

SIRGI SAAR

Belowground interactions:
the roles of plant genetic relatedness,
root exudation and soil legacies



DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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LIST OF ORIGINAL PUBLICATIONS

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

- I. **Semchenko M, Saar S, Lepik A. 2014.** Plant root exudates mediate neighbour recognition and trigger complex behavioural changes. *New Phytologist* **204**: 631–637
- II. **Semchenko M, Saar S, Lepik A. 2017.** Intraspecific genetic diversity modulates plant-soil feedback and nutrient cycling. *New Phytologist*. doi: 10.1111/nph.14653
- III. **Saar S, Semchenko M, Barel JM, De Deyn GB. 2016.** Legume presence reduces the decomposition rate of non-legume roots. *Soil Biology and Biochemistry* **94**: 88–93
- IV. **Saar S, Semchenko M, Barel JM, De Deyn GB. 2017.** Spatial heterogeneity in root litter and soil legacies differentially affects legume root traits. Manuscript.

The author's contribution to the papers:

Was responsible for ***; contributed substantially **; contributed *.

| | I | II | III | IV |
|---------------------------|-----|----|-----|-----|
| Designing the experiments | * | | *** | *** |
| Data collection | *** | * | *** | *** |
| Analysing the results | ** | ** | ** | ** |
| Manuscript preparation | ** | ** | *** | *** |

INTRODUCTION

Soil provides plants with essential nutrients and water but also contains physical obstacles, roots of the same and neighbouring individuals and a multitude of saprotrophic, pathogenic and mutualistic organisms. The ability of plants to navigate and interact with this heterogeneous environment is still poorly understood. It is increasingly recognised that the nature of plant-plant interactions and species coexistence are determined not only by the ability of interacting plants to take up resources but also by the release of diverse organic compounds into the soil (known as root exudates, Rovira 1969), and plant interactions with soil microbes (Bever et al. 2010; Inderjit et al. 2011). Besides direct effects on the growth of neighbouring plant individuals, root exudates and plant litter profoundly affect soil microbial activity and composition (Hamilton and Frank 2001; Broeckling et al. 2008). Root exudates and litter vary widely in their chemical composition and impose short- and long-term effects on microbial communities, respectively. Knowledge of how these two types of plant-derived carbon interact to shape nutrient cycling, and the role of litter chemical properties, is still limited.

Game-theoretic models and kin selection theory predict that genetic relatedness between interacting plants may affect plant phenotypes and behaviour (Gersani et al. 2001; File et al. 2012b). Behavioural changes may include intensified contesting of resources between unrelated individuals and reduced competition within genetically closely related groups. If behavioural changes involve changes in root morphology and chemical composition, these may also affect the quality of carbon available to soil decomposers and the susceptibility of plants to soil pathogens. It is therefore likely that kin recognition in plants has consequences for other trophic levels and affects nutrient cycling and plant-pathogen interactions.

Root exudates are a primary energy source for soil microbiota, and plants are known to cause significant changes to the composition and activity of microbial communities via root exudation (Haichar et al. 2008). The microbiome also releases a diverse set of compounds into the soil and modifies the chemical composition of root exudates, contributing to plant-microbe interactions (Lambers et al. 2008; Berendsen et al. 2012; Li et al. 2016). Living plants can influence nutrient and carbon cycling in soil through so-called priming effects. Plants can hasten litter decomposition by providing an additional energy source for decomposer bacteria and fungi in the form of labile carbon; however, they can also suppress microbial activity by exuding antibiotics and competing with soil microbiota for nutrients. Among legumes, exudates may be rich in nitrogen (N) and boost microbial biomass by providing an additional N source (Fustec et al. 2011). Priming effects also depend on litter quality. Root exudates may particularly hasten the decomposition of poor quality litter, such as lignin-rich roots, as microbes receive additional energy and nutrients from the living plant (Kuzakov 2002, 2010). However, the presence of living plants may shift

microbial activity and composition towards decomposition of easily degradable compounds contained within exudates and slow the decomposition of poor quality litter (Sparling et al. 1982; Kuzyakov 2002). It has been suggested that priming effects may depend on the nutrient status of living plants, with positive priming appearing in N limited systems and no significant priming occurring in soil with phosphorus-deficient plants, that use rhizodeposition, rather than soil organic matter degrading microbes, to acquire phosphorus (Dijkstra et al. 2013). Root decomposition rate also appears to depend on the precise identities of the litter and living plants, as the same plant species can increase the decomposition of one type of litter while decreasing the decomposition of another (van der Krift et al. 2002). Due to the lack of comparative empirical studies, it is currently unclear whether priming effects are generally negative or positive and what influences the direction or magnitude of the effects.

The direct effect of exudates in plant-plant interactions has mostly been demonstrated in invasive species, where effects are typically negative in the invaded range but neutral in the native communities (Callaway and Aschehoug 2000). However, root exudates and secretions with seemingly neutral effects could be important for neighbour recognition – including kin and species-level recognition – in coevolved communities (Fitter 2003; Bais et al. 2006; Biedrzycki et al. 2010). The role of root exudates in plant recognition has been debated, as microbial degradation may prevent soluble organic compounds from persisting in soil long enough to act as a signal (Jones and Darrah 1994; Kaur et al. 2009; Ehlers 2011). Alternatively, identity cues may be contained within DNA fragments (Mazzoleni et al. 2015) or proteins (Badri et al. 2012), which may be more stable in the soil environment and contain more specific information. Although no specific non-toxic compounds have been identified as cues of the genetic identity of neighbours, specific changes in plant phenotypes in response to neighbour identity have been repeatedly demonstrated in sterile media (Biedrzycki et al. 2010; Badri et al. 2012) as well as in non-sterile soil environments (Dudley and File 2007; Lepik et al. 2012). However, while root exudates represent a likely mechanism of neighbour recognition in plants, phenotypic changes could also be mediated by changes in soil resource dynamics or other as yet unidentified cues (Semchenko et al. 2007b; Hess and de Kroon 2007; File et al. 2012b). The involvement of root exudates in plant interactions has been tested by using activated carbon powder to adsorb root exudates, thus negating any effects on plants (Callaway and Aschehoug 2000; Abhilasha et al. 2008). However, activated carbon may strongly interfere with nutrient availability and microbial activity in the soil, creating unwanted artefacts (Semchenko et al. 2007a; Lau et al. 2008; Wurst et al. 2010). Therefore, novel approaches are necessary to determine if root exudates can mediate neighbour identity recognition in realistic soil conditions but without differences in nutrient levels or other artefacts.

While proximate mechanisms of belowground neighbour recognition in plants remain elusive, plant species have been found to vary widely in their responsiveness to neighbour identity and in the nature of phenotypic changes

produced. Plants can express different phenotypes depending on the genetic identities of their neighbours (known as indirect genetic effect, IGE) and such plasticity can have consequences for ecosystem processes through changes in plant traits. Plants can exhibit three broad foraging responses to perceived neighbour presence. They can aggressively confront their neighbours and try to pre-empt loss of nutrients by aggregating roots towards the neighbour's root system. Alternatively, cues of neighbour presence and identity can trigger avoidance of root competition, displayed as redirection of root growth away from space occupied by neighbours. Both aggressive and avoidance behaviours have been shown to depend on the nutrient availability in the soil and to occur in response to both conspecific and heterospecific neighbours (Semchenko et al. 2007b; Cahill et al. 2010; Schmid et al. 2015). Several studies have also reported no detectable response to the presence or identity of neighbours (Semchenko et al. 2007b; Lepik et al. 2012).

The genetic relatedness of interacting conspecifics can influence the outcome of competition and plant responses to neighbour presence. Phenotypic responses to the genetic relatedness of neighbours resulting in cooperative behaviour have been considered as evidence for kin recognition in plants. According to kin selection theory, plants should benefit from avoidance of competition with close kin as it should improve inclusive fitness by releasing individuals with shared genes from competition, but the benefit can also be direct as more resources can be allocated to reproduction and other functions instead of wasteful competition (de Kroon 2007; File et al. 2012b; Dudley et al. 2013). Several plant species have been shown to reduce investment to root growth, suffer less damage from soil pathogens and form more extensive interactions with mycorrhizal fungi when grown in groups of closely related individuals (Dudley and File 2007; Murphy and Dudley 2009; Biedrzycki et al. 2010; File et al. 2012a; Gorzelak et al. 2015; Zhang et al. 2015). These results are in agreement with theoretical predictions that interactions with kin should favour reduced allocation to competitive traits and greater investment into natural enemy defence and mutualistic interactions. Besides changes in overall root growth, little is known about the ability of plants to change root spatial distribution and morphology in response to the genetic relatedness of interacting plants. It is also unclear whether such responses are localised in their extent or cues could trigger a systemic response at the level of the whole root system.

The effects of plant individuals occupying a certain soil patch may also extend beyond their lifetime. Plant activity, exudation and litter production can modify abiotic soil properties and soil biotic communities, which in turn may affect the growth and performance of plants in subsequent generations – a phenomenon known as plant-soil feedback (PSF). Plants can produce species-specific feedback effects by accumulating autotoxic exudates, specific pathogens, mutualists or litter decomposers. PSF can be positive if soil conditions become more favourable for growth of conspecific than heterospecific plants. This may be due to improved availability of limiting resources or soil mutualists such as mycorrhizal fungi or nitrogen-fixing bacteria. Negative PSF occurs when

the depletion of limiting resources or accumulation of pathogens makes soil more favourable for the growth of other species compared with conspecifics. Most plant-soil feedback studies have subjected plants to a homogenous soil environment, while plants are likely to experience heterogeneous environments in natural conditions where root systems encounter different patches with more or less favourable microbial communities and/or abiotic conditions. Plants are known to be very responsive to soil nutrient concentrations, with higher root branching and residency time within nutrient-rich patches (Gross et al. 1993; Robinson et al. 1999; de Kroon and Visser 2003; Lamb et al. 2004). Little is known about the ability of plants to react locally to soil microbial legacies or produce systemic responses to heterogeneous soil conditions. It has been shown that grassland plants produce less root mass in soil patches conditioned by conspecific plants, which may reflect response to host-specific pathogens (Hendriks et al. 2015). However, it is unclear whether plants can modify traits other than biomass production in response to heterogeneity in soil legacies or respond differently to soil conditioned by species other than conspecifics. Moreover, it is unclear whether feedback effects on plant growth and morphology reflect responses to soil microbial communities or root litter presence and decomposition. Most experiments have used whole soil containing root litter or with litter removed, but the relative contribution of soil biota and litter to feedback effects has not been investigated. It can be predicted that decomposing litter may have additional effects on plants (e.g. via releasing nutrients or toxic compounds) to those detected in studies using soil inoculums where litter is removed.

While plant responses to soils conditioned by different species have been widely studied and their importance for species co-existence and ecosystem functioning appreciated, the consequences of within-species genetic diversity for plant-soil feedback are still poorly understood. Genetic diversity within plant populations is known to enhance multiple ecosystem functions, such as primary productivity and nutrient cycling, while also improving plant pathogen resistance and species co-existence (Booth and Grime 2003; Schweitzer et al. 2005; Barton et al. 2015). The mechanisms underlying such effects are, however, largely unidentified. Beneficial effects on productivity have been attributed to niche complementarity but are yet to be experimentally demonstrated (Crutsinger et al. 2006). Enhanced nutrient cycling and litter decomposition could be due to the provision of chemically diverse litter that can support a more diverse and active decomposer community (Schweitzer et al. 2005; Madritch et al. 2006; Crutsinger et al. 2009). Higher intraspecific diversity may also increase resistance to pathogens via associational resistance, as has been shown for resistance to insect herbivores (Bustos-Segura et al. 2017).

Effects of genetic diversity are not always additive in their nature and thus are difficult to predict due to interactions between genotypes (Hughes et al. 2008). Different phenotypes resulting from IGEs of the identities of their competitors show significant plasticity in plant responses. Plant phenotypic plasticity arising from kin recognition is one way in which plant-plant interactions

could affect litter quality. It could be expected that plants produce thinner and more extensive root systems to maximise resource uptake when competing with unrelated individuals, but that such competitive behaviour is suppressed when interacting with kin. Such effects of kin interactions could contribute to non-additive effects of genetic diversity on ecosystem functioning: changes in traits such as root diameter and specific root length in response to identity cues directly translate into different nutrient-absorbing surface area and these traits also modify quality for litter decomposers. Thinner roots are more short-lived and easier for herbivores and parasites to degrade, unless plants reinforce them with additional structural carbon and therefore increase C:N ratio. Reduction in competitive traits in response to kin recognition could lead to less resource-acquisitive growth strategy with higher root construction costs and increased recalcitrance of litter (Vivanco and Austin 2006; Reich 2014; Lemmermeyer et al. 2015). Moreover, kin recognition responses could alleviate the expected negative effects of pathogens in stands with low genetic diversity by diverting resources away from competition with kin towards defence against natural enemies. Therefore, genetic relatedness between interacting plants might significantly affect litter chemical composition and nutrient cycling and make soil conditions more or less favourable for subsequent generations of plants.

The main goals of this thesis were to determine:

- whether root exudates mediate kin recognition in realistic soil conditions and elicit localised and systemic responses in plant root systems (**I**).
- how genetic relatedness among interacting plants affects plant-soil feedback and nutrient cycling in a plant species exhibiting kin recognition (**II**).
- how living plants, via release of root exudates, affect the decomposition of dead roots with different chemical properties (**III**).
- the local and systemic responses of plant root systems to spatial heterogeneity in soil microbiota and root litter (**IV**).

MATERIALS AND METHODS

Paper I – Root exudates as a mechanism of neighbour recognition

The perennial grass *Deschampsia cespitosa* was used as a focal plant. The experiment involved subjecting plants to root exudates collected from: a) siblings of the focal plant, b) unrelated conspecifics from the same community, c) conspecifics from a distant community, d) plants of *Lychnis flos-cuculi* from the same community, and e) plants of *Lychnis flos-cuculi* from a distant community. Each treatment was replicated 10 times. Root exudates were previously collected as soil leachate and were sterilised using 0.2µm syringe filters. Exudate solution mixed with liquid fertiliser was imbibed into soil on one side of the focal plant, while the other side was treated with fertiliser solution as a control to compensate for differences in nutrient concentrations. Exudate application started after two weeks of plant growth and was repeated twice per week for 10 weeks in total. After 12 weeks of growth, plants were harvested, aboveground biomass dried (70°C for 48 hours) and weighed, and roots sampled with soil cores at the locations of exudate and control solution application. A representative sample of roots from each soil core was scanned and analysed using WinRhizo Pro 2008a (Regent Instruments, Inc., Québec, Canada) to estimate root length, diameter and branching. Scanned roots were dried and weighed as above. Root branching intensity was calculated as the ratio of the length of second-order branches to the length of the main adventitious root branch. Specific root length (SRL) was calculated as ratio of root length and dry mass from the scanned root sample. Root length density (cm/cm^3) was estimated based on SRL, root dry mass and the volume of the soil core.

To test for kin recognition responses, linear mixed models were fitted to biomass and root trait data, using exudate origin (kin or stranger from the same population) and root sample position (exudate or control core) and their interaction as fixed factors. The identity of mother lineage and pot identity were included as random factors for all models. To identify population- and species-specific effects, data from all treatments except the kin treatment were used to fit linear mixed models with community origin, species identity, sample location and their interactions as fixed factors and mother lineage and pot identity as random factors. More detailed descriptions of methods can be found within publications (I–IV).

Paper II – The effect of intraspecific diversity on nutrient cycling and plant-soil feedback

The experiment was conducted in two phases: first conditioning soil and then using it as a substrate for *D. cespitosa* in a feedback phase. In the conditioning phase, plants were grown as sibling groups (originating from the same mother plant, 10 different mother plants were used) or genetically diverse groups (multiple mother plants mixed). Fifteen plants per pot were grown, and harvested after three months. Soil from each pot was divided into two equal parts, one of which was sterilized by gamma radiation (15 kGy). Soils from the sibling groups were kept separately, while control soil and soil conditioned by genetically diverse groups was pooled within each sterilisation treatment. Root C and N content, as well as soil N, available P and available K content, were determined. To assess the effects of the conditioning treatment and sterilisation on root and soil nutrient content, linear fixed effects models were used.

In the feedback phase, seedlings from the same mother plants as used in the conditioning phase were grown in a factorial design on both sterilised and unsterilized soil that was conditioned by siblings, genetically diverse groups or no plants. Ten replicates were established for each treatment combination, resulting in 60 pots in total. Plants were grown for 58 days. Roots were then washed out of the soil and separated into roots belonging to the focal plants and dead roots that came from the conditioned soil. In this experiment, *in situ* decomposition estimation was used (Dornbush et al. 2002) to gain realistic estimates of root litter decomposition as, unlike litterbags, it allows close contact between root litter, soil and living plants. This experiment allowed relatively precise estimation of decomposition, as a comparison with sterilised soil was included. Plants and dead roots were dried at 70°C for 48h and weighed. Root C and N content of plants grown in the feedback phase were also determined. Linear mixed models were used to estimate the effects of soil conditioning and sterilisation (fixed factors) on plant biomass and N uptake, and litter decomposition. Mother plant lineage was included in the models as a random factor.

Paper III – The impact of living roots on litter decomposition

Root litter from seven grassland species (*Lolium perenne*, *Festuca rubra*, *Arrhenaterum elatius*, *Trifolium repens*, *Trifolium pratense*, *Vicia cracca*, *Cichorium intybus*) was incubated in litterbags in soil for eight weeks together with a focal plant (*T. repens*) and without a plant (control) to determine the effect of living roots on root litter decomposition. The first part of the experiment consisted of growing plants in sandy soil at 60% water holding capacity to harvest the roots for litter decomposition. The soil mixture consisted of 85% sterilised soil (gamma irradiation 25 kGray) and 15% live soil (collected from

52°04'N, 5°45'E). Plants were grown in 2L pots in a greenhouse for 12 weeks. At harvest the roots were washed carefully and dried at 40 °C for one week. Litterbags were filled with 0.5g of dry fine roots. Nutrient concentrations in soil and plant biomass were measured (bioavailable N and P in the soil using the standard CaCl₂ extraction method (Houba et al. 2000). N, P and C in the root litter prior to incubation (Novozamsky et al. 1983) were measured using Segmented Flow Analyses and a CN elemental analyser.

Litter decomposition was manipulated with the addition of a single clover (*T. repens*) plant per pot (8 replicates with and without plant presence for each litter species). Plants and litter were placed into pots that were 11cm wide, 22cm long and 12cm deep and filled with 1740g of soil mixture (10% living soil and 90% sterilised soil, same soil as above). The litterbags were inserted into the soil (oriented vertically, directly below the soil surface and at 2 cm from the pot border) ten days after planting the clover plants. Plants were harvested after 8 weeks, shoots and roots of each plant were dried separately at 40 °C for 48h and weighed. The litterbags were also removed from soil, rinsed and dried under the same conditions, and remaining litter was weighed.

Root litter decomposition rate was calculated for each litterbag as the proportion of litter mass that was lost during the experiment. Priming effect was calculated for each litter species as the difference in the mean root decomposition rates in the presence and in the absence of a living plant in the soil. Linear mixed model was used to test for species-specific root decomposition patterns in relation to plant presence using the proportion of litter decomposed as a response variable and litter species, presence/absence of the living plant and their interaction as predictor variables. Root litter replicate and block nested within root litter replicate were included in the model as random factors. For testing the effects of litter quality on decomposition rate, linear mixed models were designed with priming effect or litter decomposability as a response variable and litter N, C, C:N and P as predictor variables.

Paper IV – Local and systemic responses to spatial heterogeneity in root litter and soil legacy

Split-root plants of *T. repens* were used to determine whether plants respond locally to heterogeneity in soil conditions or integrate information originating from different parts of their root systems. Split-root plants were prepared by cutting the main root of eight-week-old plants at 2cm below the rooting point and dividing remaining roots between two pot halves. Plants were grown in the conditions described in the second phase of **III**. The pot was split with a plastic partition into two equal compartments. In the litter experiment, a litterbag filled with 0.5g root litter from one of seven grassland species (as in **III**) was added to one of the pot compartments. Both soil compartments contained sterilised soil inoculated with 10% live field soil as in **III**. The soil conditioning experiment was established by inoculating one of the pot compartments with a sterilised

soil mixture containing 10% unsterilised soil conditioned by one of seven grassland species used in **III**, while the other pot compartment was inoculated with 10% unsterilised soil collected from the original field site (representing unconditioned control soil). After eight weeks of growth, plants were harvested and a root sample from each pot compartment taken for morphological analysis and estimation of nodule abundance. Shoots and all sampled and remaining roots were dried at 40°C for 48h. Linear mixed models were used to estimate the effects of litter addition and soil inoculum on focal plant root traits, where litter or soil origin, pot compartment and their interaction were included as fixed factors. Root biomass, diameter, specific root length (SRL), branching and the number of nodules per unit of root dry mass were used as response variables.

RESULTS

Paper I – Root exudates as a mechanism of neighbour recognition

Plants responded to cues of relatedness and species identity even in the absence of actual neighbours. Exudates collected from closely related individuals reduced root proliferation of entire root systems. On the other hand, exudates produced by unrelated individuals from the same population caused focal plant roots to branch more and to produce more root length per unit of invested biomass (Fig. 1 in **I**). Irrespective of the exudate origin within the same population, greater root mass was recovered from the soil patch treated with exudates, and the roots had higher specific root length and were more branched compared with those from the soil patch treated with control solution (Table 1 and Fig. 1 in **I**). At the whole root system level, responses to root exudates displayed species- and population-specific effects. Application of conspecific exudates from plants of the same population caused higher root length density than exudates originating from individuals of different population (Fig. 2 in **I**). A spatially localised response to *D. cespitosa* exudates was mediated by a species-specific cue that was common to both examined populations. Exudates produced by a different species (*L. flos-cuculi*) did not cause a significant response independent of community origin (Fig. 2 in **I**). The treatments did not cause any significant differences in shoot and total plant biomass.

Paper II – The effect of intraspecific diversity on nutrient cycling and plant-soil feedback

Decomposition of root mass was greater in soil conditioned by genetically diverse groups compared with soil conditioned by sibling plants (Fig. 2 in **II**). No significant difference in the loss of root litter mass was detected between high and low diversity treatments in sterilised soil. Root litter collected from genetically diverse plant groups also had a significantly higher N content and a lower C/N ratio compared with root litter produced by plants grown among siblings (Table 2 in **II**). These effects carried over to the feedback stage when soil was left unsterilized: plants grown in soil conditioned by genetically diverse plant groups had higher tissue N content and lower C/N ratio compared to plants grown in soil conditioned by siblings (Fig. 3a, 3b in **II**). Total N uptake by plants was also higher in soil conditioned by genetically diverse groups than in soil conditioned by siblings. The effect on N uptake was only evident in unsterilized soil. Plant growth was equally inhibited in unsterilized soil conditioned by both sibling and diverse plant groups compared with the unconditioned control, indicating negative plant-soil feedback (Fig. 3e–3h, in **II**). Plant growth was significantly improved by soil sterilisation (Fig. 3c, 3d in **II**).

Paper III – The impact of living roots on litter decomposition

Decomposition rates of root litter originating from different species varied widely, independent of the presence of living roots: litter of *C.intybus* decomposed most by the end of the experiment, while root litter of grass species decomposed the least (Table 1 in **III**). Instead of the expected positive priming effect, there was a decline in the decomposition of grass root litter when a living plant was grown simultaneously in the soil, while the decomposition of legume roots was not affected. The strength of the priming effect was significantly influenced by the initial N and P content of the root litter, and negatively affected by the C/N ratio: decomposition of litter with low nutrient content and high C/N ratio was suppressed more in the presence of a living plant than the decomposition of higher quality litter (Fig. 1 in **III**). Litter decomposability (root litter mass loss in the absence of a growing plant) did not depend on these litter characteristics. Litter species identity or nutrient content did not significantly affect the biomass of focal *T. repens* plants.

Paper IV – Local and systemic responses to spatial heterogeneity in root litter and soil legacy

Soil legacies elicited localised responses in *T. repens* root systems. Significantly less root length was produced in the pot compartment inoculated with conditioned soil compared with the soil compartment inoculated with unconditioned soil (Fig. 1b in **IV**). However, mean root length in conditioned soil did not differ significantly from the control treatment where both pot compartments were inoculated with unconditioned soil. Species-specific localised responses were observed in response to inoculation with soil conditioned by legume *V. cracca*: root nodulation was reduced by 71% compared with the compartment inoculated by unconditioned soil (Fig. 2a in **IV**). No significant changes in root morphology or nodulation were observed in response to soil legacy of any other species. There was a trend of systemic response to soil conditioned by conspecifics: plants produced fewer nodules in both pot compartments when one of the compartments was inoculated with soil of *T. repens*.

Root litter addition affected the spatial distribution of root biomass: focal plants placed more root biomass towards the litter irrespective of litter origin, compared with the pot compartment without litter (Fig. 1c in **IV**). Also, in most species, fewer nodules were produced in pot halves with litter, indicating a significant localised response independent of litter species identity. However, this localised response did not differ from the response to an empty litterbag. Litter of *V. cracca* induced a significant systemic response in root diameter in the pot compartment that was not in direct contact with the litter: clover roots were significantly thinner in the control compartment compared with roots in contact with the root litter and compared with roots produced in the control

treatment with no litter application (Fig. 2d in **IV**). Total plant biomass above and below ground was not significantly affected by soil inoculation or litter addition.

The summary of all results is presented in Table 1.

Table 1. Research questions and main findings

| Question | Result |
|--|--|
| Is kin recognition mediated by root exudates? | Root exudates convey information about genetic relatedness of neighbours as well as population- and species-specific cues. |
| How does the presence of living plants affect litter decomposition? | The presence of living plants can inhibit the decomposition of low quality root litter. |
| What are the intergenerational effects of kin recognition and intraspecific genetic diversity? | In presence of soil biota, litter produced by genetically diverse plant groups decomposes faster than litter produced in sibling groups and results in higher N uptake in the next generation of plants. Despite higher N uptake, plant biomass accumulation suffers strongly from negative soil feedback. |
| Can plants respond to spatial heterogeneity in soil microbial legacy and litter distribution? | Plants can react locally by changing root morphology, but systemic integration of information is limited. |

DISCUSSION

Kin recognition and consequences for nutrient cycling and plant-soil feedback

The results of this study show that root exudates produced by groups of closely related *versus* genetically diverse individuals of *D. cespitosa* elicited different responses in plants exposed to the exudates (**I**). The results of this study also provide empirical evidence that root exudates can mediate neighbour recognition in natural soil conditions and in the presence of microbial communities. Observed suppression of root proliferation in response to sibling exudates implies reduced competitive behaviour, in accordance with kin selection theory, which predicts that competition among offspring decreases parental fitness and therefore should be avoided (Hamilton 1964). Additionally, there was a spatially localised response to the application of root exudates: plants allocated more root length and produced more branched roots in soil patches containing conspecific exudates independent of exudate origin (siblings, conspecifics from the same or different population). This suggests that root exudates contain multiple cues with some indicating neighbour relatedness and others conveying information about the location of potential conspecific competitors independent of relatedness. This reaction to root exudates could be expected, as it allows plants to respond to a competitor before competition for nutrients becomes intense. If such a response occurs in parallel with kin recognition, then plants can modify the degree of response to neighbour presence accordingly (Fig. 1 in **I**). As plants are more related within populations compared to between populations, different responses towards unrelated conspecifics from the same and different communities to that of the focal plant were expected. Aggressive root proliferation appeared in response to root exudate cues from plants from the same population but not to those from a different population. Population-level specificity in plant communication has previously been recorded among responses to volatile compounds originating from aboveground plant parts in the context of induced anti-herbivore defence (Moreira et al. 2015; Karban et al. 2016) and in response to root contact between plants from different geographical regions (Mahall and Callaway 1996). These results suggest that neighbour recognition operates at local geographical scales and is likely to break down if interacting plants originate from distant populations. Sourcing plants for habitat restoration within the scales at which neighbour recognition operates might allow facilitative interactions to be maintained.

The increase in root density per unit of soil volume in response to the exudates of genetically diverse plants did not involve an increase in root biomass but instead changes in root morphology (longer but thinner roots). This suggests that plants may avoid the cost of producing more biomass to achieve higher competitive ability and to maintain nutrient uptake in the face of competition by reducing allocation of resources per unit of root length. In this way, the

energetic cost of selfish behaviour is reduced but plants may face the trade-off of low-cost, thin roots being more susceptible to pathogens (Eissenstat and Yanai 1997). Differential responses to interactions with closely related and genetically diverse neighbours could also be inferred from the finding that genetically diverse groups produced roots with higher N concentrations but no difference in biomass production compared to kin groups (**II**). This change in resource acquisition resulted in root litter with higher N concentration that decomposed significantly faster than litter produced in kin groups. The faster decomposition of N-rich litter of diverse groups improved plant nutrition in the next generation (**II**). Previous studies have also recorded improved nutrition and competitive ability of fast-growing grasses when N-rich litter was added to the soil (Vinton and Goergen 2006; Hofland-Zijlstra and Berendse 2010). However, production of nutrient-rich litter may be associated with adverse effects such as nutrient loss through leaching (Phoenix et al. 2003) and higher susceptibility to herbivory (Stevens and Jones 2006). The results of this study demonstrate that genetic diversity within plant neighbourhoods can have significant consequences for nutrient cycling, particularly in ecosystems with low species diversity where intraspecific interactions are widespread. Previous studies exploring the effects of litter diversity on decomposition rates have often used litter from plants grown in isolation and have not incorporated the possible effects of plant interactions on litter quality (Schweitzer et al. 2005; Crutsinger et al. 2009). This study shows that the genetic identities of interacting plants can affect plant phenotype, including litter quality, and that such indirect genetic effects can have consequences for nutrient cycling.

Slower N cycling apparent in the sibling treatment could have been caused by increased allocation to defence-related traits, as lower specific root length implies longer-lived, thicker roots that may be more resistant to decomposers (**I**). Higher C content in roots produced in sibling groups could also be associated with pathogen defence as genetically similar plants are more susceptible to pathogen attack (Zhu et al. 2000; Rottstock et al. 2014) and therefore would benefit from allocating more to defence. However, interactions with non-siblings have been shown to upregulate the expression of genes involved in pathogen defence, though no significant effect on the resistance to pathogen infection was observed (Biedrzycki et al. 2011). As pressure from natural enemies is higher and more predictable in low-diversity stands (Tooker and Frank 2012; Barton et al. 2015), structural and constitutive defence mechanisms may be favoured when interacting with kin. Individuals in diverse stands generally experience lower levels of natural enemy attack and induced defence may be more favourable in such settings.

In this study, seedlings grown on soil conditioned by kin groups and genetically diverse groups experienced a similar level of negative soil feedback. Growth suppression was probably caused by interactions with soil pathogens as soil sterilisation improved plant growth in both sibling and diverse plant treatments, and plants grew better in soil that was not previously conditioned by any plants (**II**). Several studies have demonstrated increased natural enemy damage

in low diversity stands (Tooker and Frank 2012; Barton et al. 2015; Luo et al. 2016) and therefore more negative soil feedback could be expected in soils conditioned by siblings compared with genetically diverse groups. However, plants in this study did not grow significantly larger in soil conditioned by diverse plant groups compared to growth in soil conditioned by sibling groups despite greater N uptake in the former soil. Similar levels of growth suppression by soil biota suggest that changes in resource allocation in sibling groups may have alleviated stronger negative feedback expected in low-diversity stands and that siblings didn't accumulate deleterious soil biota faster than diverse plant groups. On the other hand, plants in diverse groups accumulated more N in their tissues but may have also attracted more soil pathogens due to low levels of investment into defence. These results demonstrate how considering the ability of plants to change their phenotype in response to neighbourhood diversity may modify predictions of the relationships between diversity and ecosystem processes.

While this study demonstrated kin recognition via root exudates, the fitness consequences of kin recognition remain to be demonstrated. The fitness benefit of cooperation with kin via root segregation will depend on the availability of unoccupied space or space occupied by non-kin, while the cost of selfish behaviour may vary depending on whether it requires additional investment of limiting resources or can be achieved via morphological changes. Regardless of fitness costs, changes in plant traits in response to the genetic relatedness of surrounding neighbours have the potential to affect ecosystem functioning. Plants of *D. cespitosa* responded to both perceived (I) and actual (II) intra-specific competitors by altering root traits in ways that affect nutrient cycling and plant-soil feedback. Advancing our understanding of kin interactions in plants has direct relevance to agricultural systems, which often involve monocultures of closely related individuals where within-crop competition is highly undesirable. A possible direction for crop breeding could be to develop varieties with diminished competitiveness towards relatives but increased pathogen resistance and seed yields (reviewed in (Murphy et al. 2017)).

Interactions between living plants, litter decomposition and soil legacies

Besides the involvement of root exudates in plant-plant communication, the results of this study demonstrate that root exudates have specific effects on soil microbial activity as demonstrated by changes in the rates of root litter decomposition (known as priming effect, III). The presence of white clover (*T. repens*) roots slowed down the decomposition of root litter produced by non-legumes. The speed of decomposition of legume root litter on average was not significantly influenced by the presence of living roots, but there was a trend towards increased decomposition of *T. repens* root litter, indicating home-field advantage of enhanced litter decomposition under influence of its origin species

(Ayres et al. 2009; Freschet et al. 2012). The absence of the originally hypothesized positive priming effect (the presence of living roots increasing decomposition) may have been due to N fixation by the white clover allowing microbes to thrive on exudates instead of mining N from root litter. In support of this hypothesis, it has been shown that N addition can decrease fine root decomposition (Solly et al. 2014). The strength of the priming effect depended on litter N and P concentrations, being most negative for the lowest quality litter. Similar negative priming effects have been obtained in a previous study where high C:N litter induced negative priming effects through a switch in microbial resource use from recalcitrant litter towards root exudates as a labile carbon source (Sparling et al. 1982; Recous et al. 1995). Additional N from *T. repens* root exudates could have facilitated this shift by providing easily available N compared with N mining from the litter (Craine et al. 2007). Legumes can also cause P deficiency as N fixation increases plant demand for P, resulting in stronger competition for P between plants and microbes (Downie 2014). P limitation in plant presence may have limited microbial activity. Yet plants in this study appeared to be more N than P limited. Considerable variation in the strength of negative priming was observed between the litters of non-legume species that could not be explained by differences in litter N, P or C:N ratios. It is likely that such differences are related to litter C quality. Further research is necessary to ascertain how differences between root exudates and litter in the content of labile and non-labile C affect the nature of priming effects.

If the negative priming effect caused by living roots operates in the field, soil C storage could be affected by the interactive effects of root exudate and litter properties such that recalcitrant litter is likely to accumulate in the soil in the presence of nutrient-rich root exudates. It has been shown that plant diversity can increase carbon accumulation in soil and, in addition to the production of litter, carbon inputs are likely affected by root exudates (Lange et al. 2015). Simultaneous manipulation of root litter and root exudate quality is required to test for the mechanisms causing negative priming effects as the main focus so far has been on litter properties alone. Priming effects could have a practical application in designing crop rotations. Different combinations of main crops and cover crops can be selected depending on whether the focus is on increasing soil organic matter content or improving nutrient cycling. As the negative priming effect retards litter decomposition, growing clover as a cover crop following grain crops might result in enhanced soil carbon storage.

The ability of plants to respond to spatial heterogeneity in litter and soil microbial properties was investigated in a split-root experiment where one half of the white clover root system experienced soil biota or root litter accumulated by different plant species (IV). Largely local effects were found, showing that plants can react to soil and root litter legacies locally but this does not cause a systemic reaction such as a change in aboveground biomass. Root length generally decreased as a response to specific soil inoculum compared with inoculation with 10% natural grassland soil inoculum, indicating avoidance of specifically conditioned soil compared to unconditioned soil. The number of

root nodules was locally suppressed in the compartment inoculated with soil of *Vicia cracca*, but not other species. This reduction could be explained by the high specificity of interactions with nodule-forming *Rhizobia* (Wang et al. 2012) as soil conditioned by other legumes may have harboured *Rhizobia* that were less suitable to form nodules on the white clover. Soil of *V. cracca* likely harboured dissimilar AMF communities and *Rhizobia* strains compared to the focal *T. repens*, but may have contained shared fungal pathogens (Gilbert and Webb 2007; Veresoglou and Rillig 2014). Sharing same pathogens, but being specialist in interactions with mutualists, could result in negative heterospecific feedback between legume plants, but less negative feedbacks from non-legume species. The only significant systemic effect that was dependent on the root litter identity appeared in response to *V. cracca* litter. In the compartment away from litter, root diameter decreased, which indicates a compensatory production of thinner roots in more favourable soil conditions as a response to local detrimental conditions in the compartment with added litter. This finding suggests that *T. repens* can compensate for local negative effects by root proliferation elsewhere in the root system. Overall, these results show that focal plants produced distinct responses to heterogeneity in soil microbial communities and root litter, and that these responses involve not only biomass, but also root morphology and nodule formation, which reflects altered symbiosis with nitrogen-fixing bacteria.

While root foraging behaviour in response to nutrient heterogeneity is widely known and investigated (Hodge 2004), less is known about the ability of plants to divert root growth in response to heterogeneity in the spatial distribution of neighbouring plant root exudates, plant litter and soil microbial communities. This ability can be expected to depend on plant biology such as root system architecture and clonal growth form. Non-clonal species have been shown to exhibit systemic control of root architecture, reacting locally to nutrients and competitors (Nan et al. 2013) as well as integrating the information about nutrient placement and variability across the whole root system (Dener et al. 2016). Stoloniferous species have been shown to integrate information and exchange limiting resources across multiple interconnected but potentially independent shoots (known as ramets, (Stuefer et al. 1996; Louâpre et al. 2012)). The two studied species, *T. repens* and *D. caespitosa*, have distinct growth forms that may contribute to their differences in response to localised cues. *T. repens* is a clonal forb with aboveground stolons rooting at the nodes. *D. caespitosa*, on the other hand, is a tussock grass with phalanx-strategy clonal reproduction: adjacent shoots are placed very closely together and do not serve a dispersal function. *T. repens* exhibited weak and predominantly localised responses to belowground heterogeneity (IV). This species was also only weakly affected by soil microbial legacy. *T. repens* may benefit from clonal mobility by placing new ramets away from soil patches with unfavourable conditions rather than investing into systemic defences within a single ramet. *D. caespitosa* can benefit more from the systemic reactions observed in this study (I) as tussocks are very long-lived and cannot escape unfavourable conditions by clonal spread.

Therefore, the spatial resolution of root reactions to soil heterogeneity may depend on clonal strategy and future research into the relationship between plant life history and response to heterogeneity may provide new insights into how local spatial reactions develop and affect fitness at the genet level.

CONCLUSIONS

The results of this thesis reveal a complex pattern of root reactions to cues originating from other plants in the form of root exudates, litter and soil microbial legacies as well as the capacity of living root systems to modify the activity of litter decomposers. Investigation of plant responses to neighbours' root exudates in the absence of competition highlighted the diversity of cues contained within root exudates and their importance in mediating plant-plant interactions: plant root systems responded locally to cues of neighbour proximity as well as systemically to cues of neighbour genetic identity by modifying root morphology and branching. Responses to root exudates were also population- and species-specific with the strongest responses observed when exposed to exudates collected from conspecifics from the same population. Plants responded to the exudates of genetically diverse plant groups by increasing root growth. Enhanced root proliferation was achieved via the production of finer roots rather than greater biomass investment, suggesting that plants can reduce the cost of allocation to apparently selfish root proliferation. However, the production of thinner roots in response to competitive interactions can predispose plants to pathogen attack and cheap but short-lived roots will only be advantageous if contested nutrient patches are quickly depleted. The ability of plants to modify root morphology and the trade-off between root construction cost and longevity could be incorporated into future modelling of plant behaviour to help to identify the full range of viable behavioural strategies. While this study identified root exudates as mediators of kin recognition, other mechanisms could potentially be involved in different species. Further studies are required to establish the generality of exudate-mediated recognition and to determine the major types of compounds involved in recognition. Future studies on kin recognition should also place more focus on estimating the actual fitness costs and benefits of selfish and cooperative behaviours in different environmental settings as these may be modified by trade-off between growth, defence and reproduction.

Kin recognition and associated changes in plant traits can have significant consequences for nutrient cycling and plant-soil feedback in species-poor habitats where conspecific interactions predominate. Experiment on plants from a species known to exhibit kin recognition demonstrated that individuals produced higher quality root litter when grown in genetically diverse groups. Such litter decomposed more rapidly and made more nitrogen available for the next generation of seedlings compared to soil conditioned by groups of siblings. Despite differences in nitrogen uptake, plant biomass accumulation was strongly suppressed in soil conditioned by both kin and non-kin groups compared with unconditioned soil. These results demonstrate that within-species genetic diversity can affect ecosystem processes via changes in plant traits, with differential effects on nutrient cycling and negative feedback with soil biota. Importantly, the ability of plants to assume a more conservative growth strategy

when interacting with closely related individuals may counteract the expected accumulation of soil pathogens in stands of low diversity.

Examination of local and systemic changes in root traits in response to soil heterogeneity revealed that plants can respond to cues of genetic relatedness from living plants as well as to the litter and soil microbial legacy left behind by previous generations of plants belonging to different species. Moreover, the presence of living roots can inhibit the decomposition of low-quality litter via effects of root exudates on microbial activity, and genetic relatedness within plant groups can affect nutrient cycling via changes in litter quality. The aim for future research should be to identify compounds involved in exudate-mediated plant-soil interactions and to determine conditions favouring negative or positive priming effects in litter decomposition by simultaneous manipulation of root exudates and litter quality.

SUMMARY IN ESTONIAN

Maa-alused interaktsioonid: taimede suguluse, juureeritiste ja mulla biotilise keskkonna roll

Lisaks otsesele konkurentsile valguse ja toitainete pärast võivad taimed üksteise kasvu pärssida või soodustada ka keemiliselt. Taimedel on erinevate mullas ja õhus levivate signaalide abil võimalik saada informatsiooni naabertaimede liigi ja sugulusastme kohta, hoiatada naabreid herbivooride rünnaku eest, meelitada kohale ohustavate herbivooride looduslikke vaenlasi, luua sümbiootilisi suhteid mullamikroobidega ja tarvidusel pärssida mikroobide elutegevust mullas. Selliste käitumismustrite olemasolu võimaldab taimede uurimisel kasutada laiemalt ökoloogilisi ja evolutsioonilisi teooriaid, mida eelkõige on käitumise seletamisel kasutatud loomadel. Taimed peavad mullas lahendama keerulisi optimeerimisülesandeid abiootiliselt ja biootiliselt heterogeenses ruumis, paigutades juuri kohtadesse, kus toitainete omastamine on optimaalne, arvestades ka naabrite juurte paigutust ja patogeenide olemasolu. Juurte paigutamisel arvestab taim ka naaberjuurte identiteeti: konkureerimine taime enda või lähisugulaste juurtega on ebasoovitav, samas kui mitesugulastest liigikaaslaste või teise liigi juurte läheduses on agressiivne ressursi hõivamine kasulik.

Konkurentsi vältimist enda lähisugulastega seletab iseka geeni ja hõimuväliku teooria, mille kohaselt tasub isendil vähendada konkurentsi geneetiliselt endaga sarnaste organismidega, kuna tänu sellele jõuab järgmisesse põlvkonda rohkem vastavate geenide koopiaid. Sealjuures tuleb jätkuvalt konkureerida mitesugulastega ja teiste liikide isenditega, millest tuleneb vajadus nende äratundmise järele. Taimedel on varasemalt näidatud enda/mitte-enda äratundmisvõimet ja välja pakutud, et sugulaste äratundmine on selle võime evolutsiooniline edasiarendus või kõrvalsaadus. Taimesisest on oluline ka reaktsiooni süsteemsus olukorras, kus taime mingis piirkonnas tajutud stiimulile (näiteks herbivooride või patogeenide rünnakule) oleks vaja kiirelt reageerida terve taime piires. Samas lokaalselt paiknevale keskkonnaerisusele, näiteks toitainelaigule, tasub reageerida samuti lokaalselt, sest taime kohasust tõstab just selles piirkonnas toitainete ammutamine.

Sugulaste äratundmist võimaldav mehhanism taimedel on jätkuvalt kindlaks tegemata. Mitmed eksperimendid laboritingimustes on näidanud, et selle jaoks on olulised juureeritised, kuid kas eritised säilitavad äratundmisfunktsiooni ka mullamikroobide olemasolul, ei ole teada. Lisaks on keeruline eristada ressurside omastamisest ja äratundmisest tulenevaid reaktsioone kooskasvatamise eksperimentides. Samuti on vähe teada taimede biotiliste interaktsioonide, nagu liigisisese ja liikidevahelise äratundmise ning mullamikroobide kaudu vahendatud interaktsioonide, tähtsusest ökosüsteemi tasemel.

Selle doktoritöö üheks eesmärgiks oli demonstreerida sugulaste äratundmise mehhanismi looduslikes mullatingimustes, kuid otsese taimedevahelise konkurentsi puudumisel, vältimaks toitainetekonkurentsisist tuleneda võivaid reakt-

kasvu- ja kaitsefunktsioonide vahel, mis võib omakorda mõju avaldada mulla tagasisidele, varise lagunemisele ja toitainete ringlusele.

Doktoritöö teises osas keskendusin taime võimele mõjutada juurevarise lagunemist ja reageerida varise ning mulla mikroobikoosluste ruumilisele heterogeensusele. Selgitamiseks elusa taime juureeritiste mõju varise lagunemisele inkubeerisin seitsmelt rohttaimeliigilt (3 kõrrelist, 3 liblikõielist ja 1 rohund) pärinevat juurevarist mullas ilma taimeta või koos valge ristiku taimega (*Trifolium repens*). Tulemused näitasid, et elus juured aeglustavad juurevarise lagunemist, mis on osaliselt seletatav varise toitainetesisaldusega. Toitainetevaese kõrreliste varise lagunemine oli oluliselt rohkem alla surutud elus juurte juuresolekul, samas kui liblikõieliste varise lagunemise kiirus ei muutunud. Siinkohal nähtud elus taime negatiivne mõju varise lagunemisele võis tuleneda sellest, et mullamikroobid eelistasid madala lämmastikusisaldusega varise lagundamise asemel kasutada energiaallikana hoopis liblikõielise juureeritisi.

Selleks, et teha kindlaks, kas taim integreerib taime eri osadest pärit informatsiooni mullatingimuste kohta süsteemselt, kasutasin jagatud juuresüsteemiga taimi, kus ühe taime juuresüsteem oli jagatud kahe poti vahel ja üks pottidest sisaldas eri liikide poolt mõjutatud mikroobikooslust või juurevarist, teine aga looduslikust kooslusest pärit mikroobidega inokuleeritud mullasegu. Süsteemse vastuse korral pidanuks vastusena ühes potis tajutud tingimustele muutuma ka taime kogubiomass ja/või juurte morfoloogia teises potis, mis ei sisaldanud juurevarist või spetsiifilist mullainokulaati. Süsteemne reaktsioon oleks kohane juhul, kui taim puutub kokku patogeeni, mis võib kiiresti levida kogu taime ulatuses. Taimedel ilmnemise peamiselt lokaalsed reaktsioonid: rohkem juurebiomassi paigutati juurevarise suunas või tühja varisekotikese poole, ning juured kasvasid pikemaks mullas, mida ei olnud inokuleeritud kindla liigi mullamikroobidega. Liikidevahelistes võrdlustes ilmnemine, et hariliku hiireherne (*Vicia cracca*) muld põhjustas valgel ristikul juuremügarate arvu vähenemist ja hiireherne juurevaris põhjustas muutusi juurediameetris juurestiku osas, mis varisega otseselt kokku ei puutunud (süsteemne reaktsioon). Teiste liikide poolt mõjutatud muld ei avaldanud negatiivset mõju ristiku kasvule ja juuremügarate arvule. Teise liblikõielise negatiivne mõju ristikule võib tuleneda sümbioosi liigispetsiifilisusest lämmastikufikseerijatega, aga ka mullapatogeenide sarnasusest liblikõieliste vahel.

Kokkuvõttes näitavad doktoritöö tulemused, et taimed on võimelised tajuma mitmekesiseid signaalide naabertaimede geneetilise erisuse, asukoha ja mullakvaliteedi kohta ja neile vastavalt reageerima. Peale selle mõjutavad taimed juureeritiste kaudu varise lagunemise kiirust ja varise kvaliteedi kaudu toitaineteringlust ning järgmise põlvkonna taimede kasvu. Need leiud juhiivad tähelepanu vajadusele võtta ökoloogiliste protsesside mõistmisel ja ennustamisel ka taimede puhul arvesse nii liikidevahelist varieeruvust funktsionaalsetes tunnustes kui ka genotüübilist varieeruvust ja eri genotüüpide vastastikmõjusid fenotüübile.

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