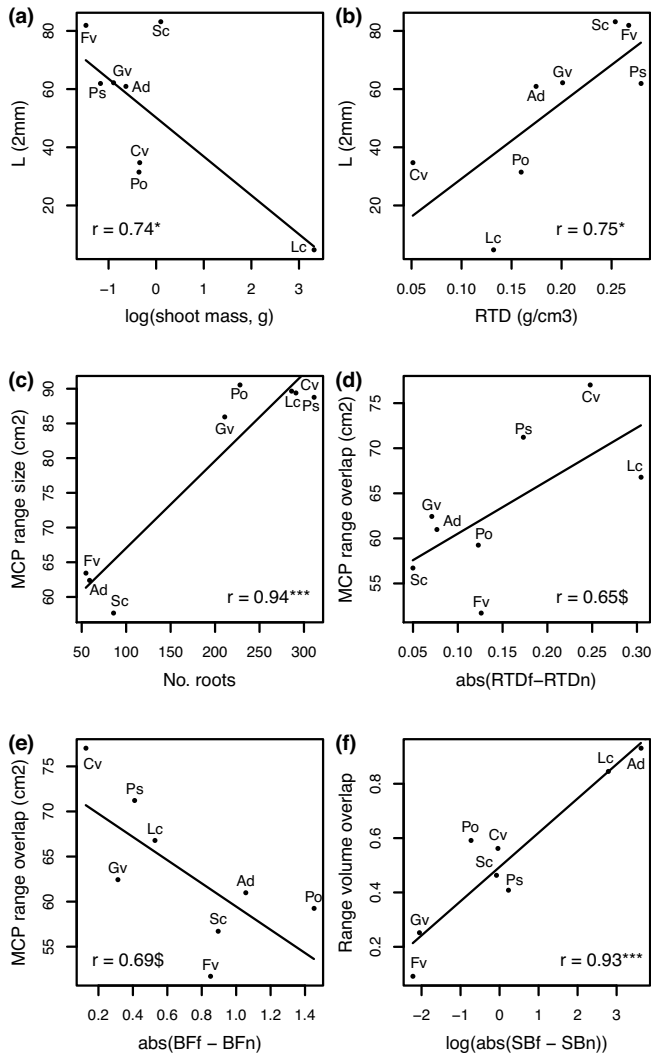


Figure 8. Correlations between root spatial patterns and plant traits. a) Root aggregation at 2mm spatial scale in species monocultures and total pot shoot mass; b) Root aggregation at 2mm spatial scale in species monocultures and root tissue density; c) Minimum convex polygon home range and total number of roots recorded for the focal plant in species mixtures; d) Minimum convex polygon home range overlap and absolute difference in root tissue density between focal plant and neighbours in species mixtures; e) Minimum convex polygon home range overlap and absolute difference in branching frequency between focal plant and neighbours in species mixtures; f) Total kernel volume overlap and absolute difference in shoot mass between focal plant and neighbours in species mixtures. All values represent predicted means at mean neighbour density (four neighbours) at soil depth of 5cm. Focal species names are indicated with initial letters for genus and species names (Table 1). Pearson correlation coefficients and their significance are shown ($\$ P < 0.1$, $* P < 0.05$, $*** P < 0.001$) (Paper II).

3.3. Kin recognition in temperate grassland plant species

Genetic relatedness did not significantly affect plant shoot mass at any plant density for any of the studied plant species. However, marginally significant effects of relatedness were detected in two species: *Deschampsia caespitosa* had 22% greater shoot mass when grown with siblings compared to non-sibling neighbours, whereas *Leontodon hispidus* lost 24% of shoot mass when neighbouring plants were siblings compared to non-sibling neighbours (Table 6).

Table 6. The results of linear mixed models assessing the effects of neighbour density (low or high) and genetic relatedness (siblings or non-siblings) on the phenotype of eight plant species. In analyses of reproductive biomass, leaf elongation, specific leaf area (SLA) and root density, shoot dry mass was included in the models as a covariate. All traits were measured for a single focal plant in each pot, except for root density, which could only be measured at the pot level. For the analysis of root density, the combined shoot mass of all plants in a pot was used as a covariate. Due to the restricted availability of sibling seedlings of *M. lupulina*, only the low density treatments could be created for this species. The family line of the focal individual was included in models as a random factor. Wald chi-squared test statistics and their significance are shown in the table. Degrees of freedom are shown on the species name lines. \$ $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (Paper III).

	Shoot mass		Inflorescence mass		Elongation		SLA		Root density	
	X ²		X ²		X ²		X ²		X ²	
<i>Achillea millefolium</i>	1,27		1,7		1,26		1,26		1,26	
Density	32.7	***	<0.01		6.3	*	2.3		7.8	**
Relatedness	0.1		0.7		2.3		1.2		0.3	
Density × relatedness	0.1		1.3		2.5		<0.01		1.1	
Biomass			9.8	**	5.5	*	4.1	*	14.1	***
<i>Deschampsia caespitosa</i>	1,27				1,26		1,26		1,26	
Density	115.2	***			6.3	*	6.0	*	4.6	*
Relatedness	3.0	\$			0.04		0.5		0.8	
Density × relatedness	0.04				0.2		1.8		3.5	\$
Biomass					7.2	**	3.8	\$	5.1	*
<i>Leontodon hispidus</i>	1,27		1,24		1,26		1,26		1,26	
Density	32.0	***	3.3	\$	6.0	*	4.4	*	2.5	
Relatedness	3.7	\$	0.9		0.03		<0.01		0.2	

	Shoot mass		Inflorescence mass		Elongation		SLA		Root density	
	X ²		X ²		X ²		X ²		X ²	
Density × relatedness	0.6		1.8		0.05		0.02		<0.01	
Biomass			138.8	***	1.5		0.9		28.3	***
<i>Lychnis flos-cuculi</i>	1,27		1,6		1,26		1,26		1,26	
Density	15.1	***	3.1	\$	17.9	***	0.4		2.0	
Relatedness	0.02		2.2		2.9	\$	1.1		3.1	\$
Density × relatedness	1.0		0.05		1.2		8.9	**	0.03	
Biomass			14.1	***	129.6	***	30.3	***	69.6	***
<i>Medicago lupulina</i>	1,9		1,7		1,8		1,8		1,8	
Relatedness	1.3		0.5		3.0	\$	0.6		0.01	
Biomass			0.2		0.8		1.2		13.5	***
<i>Peucedanum palustre</i>	1,14				1,13		1,13		1,13	
Density	0.8				16.4	***	0.2		1.4	
Relatedness	0.03				2.2		0.5		0.5	
Density × relatedness	1.5				0.4		1.2		3.0	\$
Biomass					78.4	***	3.5	\$	22.3	***
<i>Phleum pratense</i>	1,27		1,12		1,26		1,26		1,26	
Density	33.9	***	3.5	\$	1.6		8.4	**	5.2	*
Relatedness	0.9		1.8		0.4		1.0		<0.01	
Density × relatedness	0.8		0.1		0.03		0.01		0.08	
Biomass			39.4	***	2.0		12.2	***	10.6	**
<i>Trifolium repens</i>	1,17		1,14		1,15		1,16		1,16	
Density	122.9	***	2.3		2.1		3.7	\$	<0.01	
Relatedness	0.1		0.1		0.01		8.2	**	0.1	
Density × relatedness	1.4		6.9	**	5.5	*	8.7	**	0.03	
Biomass			9.0	**	<0.01		13.0	***	9.9	**

Clear differences in plant phenotypes between sibling and non-sibling groups were observed in *Trifolium repens* (Table 6), but these differences were conditional on neighbour density. Plants growing with siblings significantly increased allocation to inflorescence mass and increased their SLA with increasing neighbour density, while plants in non-sibling groups showed little change in these traits (Fig. 9a, c). On the other hand, plants from non-sibling groups increased petiole elongation at high neighbour density – a response absent in plants growing among siblings (Fig. 9b).

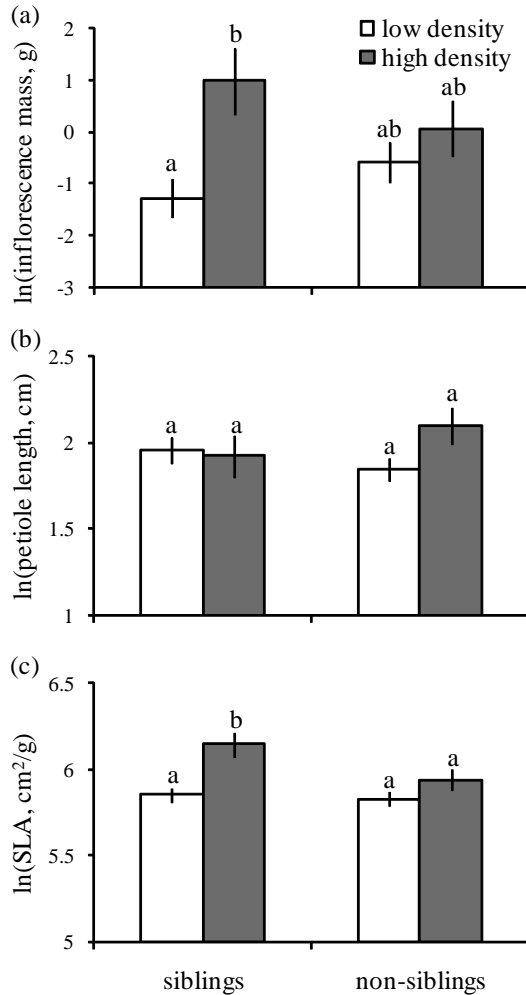


Figure 9. The effects of neighbour density and genetic relatedness on the (a) allocation of biomass to inflorescences, (b) petiole elongation and (c) specific leaf area of *Trifolium repens*. Predicted trait means \pm SE derived from models containing plant shoot mass as a covariate are presented. Therefore, the bars display differences in trait means that could not be attributed to differences in plant shoot size. Different letters indicate significant differences between means ($P < 0.05$, Tukey's test) (Paper III).

There was a significant interaction between the effects of neighbour relatedness and density on SLA in *Lychnis flos-cuculi*. At low density, plants grown with non-siblings had a significantly larger SLA than plants grown with siblings, while the opposite pattern was observed at high neighbour density (Table 6, Fig. 10).

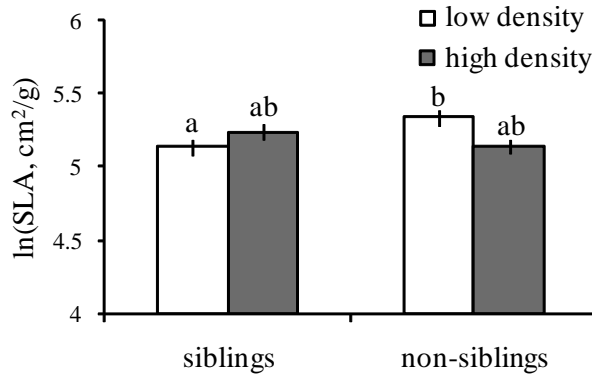


Figure 10. The effects of neighbour density and genetic relatedness on specific leaf area of *Lychnis flos-cuculi*. Predicted trait means \pm SE are presented and are derived from models containing plant shoot mass as a covariate. Therefore, the graph demonstrates differences in trait means that could not be attributed to corresponding differences in plant shoot size. Different letters indicate significant differences between means ($P < 0.05$, Tukey's test) (Paper III).

3.4. Effects of plant genetic diversity on plant-soil feedback

Both groups of plants (siblings or genetically diverse) produced similar total aboveground biomass by the end of the conditioning stage (mean mass 25.3 g and 24.7 g, respectively; t -test $P = 0.7$). Roots in diverse groups had 28% higher N content compared to sibling groups (Table 7).

Table 7. Root carbon (C) and nitrogen (N) content of *Deschampsia cespitosa* plants grow in either groups of siblings or genetically diverse individuals from the same population. F-values, the significance of the treatment (^s, $P < 0.1$; *, $P < 0.05$), raw means and standard errors (in parentheses) are shown (Paper IV).

	Treatment	Siblings	Diverse
C %	$F_{1,10} = 3.8^s$	45.45 (0.14)	44.77 (0.32)
N %	$F_{1,10} = 6.0^*$	0.57 (0.02)	0.74 (0.06)
C : N	$F_{1,10} = 8.7^*$	80.31 (3.31)	62.76 (4.94)

These differences carried over to the feedback stage of the experiment via litter decomposition and plant N uptake, but were only detectable in the unsterilised soil treatment (Table 8).

Table 8. The effect of soil conditioning (siblings of genetically diverse groups) and soil sterilization of *Deschampsia cespitosa* seedlings growth at 2 week, total plant dry mass and nitrogen (N), root N% and the proportion of litter mass remaining in soil after 8 week of incubation. F-values and their significance are shown: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ (Paper IV).

	df	Prop. litter remaining	Root N%	Total N (g)	Seedling length (cm)	Plant mass (g)
Conditioning (C)	1	4.9*	8.4**	1.2	0.1	0.6
Sterilization (S)	1	33.8***	54.0***	49.5***	25.8***	101.6***
C × S	1	6.5*	8.9**	13.9***	2.0	0.1
Residuals	27					

Soil sterilisation significantly suppressed litter decomposition and the proportion of root litter remaining in the soil by the end of the feedback stage was not significantly different between plant diversity treatments. When soil was left unsterilised, more litter was decomposed when the soil was conditioned by a more diverse group of plants than by siblings (Table 8, Fig. 11).

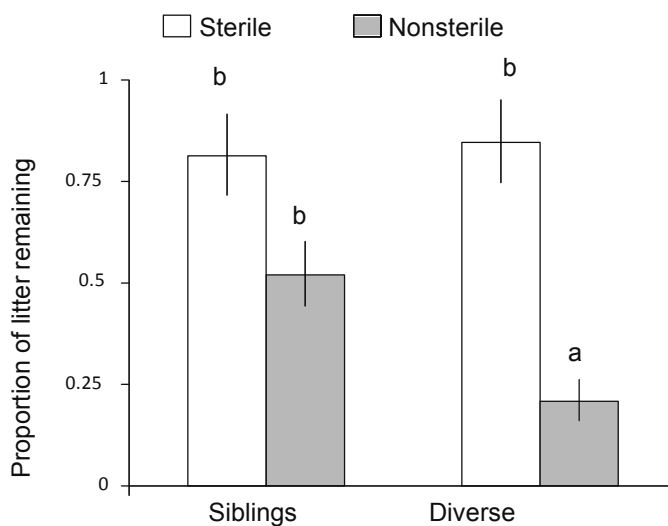


Figure 11. The effect of soil conditioning and sterilization on the proportion of *Deschampsia cespitosa* root litter mass remaining in soil after 8 week of incubation. Soil was conditioned by either siblings or a mixture of genotypes originating from different mother plants from the same population, and was either left unsterilised (closed bars) or sterilized by gamma radiation before incubation (open bars). Mean \pm SE are shown. Statistical analysis was performed on square-root transformed data. Different letters indicate significant differences between means ($P < 0.05$, Tukey's test) (Paper IV).

In the unsterilised treatment, plants grown in soil that was conditioned by a genetically diverse group of plants had a significantly higher root N content and total N uptake compared to plants grown in soil conditioned by a group of sibling plants (Fig. 12a).

Plant growth was similar in soil conditioned by different plant groups and soil not conditioned by any plants when the soil was sterilised prior to the feedback stage of the experiment. However, plants grown in unsterilised soil attained significantly lower biomass when grown in soil conditioned by both siblings and diverse plant groups compared to soil that was not previously occupied by any plants (Table 8, Fig. 12h). Therefore, plants experienced a negative plant-soil feedback on plant growth from both soils conditioned by siblings and diverse plant mixtures. However, plant-soil feedback on N uptake was more negative for plants grown in soil previously occupied by siblings than by diverse plant groups (Fig. 12f).

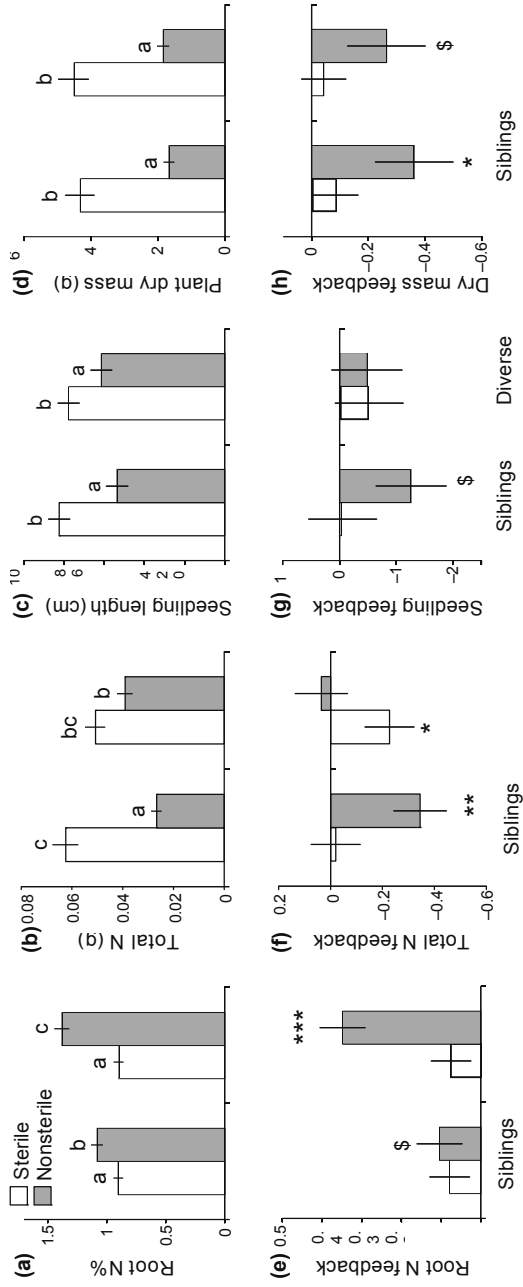


Figure 12. The effect of soil conditioning and sterilization on (a) root nitrogen (N) content, (b) total plant N, (c) seedling length after 2 week of growth, and (d) plant dry mass after 8 weeks of growth and soil feedback for (e) root N content, (f) total N, (g) seedling length and (h) plant mass of *Deschampsia cespitosa* in comparison to an unconditioned control treatment. Plants were subjected to soil that was conditioned by either siblings from the same mother plant or a mixture of genotypes originating from different mother plants from the same population. Conditioned soil was either left unsterilized (closed bars) or sterilized by gamma radiation before planting the next generation of seedlings (open bars). For plant mass and N data, statistical analysis was performed on log_e-transformed data. Different letters indicate significant differences between means ($P < 0.05$, Tukey's test). Soil feedback was calculated as log_e-transformed ratio of mean root N (e), total N (f) or plant dry mass (g) or as the difference in mean seedling length (h) between conditioned soil and unconditioned control. Means \pm SE are shown. Symbols indicate significant differences from the control \$, $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (t-test) (Paper IV).

4. DISCUSSION

To be successful members in a community, plants have to be good “fighters”, acquiring resources at the expense of their neighbours, and be resilient “sufferers” in order to withstand suppression from neighbouring plants. Having larger plant size and higher growth rates, both above- and belowground, has been considered the most successful strategy in competition (Goldberg & Landa 1991; Goldberg 1996; Keddy et al. 2002; Wang et al. 2010; Herben & Goldberg 2014; Ravenek et al. 2016). In our experiment (I), we found supporting evidence for the importance of size and growth rate in competition. The focal plant suffered more when the neighbouring species had a larger and horizontally wider root system, suggesting that these neighbouring plants had a great competitive effect on the focal plants. Strong competitive effects were also associated with low tissue density, which is known to reflect a plant life history characterised by fast growth, low levels of stress tolerance and short lifespan (Ryser, 1996; Kramer-Walter *et al.*, 2016). Furthermore, the examination of fine-scale root spatial patterns (II) showed that combinations of species with contrasting root tissue densities or plant sizes resulted in most extensive root system overlap, confirming that these traits play an important role in the contest of belowground space. We also found that species characterised by the lowest levels of root spatial aggregation possessed low tissue density and achieved the highest aboveground productivity in monocultures conditions, indicating most efficient space use and nutrient capture. In species mixtures, species with lower levels of root aggregation attained higher above- and belowground biomass and larger home ranges, suggesting competitive superiority of such species (II). These findings demonstrate that the efficiency of root spatial placement plays an important role in determining plant productivity and competitive success and may underlie some of the relationships between plant performance and root system size and tissue density.

While increasing plant size seems to be an efficient way to suppress neighbouring individuals, we found that greater size did not enhance the ability to tolerate competition from neighbours; therefore, fast resource acquisition and growth confer only a partial advantage in competition (I). The other part of competition is tolerance to neighbours’ suppression, but the mechanisms behind this ability are still largely unclear (Wang et al. 2010). Moreover, recent theoretical modelling demonstrated that the ability to tolerate competition is far more important in competitive success than the ability to suppress neighbours. Therefore, it is critical to determine which species characteristics confer competitive tolerance (Hart et al. 2018). It has been suggested that root traits could be key to explaining variation in the ability to tolerate competition (Goldberg 1996; Keddy et al. 1998; Belter & Cahill Jr. 2015; Ravenek et al. 2016). In our experiment, we found that species with a deeper and less branched rooting system and lower specific root length were most tolerant to competitors (I). Deeper roots enable access to nutrients from deeper soil layers while reduced

branching and lower specific root length may be associated with higher levels of mycorrhizal colonisation, which may compensate for nutrient shortage in competitive situations and improve nutrient acquisition efficiency (Maherali 2014; Koziol & Bever 2015; Cortois et al. 2016). Using available data on mycorrhizal prevalence among plant species (Hempel et al. 2013), we found support for this association as plant species with less branched root systems in our study are generally more colonised by mycorrhizal fungi. We also found that species with different branching frequencies exhibited reduced root system overlap (II). This suggests that traits contributing to competitive tolerance may also reduce the intensity of direct resource competition and may affect the efficiency of resource uptake.

Root spatial mapping showed that plant roots of most species were strongly aggregated at fine and intermediate spatial scales (II), likely reflecting constraints on root architecture. Contrary to modelling studies, which predict that large root systems should be less efficient in root spatial positioning (Berntson 1994; Pagès 2011), we found that interspecific variation in levels of aggregation could not be explained by overall root system size (II). Variation among species may be related to root branching angles and frequencies such as the continuum between herringbone and dichotomous root architectures (Fitter et al. 1991; Ge et al. 2000; Lynch & Brown 2001; Dunbabin et al. 2004). We found that root aggregation declined with increasing spatial scale, suggesting that plant root systems are less developmentally constrained and able to occupy available space evenly at larger spatial scales. Root spatial aggregation patterns changed when species were grown in mixtures. Three species out of eight intensified root aggregation in species mixtures compared to monocultures. This kind of change is contrary to the expectations which predict complementary space use (Berendse 1982; Postma & Lynch 2012; Hoekstra et al. 2015). Even though overall root aggregation increased, roots belonging to different species were positioning randomly with respect to each other in the area of species overlap. Such pattern could occur if plants detected the presence of heterospecific competitors but root aggregation response was triggered systematically across the whole root system instead of being constrained to the vicinity of heterospecific roots. This behaviour is contrary to what could be expected if root spatial distribution were optimised for resource uptake, which would result in ideal free distribution within and between species. Conversely, if plants engaged in the tragedy of commons and maximised individual fitness, root overproduction in the area of species overlap should have been observed (O'Brien et al. 2007; McNickle & Brown 2014). Increased aggregation across the whole root system may be a strategy to consolidate occupied space and prevent further intrusion by heterospecific roots. We also found that focal plant minimum convex polygon (MCP) ranges declined with increasing neighbour density, while core areas remained stable. This also suggests that plants held on to their core foraging areas and ceded space at the limits of their ranges with increasing competitive pressure, rather than engaged in competitive contest of space in the presence of neighbours.

Plants have to compete with neighbours of different identities and can benefit from different behavioural strategies depending on neighbour identity. In addition to encountering and responding to neighbours belonging to different species (I and II), plants also experience variation in the genetic composition of conspecific neighbours. It has been shown that some species exhibit kin recognition and modify their growth and morphology when grown with siblings versus non-siblings (Dudley & File 2007; Murphy & Dudley 2009; Biedrzycki et al. 2010; Bhatt et al. 2011; Biernaskie 2011). However, it remains unclear how common such ability is among plant species. We tested eight common temperate grassland plant species with different growth forms and reproduction strategies for the ability to modify their morphology and biomass allocation in response to growing among siblings or non-siblings (III). We found that only one species, *Trifolium repens*, exhibited significant differences in multiple measured traits in response to the genetic relatedness of neighbouring plants. When growing with siblings, *T. repens* increased biomass allocation to inflorescence production at high neighbour density; at lower levels of competition, this reaction was absent. Increased flowering in response to competition with siblings has been detected before (Biernaskie 2011). This reaction may also be related to growth form, as previous studies have shown that clonal plants may respond to unfavourable conditions (e.g. low light conditions) by increasing the investment into flowering (Watson 1984; Geber et al. 1992; Newton et al. 1992). This investment into flowering could be construed as an attempt to escape the inhospitable area and provide offspring with a chance to grow in better conditions. Furthermore, competitive organs are expensive to grow – it may be more economical to be cooperative rather than selfish by reducing competition between neighbours (Gersani et al. 2001). The more cooperative behaviour towards siblings is also supported in our study by the observation that plants increased specific leaf area (SLA) in high-density conditions with sibling neighbours, accompanied by no changes in petiole elongation. On the contrary, when plants were grown with unrelated neighbours, we observed enhanced petiole elongation and only a slight increase in SLA. Increased SLA improves plants' shade tolerance and allows for more efficient light capture (Ballaré et al. 1994; Griffith & Sultan 2005), while elongated petioles are usually the result of competition for light and a strategy to overtop surrounding plants (Schmitt et al. 1995; Leeftang et al. 1998; Weijschedé et al. 2006).

As kin recognition may not be a very common phenomenon in plant communities, the choice of studied species may significantly affect research findings. Due to the inherent difficulty of publishing negative results and the tendency to use only a single focal species (Dudley & File 2007; Murphy & Dudley 2009; Biedrzycki et al. 2010; Bhatt et al. 2011; Biernaskie 2011), data on kin recognition may be biased, which is why it is very difficult to generalise how widely kin recognition in plants is spread. Moreover, morphological changes in response to competition may only occur in certain environmental settings, such as high neighbour density (Willson et al. 1987; Escarre et al. 1994; Donohue 2004), while many studies restrict experiments to a single environmental

context. Our study included multiple common species and manipulations with different plant densities to address previous shortcoming in experimental design. Our findings demonstrate clear density-dependence in kin recognition responses and suggest that kin recognition may not be widespread among temperate grassland plants.

The factors that favour the evolution of kin recognition remain unknown, but preliminary data from research on interspecific competition suggests that the frequencies of interactions with different neighbours may be a key factor. In previous studies, we found that plant competitive ability is strongly influenced by the frequency of encountering conspecific or heterospecific neighbours in the field (Semchenko et al. 2013) and that plants are capable of responding differentially to conspecific and heterospecific neighbouring plants only when plant populations are exposed to heterogeneous neighbourhoods where both neighbour types are encountered at similar frequencies (Abakumova et al. 2016). These findings are in line with theoretical predictions that two types of responses will evolve only in species that in nature encounter both kinds of neighbour at similar frequencies (Moran 1992). If a plant species encounters predominantly only one type of neighbours, then a fixed behavioural strategy most compatible with that neighbour type will be favoured (Alpert & Simms 2002; Givnish 2002). The probability of plants meeting kin depends on species' life-history traits, especially offspring dispersal (Lovett-Doust 1981; Cheplick 1992). Our field measurements showed that the nearest neighbours of *T. repens* often belonged to the same species (44% of the time) and it is often the result of clonal propagation. Therefore, we may suggest that it may be beneficial for this species to avoid competition with the same clone and kin recognition ability that we observed in our study is the result of frequent interactions with ramets of the same clone and other conspecifics. Interestingly, *Deschampsia cespitosa* did not show any changes in the measured traits in response to growing with siblings or non-siblings but plants grew bigger in sibling than non-sibling groups (22 % greater shoot mass). The field survey showed that *D. cespitosa* encountered conspecific neighbours 95% of the time, which may frequently correspond to kin interactions. While this study did not provide evidence for kin recognition for this species, differential responses to neighbour relatedness were subsequently described to operate belowground (Semchenko et al. 2014).

As demonstrated by our previous experiments (I, III) and other studies (Mahall & Callaway 1992; Semchenko et al. 2007a; Murphy & Dudley 2007; Biedrzycki et al. 2010; Abakumova et al. 2016), plants have the capability to recognise their neighbouring species or even kin and change their above- and belowground traits in response to neighbour identity. Such changes in plant morphology may also reflect changes in tissue chemical composition and affect litter quality, decomposition rates and nutrient cycling (Genung et al. 2013). In our next experiment (IV) with *D. cespitosa*, we looked for evidence whether phenotypic plasticity in response to the identity of neighbouring plants can trigger changes in root chemical properties, thus affecting nutrient cycling and plant-soil interactions. Indeed, we found changes in litter quality depending on

the identity of neighbours. If plants were grown among genetically diverse individuals, they produced roots with higher N content compared to plants grown with kin. This N-rich litter decomposed faster and led to higher N uptake by the next generation of seedlings, but only in unsterilized soil treatment. This finding indicates that extra N uptake by the next generation was facilitated by soil biotic activity (litter decomposers). The population of *D. cespitosa* that we studied came from a species-poor, productive grassland where this species strongly dominates and frequently interacts with conspecific neighbours (III). It is therefore possible that genetic diversity of such species can play an important role in ecosystem functioning, with genetically diverse stands of *D. cespitosa* not only increasing litter quality but also supporting a more diverse and metabolically active soil biotic community.

Besides faster nutrient cycling in genetically diverse plant communities, higher genetic diversity of a plant population can also lower natural enemy spread and has been shown to result in lower levels of damage by aboveground enemies (Zhu et al. 2000; Tooker & Frank 2012; Barton et al. 2015). Therefore, if closely related plants grow together, pathogens are expected to accumulate faster and cause greater damage (Luo et al. 2016). In our study (IV), the growth of plants in soil previously inhabited by either genetically closely related or diverse neighbours were suppressed compared to the control group grown in soil that was not occupied by any plants during the conditioning stage. In sterilized soil conditions, plant growth was no longer suppressed, suggesting that the negative feedback was caused by soil biota such as pathogenic fungi (Schnitzer et al. 2011; Maron et al. 2011). Therefore, even though there was a positive effect of litter decomposers on plant nutrition, other soil organisms seemingly prevented plants from achieving greater biomass. Contrary to predictions, we observed equally negative effects of soil pathogens on plant growth in soils conditioned by siblings and genetically diverse plants. These findings may be explained by more conservative root traits in sibling groups. Plants in sibling groups had roots with a higher C : N ratio (IV) and lower specific root length (Semchenko et al. 2014) compared to the diverse groups. Such root characteristics have been shown to confer longer lifespan and be less vulnerable to pathogens (Herms & Mattson 1992; Tjoelker et al. 2005; Reich 2014; Lemmermeyer et al. 2015). Therefore, it is possible that kin recognition triggered investment into root longevity and better defence against pathogens, which negated the disadvantage of growing in low diversity groups.

The studies presented in this thesis contribute to the growing body of evidence that plants have evolved diverse behavioural strategies of interacting with competitors (Semchenko et al. 2007a; Semchenko et al. 2010; Valverde-Barrantes et al. 2013; Belter & Cahill Jr. 2015). Species may possess equivalent competitive ability via different trait combinations, which could provide a mechanism for species co-existence. However, additional processes and trade-offs have to operate to prevent the evolution of a perfect competitor with optimal values in all traits. We found little evidence for niche differentiation based on trait differences either between species or between genotypes within

species (MacArthur & Levins 1967; Silvertown 2004). Instead we found that competitive suppression was weaker for species with more similar root trait combinations. Within species, competition among closely related genotypes should be more intense than competition between genetically diverse neighbours due to greater niche overlap, resulting in lower productivity in closely related neighbourhoods. No significant differences in productivity were detected in our study. However, we found that plants adopted different phenotypes when growing in closely related or genetically diverse neighbourhoods. Our results also suggest that there might be a trade-off between fast resource acquisition and resistance to natural enemies and that genetically diverse neighbourhoods favour resource-acquisitive phenotype while low genotypic diversity favours tissue conservation over fast resource acquisition. Such intraspecific variation in plant traits has significant consequences for litter quality and nutrient cycling and may play an important role in ecosystems characterised by low species richness.

CONCLUSIONS

The studies presented in this thesis explored which belowground traits contribute to the ability of plants to suppress and tolerate their competitors, how neighbour identity and density affect plant root spatial distribution and how genetic relatedness between competing plants modifies plant traits and nutrient cycling. Experimental assessment of competitive ability across 26 common grassland species confirmed observations of previous studies that plant competitive ability is higher in species with larger size. We found that traits enabling fast and extensive soil space occupation were strongly related to competitive effect: plants with higher root biomass, more horizontally spread roots and lower tissue density were better at suppressing their neighbours. We did not find any significant connection between these traits and plants' ability to tolerate competition from their neighbours. On the other hand, traits that were unrelated to root system size, such as a deeper root system, lower specific root length and less branched roots, were related to greater ability to withstand competition from neighbouring plants (competitive response). However, these traits did not affect the ability to suppress competitors, indicating that different sets of traits contributed to competitive effect and response ability. When searching for the best model to describe competitive outcome, we found that the set of best predictors included root morphological traits, rather than root system size. We also found that differences in belowground traits did not contribute to niche differentiation and plant species co-existence. On the contrary, competitive suppression was weaker for species with more similar trait combinations.

In the second study, we mapped root spatial distribution of eight grassland species and described plant foraging and home range behaviour with approaches previously used to describe animal behaviour. We observed a wide range of root aggregation intensities and home range behaviours. Species with higher above-ground productivity and traits associated with fast growth were characterised by more uniform placement of roots in soil, indicating more efficient space use and resource capture. With increasing plant density, soil exploration efficiency was enhanced, suggesting that plant mortality and resulting plant density may significantly affect the efficiency of nutrient uptake at the plant community level. Plant root systems overlapped extensively in species mixtures and roots belonging to different species distributed randomly with respect to each other, demonstrating a lack of territoriality in examined grassland species.

In the third experiment, the ability to recognise kin was examined in an array of temperate grassland plant species. Results from this experiment suggest that kin recognition may not be very widespread, as only one species of eight, *Trifolium repens*, exhibited recognition of kin as indicated by changes in plant morphology and biomass allocation in response to neighbour relatedness. When *T. repens* was grown in groups of siblings, plants exhibited responses indicative of avoiding competition with neighbours: plants enhanced light capture

efficiency by increasing specific leaf area and allocated more resources into inflorescence mass at the expense of vegetative biomass when grown among siblings. On the contrary, if individuals of *T. repens* were grown next to genetically diverse neighbours, they invested in enhanced petiole elongation, which is known as a behaviour aimed at overtopping neighbouring individuals. Notably, differences in plant behaviour among kin and non-kin groups were only detectable when observing plants at a range of neighbour densities.

The last experiment explored the consequences of kin recognition for soil processes and feedback between plants and soil biota. We found that plants produced roots with higher nitrogen content when grown in genetically diverse neighbourhoods compared with groups containing only siblings. Such roots decomposed faster and led to higher N uptake by the next generation of seedlings, indicating faster nutrient cycling in genetically diverse neighbourhoods. Contrary to our predictions, low genetic diversity among plants did not cause faster spread and damage from soil pathogens, suggesting that plants may preclude pathogen spread by kin recognition responses that make tissues less susceptible to attack by natural enemies.

Collectively, these findings indicate that competitive outcomes may be best predicted by differences in traits related to the ability to tolerate competition, rather than size-related traits associated with the ability to suppress neighbours. In addition to widely measured size and morphological traits, plant species vary widely in their root spatial placement and the degree of root system overlap in species mixtures, with low levels of fine-scale root aggregation conferring higher productivity and contributing to competitive success. Plant competitive interactions also vary within species. Though not very common among grassland species, kin recognition may significantly modify plant morphology and litter quality, with significant consequences for interactions with soil pathogens and decomposers. Kin recognition may play an important role in species-poor communities, where responses to genetic relatedness in the dominant species may significantly alter ecosystem processes.

SUMMARY IN ESTONIAN

Taimedevaheline konkurents ja selle seosed taimetunnuste ja mullaprotsessidega

Paikse eluviisi tõttu ei ole taimedel võimalik valida, kes on nende naabriteks – kas liigikaaslased (geneetiliselt lähedased või kauged isendid) või teise liigi esindajad. Kuna kõik taimed vajavad kasvamiseks samu ressursse, oleks taimedel konkurentsi tingimustes otstarbekas suurendada eelkõige just ressursside hankimise võimet. Selleks, et olla edukas ning konkrentsis teiste taimedega vastu pidada, peavad taimeisendid olema head „võitlejad“, et naabreid võimalikult palju alla suruda ning võimalikult palju ja kiiresti ressursse endale haarata. Teisalt on taimedel vaja olla ka head „kannatajad“, et naabertaimede poolt tekitatud survele võimalikult hästi vastu pidada.

Üheks käesoleva doktoritöö eesmärgiks oli välja selgitada, millised juurte tunnused aitavad taimedel konkurente alla suruda ning millised tunnused võimaldavad konkrentsile võimalikult edukalt vastu seista. Selleks viisime läbi potikatse, kus kasvasime fokaaltaimedena 26 erinevat parasvöötme rohttaime liiki, millele lisasime erineva tihedusega naabertaimi. Katse tulemusel selgus, et uuritavad taimeliigid kaotasid oma kasvus kõige rohkem kui nende naabertaimedel oli suurem ja horisontaalselt laiem juurestik. Samuti leidsime, et liikidel, millel on suurem konkurente alla suruv mõju, on madalam juurekoe tihedus, mida on seostatud kiire kasvuga. Teisisõnu taimede kasvustrateegia, mis võimaldab rohkem mullaressursse kiiresti endale haarata, andis konkurentide allasurumisel kindla eelise.

Ehkki taimede suurusel on ilmne mõju konkurentide allasurumisel, leidsime oma töös, et suurem juurestik ei tõsta taimede võimekust konkrentsi negatiivsele mõjule vastu seismisel. Konkrentsi suhtes tolerantsemateks osutusid hoopis sügavama ja vähem harunenud juurestikuga ning väiksema juure eripinnaga taimeliigid. Sügavam juurestik aitab taimedel toitaineid kätte saada ka sügavamatest mullakihtidest, kus konkrents on eeldatavasti nõrgem. Vähem harunenud juured ning väiksem juure eripind aga võivad olla seotud hoopis mükoriisiga, mille abil saavad taimed kergemini mullast kätte vajalikud toitained ja vee ning saavad endale seetõttu lubada väiksemat juurte adsorbeerivat pinda. Võrreldes neid liike varem avaldatud andmetega leidsime, et katses konkrentsi paremini taluvad taimeliigid on tugevamalt mükoriissed. Kokkuvõtlikult võib meie katse tulemuste põhjal öelda, et juurestiku suurus määrab taimede võime naabreid alla suruda, kuid vastupanuvõime konkrentsile on seotud juurte morfoloogiliste tunnustega ja juuresüsteemi sügavusega. Kõiki tunnuseid koos vaadates, olid konkrentsitulemuse parimateks ennustajateks just konkrentsi tolereerimisega seotud tunnused, mitte taimede suurus.

Taime juurestik on kompleksne süsteem, kus juurte kogupikkus võib ulatuda kilomeetriteni ja samaaegselt kasvavate juuretippude arv tuhandeteni. Juurte ruumiline paigutus mullas määrab toitainete omastamise efektiivsust ja konku-

rentsitingimustes toime tulekut. Taimede juurte ruumilise jaotuse mõõtmiseks ja kirjeldamiseks puuduvad aga seni kergesti kasutatavad meetodid. Järgmises katses kasutasime taimede juurte käitumise mõõtmiseks taimeökoloogias uudset metoodikat, mis on eelnevalt kasutatud leidnud loomaökoloogias uurimaks loomade toitumist ning territoriaalselt käitumist. Eksperimendis kasvatasime kaheksat parasvöötme rohttaime liiki erinevatel tihedustel nii samast liigist naabritega kui ka teisest liigist naabritega. Registreerides iga juure ruumilist asukohta pottides (kahel sügavusel) saime põhjaliku informatsiooni juurte horisontaalsest paigutusest mullas. Saadud andmetega saime kirjeldada kuivõrd efektiivselt juured hõivavad mullaruumi, kui suur on taime kodupiirkond ja mis juhtub kui eri liikide kodupiirkonnad kattuvad. Leidsime erinevaid käitumusmustreid nii juurte paigutuse kui ka kodupiirkonna suuruse osas. Selgus, et suurema maapealse biomassi ja kiiremat kasvu peegeldavate tunnustega taime liikide juuri iseloomustab ühtlasem ja seega toitainete omastamiseks efektiivsem juurte paigutus. Ühtlasem juurte jaotus mullas andis eelise ka konkurentsisis teiste liikidega. Taimede kasvutiheduse kasvades muutus juurte jaotus mullas ühtlasemaks, mis loodusesse ülekantuna osutab taimede suremuse ja kasvutiheduse olulisele rollile koosluse võimes toitaineteid efektiivselt mullast omastada. Koos teisest liigist naabritega kasvades kattusid taimede juurestikud suurel määral ja juured kippusid ruumis kuhjuma võrreldes ühe liigi monokultuuridega. Selle põhjal võib järeldada, et uuritud taimeliigid ei näidanud territoriaalset käitumist tõrjudes konkurente oma kodupiirkonnast. Samas kaitsesid mitmed taimeliigid ressursse väiksemal skaalal kuhjates oma juuri kui naabruses esines teise liigi juuri.

Lisaks liikidevahelisele konkurentsile kogeivad taimed olelusvõitlust ka samast liigist konkurentidega, mis võivad olla mõnel juhul geneetiliselt lähisugulased ning teinekord mitte. Pole veel selge, kas liigikaaslase geneetiline sugulus muudab taimede käitumist ja kui levinud selline võime on. Et saada selgust, kui levinud on parasvöötme rohttaimede seas võime eristada naabrite hulgast geneetiliselt lähedasi isendeid ning kuidas muudavad taimed vastusena naabri identiteedile oma morfoloogiat, viisime läbi potikatse, kus kasvatasime erinevatel konkurentsitasemetel kaheksat liiki taimi koos kas samalt emataimelt või teistelt samas populatsioonis kasvavate taimedelt pärit isenditega. Vaid üks liik kaheksast näitas selget sugulaste äratundmist ning muutusi morfoloogias. Kasvades koos geneetiliselt lähedaste naabritega, investeeris valge ristik (*Trifolium repens*) ressursse rohkem õitesse, kuid seda vaid suure naabrite tiheduse juures. Investeerimine õitesse ja seeläbi suuremasse seemneproduktiooni võiks olla märk soovist kaugemale levida ning mitte tekitada konkurentsi sugulaste vahel ega raisata ressursse kulukatele konkurentsetele organitele. Seda kinnitas ka tõik, et geneetiliselt kaugete naabritega koos kasvades olid valge ristiku lehe rootsud pikemad viidates agressiivsele naabertaimede varjutamisele. Samas sugulastega kasvades suurendasid taimed lehe eripinda, mis tõstab taime varjutaluvust. Ka lehe morfoloogilised muutused ilmnesis vaid tiheda konkurentsi tingimustes.

Kokkuvõtlikult võib katse põhjal arvata, et valge ristik käitub sugulastega koos kasvades kooperatiivselt, püüdes vähendada otsesest konkurentsi ning investeerida kaugemale levimisse, kuid koos mittersugulastega kasvades panustavad taimed pigem ressursside haaramisse. Kuna meie katses näitas selgeid muutusi morfoloogias vaid üks liik, võib ka järeldada, et sugulaste äratundmine ei pruugi olla taimekooslustes väga tavaline nähtus. Kuna aga negatiivseid tulemusi on väga raske publitseerida ning korruga uuritakse sageli vaid ühte taimeliiki, on üldistuste tegemine varasemate uuringute põhjal kallutatud. Seda enam, et meie katsest selgus, et muutused võivad ilmnedagi vaid tugeva konkurentsi tingimustes. Seega on määrava tähtsusega, mis taimeliiki ja milliseid tunnuseid parasjagu uuritakse ning kui suurt konkurentsi pakuvad naabertaimed.

Sugulaste äratundmisel toimuvad muutused taime morfoloogias võivad kaasa tuua ka muutusi taimekudede koostises, mõjutades seeläbi ka varise kvaliteeti ja kõdnemise kiirust ning muutes toitainete ringlust mullas. Kolmandas katses küsisime, kuidas mõjutab taime liigisisene geneetiline mitmekesisus ning sugulaste äratundmine juurevarise keemilist koostist ja lagunemist ning milline mõju on sellel taime ja mullaorganismide interaktsioonidele. Uuritavaks taimeliigiks valisime luht-kastevarre (*Deschampsia cespitosa*), mis varasemalt läbi viidud juureeritiste katses näitas sugulaste eristamise võimet. Selgus, et kui luht-kastevars kasvas koos geneetiliselt mitmekesisete naabritega, oli fokaaltaimede juurtes kõrgem lämmastikutase ja ka juurevaris oli madalama süsiniku ja lämmastiku suhtega võrreldes taimedega, mis kasvasid koos geneetiliselt lähedaste sugulastega. Võib eeldada, et geneetiliselt mitmekesisuses koosluses kasvades pakuvad taimejuured mikroobsetele lagundajatele mitmekesisemat substraati ja naabrite äratundmise tulemusena ka morfoloogialt ja keemiliselt koostiselt kergemini kättesaadavamad energia allikat. Me leidsime, et lämmastikurikas juurevaris kõdnus mullas kiiremini, mis parandas lämmastiku ringlust ja kättesaadavust järgmisele taime põlvkonnale. Kuna luht-kastevarre seemned korjasime liigivaeselt rohumaal, kus liik on ise domineeriv ning koosluses on naabrid tihti sama liigi esindajad, siis saadud tulemustest võiks järeldada, et toitainete ringlust ökosüsteemis mõjutab oluliselt mitte ainult taime liigirikkus, vaid ka liigisisene geneetiline mitmekesisus.

Käesolevas doktoritöös läbiviidud katsete tulemuste põhjal võib järeldada, et taime konkurentsis ja liikide kooseksisteerimises võib olla kriitiliseks just konkurentsi tolereerimine, mitte naabrite allasurumine. Kasutades uut lähene-mist taimejuurte ruumilise paigutuse uurimiseks, avasime uusi aspekte taime käitumise mitmekesisusest ja strateegiatest. Samuti leidsime, et sugulaste äratundmine ei pruugi parasvöötme rohumaa taimeliikide hulgas olla väga levinud ning võib suuresti sõltuda taime looduslike naabrite kohtumissagedusest. Siiski võib sugulaste äratundmine osutada oluliseks liigivaestes kooslustes, kus dominantse liigi geneetiline varieeruvus võib mõjutada varise keemilist koostist ja mitmekesisust ning seeläbi mullas toimuvat aineringlust.

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ACKNOWLEDGEMENTS

First and foremost, I thank my supervisor Marina Semchenko, for all patience, guidance and support since my master studies. Also I am very grateful to my second supervisor Kristjan Zobel for introducing me to the field of plant ecology and all of the support during my long studies. I am grateful to all of our workgroup members whom I have worked together with during these experiments and big thanks to all co-authors and technical supporters who helped me with papers. My special thanks goes to John Davison for providing valuable comments, incredible statistical ideas and linguistic corrections.

I am particularly thankful to Siim-Kaarel for believing in me and all his support, help and guidance when it was most needed. I am grateful to my daughters, Hanna and Tuule, for their understanding and patience.

This study was supported by Estonian Science foundation (grants 9332 and 9269), Institutional Research Funding (IUT 20–31) of the Estonian Ministry of Education and Research, University of Tartu (0119) and the University of Manchester.

PUBLICATIONS

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- Nettan, S., Thetloff, M., Lepik, A., Semchenko, M. & Zobel, K. (2019). Manipulation of vegetation with activated carbon reveals the role of root exudates in shaping native grassland communities. *Journal of Vegetation Science*, 30:1056–1067. 10.1111/jvs.12808
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Popular-scientific publications:

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- Mägi, M., Lepik, A. (2014). Tavituvate rasvatihaste (*Parus major*) kehakaalu ööpäevased erinevused. *Hirundo*, 27 (1), 9–20.

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