

MARIA ABAKUMOVA

The relationship between competitive
behaviour and the frequency and identity of
neighbours in temperate grassland plants



DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

341

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behaviour and the frequency and identity of
neighbours in temperate grassland plants



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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** **Abakumova M**, Zobel K, Lepik A, Semchenko M. 2016. Plasticity in plant functional traits is shaped by variability in neighbourhood species composition. *New Phytologist* **211**: 455–463.
- II** Semchenko M, **Abakumova M**, Lepik A, Zobel K. 2013. Plants are least suppressed by their frequent neighbours: the relationship between competitive ability and spatial aggregation patterns. *Journal of Ecology* **101**: 1313–1321.
- III** Lepik A, **Abakumova M**, Zobel K, Semchenko M. 2012. Kin recognition is density-dependent and uncommon among temperate grassland plants. *Functional Ecology* **26**: 1214–1220.

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	I	II	III
Planned and designed the study	MS	MS, KZ	MS, KZ
Performed fieldwork and experiments	MA , KZ, AL, MS	MS, MA , AL, KZ	AL, MA , KZ, MS
Data analysis	MA , MS	MS, MA	AL, MS
Responsible for writing of the manuscript	MA , MS	MS	AL, MS
Contributed to revisions	MA , KZ, AL, MS	MS, MA , AL, KZ	AL, MA , KZ, MS

1. INTRODUCTION

Owing to sessile lifestyle, the performance of plants is strongly influenced by the surrounding environment. Plants are known to modify their morphology in response to variation in abiotic factors, and extensive research has revealed the molecular mechanisms involved, the adaptive value of plasticity and the factors that promote or inhibit the evolution of plasticity (e.g., Pigliucci, 2001; Alpert & Simms, 2002; Givnish, 2002). It has recently become evident that plants respond plastically also to the presence and identity of neighbouring individuals. Plants can discriminate between roots belonging to themselves and a physiologically independent individual, the same and different genotypes, and sibling and non-sibling neighbours (Gruntman & Novoplansky, 2004; Dudley & File, 2007; Semchenko *et al.*, 2014). While diverse patterns of plant behaviour have been described, the factors driving the evolution of different behaviours in plants are still poorly understood.

When considering responses to the presence of competitors, the frequencies of encountering neighbours of different genetic identities may play a central role in shaping competitive behaviour. In plants, neighbour identity will strongly depend on species life history traits and community characteristics. Neighbouring individuals may be predominantly conspecific as a result of limited seed dispersal or spatial aggregation of vegetatively propagated offspring (Lovett Doust, 1981; reviewed in Cheplick, 1992; Herben & Hara, 2003). Community species richness and evenness of species abundances also influence the probability of encountering any particular neighbouring species with high richness increasing neighbourhood diversity and variability and low community evenness making dominant species the most likely neighbours (Oksanen, 1997; Perry *et al.*, 2009).

Theoretical and empirical studies show that frequent within-species interactions due to spatial aggregation of conspecifics can promote coexistence by improving the performance of inferior competitors and putting greater competitive pressure on superior competitors (Pacala, 1997; Stoll & Prati, 2001; Turnbull *et al.*, 2007; Wassmuth *et al.*, 2009). Competitive ability of different species can be viewed as a behavioural trait and can be considered in the context of evolutionary game theory: the presence of neighbours should trigger increased investment into competitive organs at the expense of reproduction as such selfish behaviour ensures superior competitive ability (Gersani *et al.*, 2001; Anten, 2002; Falster & Westoby, 2003). On the contrary, if all individuals exercised cooperative restraint in the use of common resources, higher fitness would be achieved (Pepper & Smuts, 2002; Kerr *et al.*, 2006; Nahum *et al.*, 2011). However, cooperative behaviour can only spread in a population if it is primarily directed towards other cooperators. Spatial aggregation of genetically closely related individuals due to limited dispersal can be one way to fulfil this condition (Doebeli & Hauert, 2005; also known in the context of kin selection theory, Hamilton, 1964; Gardner *et al.*, 2011). In such neighbourhoods, the

restriction of root and shoot proliferation can increase a plant's inclusive fitness directly by allowing more resources to be invested into reproduction and indirectly by reducing competitive effect and promoting the fitness of neighbouring kin (Kelly, 1996; Holzapfel & Alpert, 2003; Dudley & File, 2007; Semchenko *et al.*, 2007). The importance of dispersal patterns for the evolution of cooperative versus selfish behaviour is supported by theoretical models that demonstrated simultaneous evolution of altruism and dispersal behaviour such that altruists maintain short distance dispersal, while individuals adopting selfish behaviour evolve towards longer dispersal distances (van Baalen & Rand, 1998; Koella, 2000). However, it is also possible that competitive and dispersal abilities form a trade-off, so that plants cannot simultaneously be good competitors and dispersers due to associated costs (Holmes & Wilson, 1998; Bolker *et al.*, 2003; Jakobsson & Eriksson, 2003). In this case, most aggregated species should be the strongest competitors. Despite strong theoretical support, empirical data testing for the relationships between plant competitive behaviour and dispersal ability and resulting community spatial patterns are still lacking.

Instead of possessing a fixed competitive strategy that is most successful in the most frequent neighbourhood environment, plants may evolve a flexible behaviour if the genetic identity of neighbours varies and these neighbours impose different selective pressures on plant phenotypes. Different neighbouring species or conspecifics of different levels of genetic relatedness can be viewed as alternative biotic environments, and the factors favouring the evolution of flexible behaviour towards different neighbours are likely to match those favouring any other type of adaptive phenotypic plasticity. It has been shown that, when the identity of neighbours is stable in space and time, plant neighbourhoods select for specific phenotypes and lead to genetic differentiation and local adaptation (Turkington, 1989; Callaway *et al.*, 2005; Lipowsky *et al.*, 2011). Theoretical models and limited empirical evidence suggest that plasticity is likely to evolve if plants experience spatial or temporal environmental variation that is similar in scale to the size or generation time of an individual (Bradshaw, 1965; Baythavong, 2011) and the alternative environments (in this case, different neighbour identity) are common and occur at even frequencies (Moran, 1992). Plasticity is expected to be greatest if each of two alternative environments is experienced 50% of the time. Conversely, a fixed developmental strategy that maximizes fitness in the predominating environment is likely to be favoured if one of two alternative environments is rare (Alpert & Simms, 2002; Givnish, 2002).

Lastly, plants may not only possess plasticity to the species identity of their neighbours but also discriminate between individuals of the same species of different levels of genetic relatedness, phenomenon known as kin recognition. Despite increasing interest in the ability of plants to recognize kin, it remains impossible to draw conclusions about the generality of this phenomenon. Some studies reported lower shoot mass and reproductive output in sibling groups (Escarre *et al.*, 1994; Cheplick & Kane, 2004), while others have demonstrated greater seed germination and seedling survival (Willson *et al.*, 1987), higher

flowering probability (Tonsor, 1989) and greater allocation to reproduction (Donohue, 2004; Biernaskie, 2011). However, the vast majority of studies on sibling competition have reported no significant differences in either total plant mass or absolute reproductive yield between sibling and non-sibling groups (Schmitt *et al.*, 1987; Argyres & Schmitt, 1992; Dudley & File, 2007; Monzeglio & Stoll, 2008; Milla *et al.*, 2009; Murphy & Dudley, 2009; Masciaux *et al.*, 2010; Biernaskie, 2011). Most studies on kin recognition have employed artificial growth conditions and examined behaviour of single species. Furthermore, the intensity of resource competition will depend on plant density, which may affect the cost and benefit of cooperative behaviour towards kin, but it has not been manipulated in studies on kin recognition.

To address these knowledge gaps, we performed an extensive survey of temperate grassland sites to determine the relative frequency of neighbour encounters for a wide range of species and combined these spatial data with common garden experiments to estimate plant competitive ability and morphological responses to neighbours of different genetic relatedness and species identity.

The objectives of studies reported in this thesis were:

- (1) to investigate how the frequency of encountering conspecific and hetero-specific neighbours in the field shapes the degree of morphological plasticity in response to neighbour identity **(I)**;
- (2) to determine whether morphological plasticity to neighbour identity is affected by species abundance in the community, with dominant species either exhibiting or triggering greater plasticity **(I)**;
- (3) to examine the dependence of species competitive ability on the degree of spatial aggregation with conspecifics and frequency of interactions with other species **(II)**;
- (4) to investigate how widespread is kin recognition among plant species common to temperate grassland communities **(III)**;
- (5) to examine the interactive effects of genetic relatedness and neighbour density on the focal plant morphology and biomass allocation **(III)**.

2. MATERIALS AND METHODS

2.1 Study sites and species

For the experiment examining responses to species identity, seven study sites in Estonia were selected to represent a range of different semi-natural grasslands (Table 1). The sites differed in species richness and composition, soil fertility, pH and management history. Twenty-seven focal species were used for study of plasticity in response to neighbours' frequency (all species in Table 2 except for *Knautia arvensis*); twenty-eight focal species were used for competitive ability study (Table 2). Seven species, not used as focal species, were additionally grown as neighbouring species (Table 2).

Table 1. The location and characteristics of the studied grassland communities. S – Chao estimator of species richness (Chao 1987). Redrawn from Table 1 in II.

No	Location	General description	Dominant species	Soil properties					
				S	pH	N %	P mg/kg	K mg/kg	Ca g/kg
1	58°35'03"N 23°34'09"E	Calcareous grassland, managed for ca 200years	<i>Carex tomentosa</i> <i>Sesleria caerulea</i>	88	6.7	0.60	30	72	3.2
2	58°38'31"N 23°30'55"E	Alvar grassland, managed for ca 200years	<i>Sesleria caerulea</i> <i>Carex tomentosa</i>	61	6.9	0.54	24	103	2.4
3	58°25'28"N 26°31'05"E	Mesophytic meadow, probably has been ploughed and forested in the past	<i>Festuca rubra</i> <i>Dactylis glomerata</i>	46	6.4	0.27	27	74	1.7
4	58°06'36"N 27°04'15"E	Mesophytic meadow, probably has been forested in the past	<i>Festuca rubra</i>	32	5.2	0.16	16	46	0.4
5	58°30'47"N 23°40'19"E	Islet, disturbed by ice and water	<i>Urtica dioica</i>	30	6.7	0.68	442	279	2.7
6	58°25'32"N 26°30'40"E	Flood-meadow, disturbed by ice and water	<i>Deschampsia caespitosa</i>	23	6.3	0.74	27	49	4.0
7	58°44'20"N 23°39'26"E	Coastal meadow, disturbed by ice and water	<i>Juncus gerardii</i> <i>Plantago maritima</i>	8	6.2	0.61	72	350	1.4

For the kin-recognition experiment, two study sites out of seven above-mentioned (moist and dry meadows at Kärevere, Estonia; 58°25'N, 26°31'E) were chosen, and eight species were examined in total: *Achillea millefolium* L. (Asteraceae), *Deschampsia cespitosa* (L.) P. Beauv. (Poaceae), *Leontodon hispidus* L. (Asteraceae), *Lychnis flos-cuculi* L. (Caryophyllaceae), *Peucedanum palustre* (L.) Moench (Apiaceae), *Phleum pratense* L. (Poaceae), *Trifolium repens* L. (Fabaceae) and *Medicago lupulina* L. (Fabaceae) (III).

All studied species were perennial herbs (exceptionally *Carlina vulgaris* may be biennial) and belonged to graminoids (i.e. Poaceae, Cyperaceae, Juncaceae; seven species), legumes (four species) or non-leguminous forbs (17 species).

2.2 Field survey

Plant community composition was estimated for each study site by sampling along randomly placed 10-m-long transects and recording the species identity of the shoots closest to metal poles inserted every 33 cm. Focal species were selected aiming to provide a representative sample of the studied communities; the abundances of the focal species ranged from rare (< 1%) to dominant (up to 34%) based on shoot counts. The species identity of the nearest neighbour was recorded in the field for 100 individuals of each focal species.

Table 2. List of focal and neighbour species and the sites where their spatial patterns were studied (see Table 1 for site descriptions). Modified from Table 1 in I.

No	Focal species	Abbreviation	Family	Neighbour species	Family	Site
1	<i>Achillea millefolium</i>	Achmil	Asteraceae	<i>Festuca rubra</i>	Poaceae	3
2	<i>Antennaria dioica</i>	Antdio	Asteraceae	<i>Lotus corniculatus</i>	Fabaceae	2
3	<i>Briza media</i>	Brimed	Poaceae	<i>Festuca rubra</i>	Poaceae	1
4	<i>Carex ornithopoda</i>	Carorn	Cyperaceae	<i>Trifolium pratense</i>	Fabaceae	1
5	<i>Carlina vulgaris</i>	Carvul	Asteraceae	<i>Sesleria caerulea</i>	Poaceae	2
6	<i>Centaurea jacea</i>	Cenjac	Asteraceae	<i>Anthoxanthum odoratum</i>	Poaceae	3
7	<i>Deschampsia cespitosa</i>	Descae	Poaceae	<i>Peucedanum palustre</i>	Apiaceae	6
8	<i>Festuca rubra</i>	Fesrub	Poaceae	<i>Poa angustifolia</i>	Poaceae	4
9	<i>Filipendula</i>	Filvul	Rosaceae	<i>Sesleria</i>	Poaceae	2

No	Focal species	Abbreviation	Family	Neighbour species	Family	Site
	<i>vulgaris</i>			<i>caerulea</i>		
10	<i>Galium verum</i>	Galver	Rubiaceae	<i>Filipendula vulgaris</i>	Rosaceae	2
11	<i>Inula salicina</i>	Inusal	Asteraceae	<i>Sesleria caerulea</i>	Poaceae	1
12	<i>Juncus gerardii</i>	Junger	Juncaceae	<i>Agrostis stolonifera</i>	Poaceae	7
13	<i>Leontodon hispidus</i>	Leohis	Asteraceae	<i>Sesleria caerulea</i>	Poaceae	1
14	<i>Lotus corniculatus</i>	Lotcor	Fabaceae	<i>Sesleria caerulea</i>	Poaceae	2
15	<i>Lychnis flos-cuculi</i>	Lycflo	Caryophyllaceae	<i>Deschampsia cespitosa</i>	Poaceae	6
16	<i>Medicago lupulina</i>	Medlup	Fabaceae	<i>Festuca rubra</i>	Poaceae	3
17	<i>Peucedanum palustre</i>	Peupal	Apiaceae	<i>Deschampsia cespitosa</i>	Poaceae	6
18	<i>Phleum pratense</i>	Phlpra	Poaceae	<i>Anthoxanthum odoratum</i>	Poaceae	3
19	<i>Pilosella officinarum</i>	Piloff	Asteraceae	<i>Sesleria caerulea</i>	Poaceae	2
20	<i>Pimpinella saxifraga</i>	Pimsax	Apiaceae	<i>Sesleria caerulea</i>	Poaceae	2
21	<i>Rumex acetosa</i>	Rumace	Polygonaceae	<i>Festuca rubra</i>	Poaceae	4
22	<i>Sesleria caerulea</i>	Sescae	Poaceae	<i>Pilosella officinarum</i>	Asteraceae	2
23	<i>Succisa pratensis</i>	Sucpra	Caprifoliaceae	<i>Carex flacca</i>	Cyperaceae	1
24	<i>Trifolium montanum</i>	Trimon	Fabaceae	<i>Festuca rubra</i>	Poaceae	1
25	<i>Trifolium repens</i>	Trirep	Fabaceae	<i>Poa pratensis</i>	Poaceae	3
26	<i>Urtica dioica</i>	Urtdio	Urticaceae	<i>Artemisia vulgaris</i>	Asteraceae	5
27	<i>Veronica chamaedrys</i>	Vercha	Plantaginaceae	<i>Rumex acetosa</i>	Polygonaceae	4
28	<i>Knautia arvensis</i>	Knaarv	Dipsacaceae	<i>Poa angustifolia</i>	Poaceae	4

The seeds of focal and potential neighbouring species were collected at each study site on several occasions during the vegetation season in 2008. The seeds were air-dried, stored at 4 °C and used the following year in a pot experiment.

Three soil cores were taken from random locations in each study community. Soil pH, Ca, N and available P and K contents were determined from the samples. The same parameters were calculated for three samples of commercial soil that was used in the common garden experiment described below.

2.3 Common garden experiment

In the experiments examining responses to species identity (**I**, **II**), each focal species was subjected to a combination of two treatments: (i) neighbour identity (conspecific or heterospecific) and (ii) neighbour density (0, 1, 2, 3, 4, 6 or 8 neighbours). Each neighbour identity by density combination was replicated twice. In the heterospecific treatment, each focal species was grown together with a single species that it frequently encountered in the field as its nearest neighbour. As a result of poor germination and seedling mortality, fewer pots were measured at the end of the experiment than was planned: 731 pots instead of 756 pots in the study of plasticity in response to neighbours' frequency (27 focal species × two neighbour identities × seven neighbour densities × two replicates; **I**), and 757 pots instead of 784 pots in the competitive ability study (28 focal species × two neighbour identities × seven neighbour densities × two replicates; **II**). 27 seven species were used in the plasticity study due to very slow growth and establishment of a single species, *Knautia arvensis*, which was harvested a year later than other species and morphological traits were not measured (**I**).

In the kin-recognition experiment, plant density (low and high) and plant relatedness (siblings and non-siblings) treatments were employed. Two seedlings per pot were planted in the low-density treatment and 14 plants per pot in the high-density treatment (Fig. 1). At each planting density, focal plants were grown together with either (i) seedlings originating from the same mother plant (siblings; probably half-siblings) or (ii) a mixture of randomly selected seedlings from different mother plants (non-siblings; some degree of relatedness is possible). There were 10 replicates of each species × density × relatedness combination (i.e. 40 pots per species in total). Seedlings of 10 mother plants per species were used so that every mother plant was represented once in every treatment as a focal plant. Owing to the limited number of seeds, *Medicago lupulina* was only grown at low density (i.e. 20 pots in total) and *Trifolium repens* was represented by fewer replicates at high plant density (i.e. 30 pots in total). A combination of poor germination and high seedling mortality in *Peucedanum* enabled to examine 27 pots in total with varied density of plants at harvest (between nine and 14 in high-density pots).

Pots contained a mixture of commercial soil, sand, lime powder and natural soil inoculum prepared separately for species from each study site to match the

nitrogen (N) content and pH of soil from the corresponding site. No fertilizer or herbicide was applied during the experiment. In the experiments examining responses to species identity, three pot sizes were used to account for differences in productivity and average plant size in different study communities (3.5 L pots, 5 L pots, and 7.5 L pots; **I**, **II**). In the kin-recognition experiment, only 5 L pots were used (**III**). Seed germination was initiated in April – May, and seedlings were transplanted into pots at the end of May – the beginning of June.

Pots were placed randomly in an outdoor paved area, and their positions were re-randomized twice during the experiment. Pots received natural precipitation, but were watered daily in dry and sunny weather. Plants were harvested after 11–14 weeks of growth (**I**, **II**) or 71–80 days of growth (**III**). The pot experiment was carried out in Tartu, Estonia.

2.4 Plant measurements

2.4.1 Papers I, II (responses to species identity)

Before harvesting, the maximum vegetative height of the focal plants was measured. Plants were cut at the rooting point and were placed in airtight polyethylene bags, with the cut ends of the stems submerged in water. The plants were stored upright in the dark at 4 °C for at least 24 h. Two fully expanded leaf blades were selected from each focal plant to determine their fresh mass. More leaves were weighed for species with small leaves (*Carex ornithopoda*, *Juncus gerardii*, *Veronica chamaedrys*, *Antennaria dioica*, *Lotus corniculatus*, *Galium verum*). Leaf water content was calculated by dividing the difference between fresh and dry mass by the fresh mass of the leaf blades. To calculate the specific leaf area (SLA), the fresh leaves used for the water content measurements were scanned (Epson perfection V700 Photo, Long Beach, CA, USA) and the leaf area was calculated using the program WinRhizo 2008a (Regent Instruments Inc., Sainte Foy, QC, Canada). SLA was calculated as the ratio of leaf area and leaf dry mass. All remaining leaves of the focal plants were also scanned and the total leaf area was calculated (see **I** for details). The dry mass of the supportive structures was calculated by summing the dry mass of stems, leaf petioles and leaf sheaths. All aboveground parts of each focal plant and its neighbours were oven-dried at 70 °C for 48 h and weighed separately as necessary for calculations.

Root density data were obtained for a subset of species from Site 2. Each pot was frozen at –18 °C and sliced horizontally at depths of 5 cm and 10 cm below the soil surface. The number of cut root tips present on the sliced soil surface in the area between the focal plant and its neighbours was recorded.

2.4.2 Paper III (kin recognition study)

Plant shoots were cut at the soil level and the pots were frozen at -18°C . To measure specific leaf area (SLA), two fully expanded leaves were selected and their area calculated using a scanner and program WinRhizo 2008a. The dry mass of scanned leaves was determined and SLA was calculated as above. To estimate leaf elongation, the mean length of five fully expanded leaves was calculated using a scanner and program UTHSCSA Image Tool v3.0. Petiole length was used as an estimate of leaf elongation in *Medicago lupulina* and *Trifolium repens*. Plant shoots were oven-dried at 75°C for 48 h, and the vegetative parts and inflorescences weighed separately.

To estimate root density in the soil, the frozen soil blocks were removed from pots and sliced at a depth of 5 cm below the soil surface. The surface of the frozen slices was then lightly cleared and scanned. To estimate root density, the number of roots was recorded in 16 sampling plots distributed in a hexagonal pattern across each scanned image (Fig. 1).

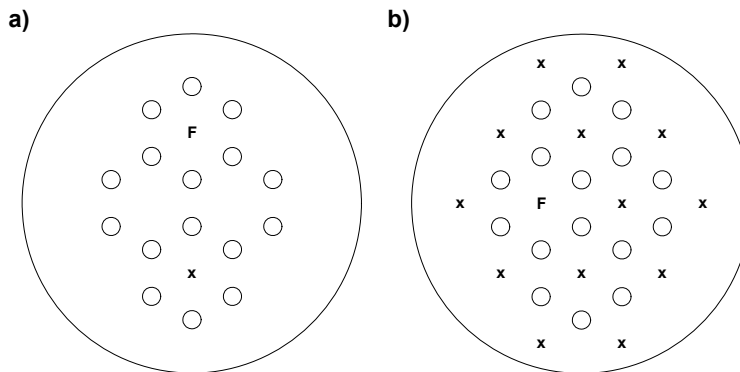


Fig. 1. Planting patterns used in a) low density and b) high density treatments. “F” signifies the position of the focal plant and crosses represent positions of neighbour plants. Distance between plants was 10 cm in the low density pots and 5 cm in the high density pots. Circles represent the positions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

2.5 Statistical analysis

2.5.1 Paper I (plasticity in response to neighbours' frequency)

For each of the focal species, linear models were constructed with one of the five measured traits (dry mass of supportive structures, maximum vegetative height, total leaf area, SLA, leaf water content) as a response variable and neighbour identity, neighbour density and the interaction term between the two as predictor variables. Before analysis, all trait values were \log_e -transformed. On the basis of five measured traits, an overall plasticity estimate for each focal

species was calculated the average of five absolute values of coefficients for the interaction term between neighbour identity and density (see **I** for details). In addition, *biomass plasticity* (change in focal biomass in response to neighbour identity) was calculated as described above.

To describe the frequency and evenness of neighbour encounters for each focal species in its community, Shannon's diversity index (index of interaction frequencies, H') was calculated as:

$$H' = -(p_{\text{con}} \times \log_e(p_{\text{con}}) + p_{\text{het}} \times \log_e(p_{\text{het}}))$$

where p_{con} and p_{het} denote the proportions of total nearest neighbour encounters in the field that represented the conspecific or the heterospecific neighbour, respectively. The index was unimodally related to the empirical probabilities of conspecific as well as heterospecific neighbour encounters across the 27 focal species (all species in Table 2 except for *Knautia arvensis*). The index reaches its highest value when neighbours of both identities are encountered at even and intermediate frequencies, satisfying a condition necessary for the evolution of plasticity to alternative environments (Moran, 1992).

To assess the relationship between plasticity and the index of interaction frequencies, the *mean plasticity* was used as a response variable, whereas H' and its second-order polynomial were used as predictor variables. To account for focal plant size effects, *biomass plasticity* was added to the model as a covariate. In addition, the difference in mean neighbour mass was included as a covariate to test whether plasticity to neighbour identity was mediated by differences in neighbour size. The difference in neighbour size was calculated as the absolute value of the difference between the mean \log_e -transformed above-ground mass of neighbours in the conspecific and heterospecific treatments. Study site and pot size were excluded from the final model as these did not significantly improve the fit of the model.

To visualize the relationship between plasticity and H' , residuals from a model with mean morphological plasticity as a response variable and biomass plasticity as an explanatory variable were used.

A model with and without a correlation structure that accounts for phylogenetic dependences between species were compared to assess the significance of phylogenetic signal in studied relationships (Revell, 2010; see for details **I**). A phylogeny containing our study species was obtained from Durka & Michalski (2012).

In addition to H' , conspecific and heterospecific encounter frequencies, species abundances and the spatial association of focal species with their heterospecific neighbours and overall neighbour diversity were also tested as alternative explanatory variables for variation in plasticity.

2.5.2 Paper II (competitive ability study)

The observed probability of conspecific encounter, species abundance in its home community, the degree of conspecific aggregation, and the probability of encountering the species used as a neighbour in the heterospecific treatment were calculated for each focal species. Linear mixed models were performed with \ln -transformed aboveground dry mass of focal plants as a response variable and the following predictors: neighbour density, neighbour identity and one of the parameters of the focal species (growth form and each of the characteristics described above). Species, nested within community, was included in the models as a random factor. In addition, the same models were run for each community separately, excluding two communities where only one focal species was examined (Sites 5 and 7). A significant three-way interaction was interpreted as evidence for a role of the above-mentioned parameters in determining the difference in competitive response of the focal plants to conspecific *versus* heterospecific neighbours. To illustrate the three-way interaction, the difference in competitive response was calculated as the difference between the regression slopes of the relationship between neighbour density and \ln -transformed focal plant mass in the heterospecific and conspecific treatments (Fig. 2). The difference in slopes was plotted against the focal species characteristic involved in the interaction term.

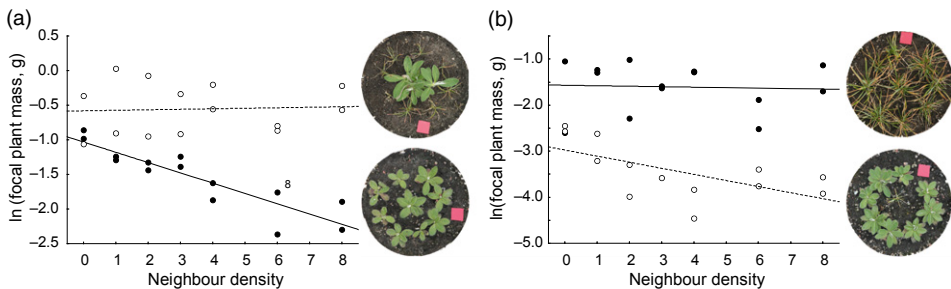


Fig. 2. An example of the effects of neighbour density and identity on the dry mass of focal plants. (a) *Pilosella officinarum* as a focal species grown with conspecifics or surrounded by *Sesleria caerulea* ($n = 28$). (b) *S. caerulea* as a focal species grown with conspecifics or surrounded by *P. officinarum* ($n = 27$). The closed symbols and unbroken line denote the conspecific treatment and the open symbols and dashed line represent the heterospecific treatment. The red squares on the photos are 2×2 cm and are provided for scale. The difference in competitive response to heterospecifics *versus* conspecifics shown in subsequent figures in this paper was calculated as the difference between the slopes of the regression lines in the heterospecific and conspecific treatments (heterospecific – conspecific). A positive difference between slopes (panel a) indicates that the growth of the focal species is suppressed more by conspecifics than by heterospecific neighbours (i.e. higher than average competitive ability). A negative difference between slopes (panel b) indicates that the growth of the focal species is suppressed by heterospecific neighbours more than by conspecifics (i.e. lower than average competitive ability). Redrawn from Fig. 1 in **II**.

Similarly, below-ground data were used instead of above-ground biomass, and linear mixed models were performed for ln-transformed root density from focal plants of Site 2 (response variable) with neighbour density, neighbour identity and degree of conspecific aggregation included as predictor variables and species as a random factor.

Data analyses were performed using R 2.15.0 (R Development Core Team, 2012). Mixed models were implemented using R package nlme (Pinheiro *et al.*, 2012).

2.5.3 Paper III (kin recognition study)

For each focal species, different dependent variables were modelled using random intercept linear mixed models, with neighbour density and genetic relatedness as fixed factors and the family line of the focal species as a random factor. Shoot dry mass was used as a dependent variable to determine whether plants attained greater size when grown with siblings than non-siblings. To assess size-independent changes in plant morphology and biomass allocation, inflorescence mass, leaf length, SLA and root density were used as dependent variables and shoot dry mass was included in the models as a covariate. As root density could only be measured at the pot level, the combined shoot mass of all plants in a pot was used as a covariate in the analysis of root/shoot allocation.

Data analysis was performed using R 2.11.1 (R Development Core Team, 2010).

3. RESULTS

3.1 Paper I (plasticity in response to neighbours' frequency)

There was a significant nonlinear relationship between mean plasticity to neighbour identity and the index of interaction frequencies (H') based on field data (Fig. 3). No significant phylogenetic signal was detected for the relationship between plasticity and H' (Table 3). The relationship was overall positive in nature: the greater the index describing the commonness and evenness of interactions with the two neighbours, the greater the observed plasticity to neighbour identity. The species with the highest degree of plasticity originated from different study sites, indicating that plasticity to neighbour identity was not restricted to a particular grassland or taxonomic group (Fig. 3).

H' described 56% of the variation in the mean plasticity after accounting for biomass effects; the frequencies of conspecific and heterospecific encounters separately described considerably less variation (8% and 17%, respectively; Fig. 4). The degree of plasticity showed no significant relationship with the difference in neighbour mass between conspecific and heterospecific treatments (Table 3) or the neighbour diversity index based on all neighbouring species encountered in the field ($F_{2,24} = 0.28$, $P = 0.758$, $R^2 = 0.02$).

When examining responses to neighbour identity in each measured trait separately, similar positive relationships with the index of interaction frequency were observed for each of the measured traits (Fig. 5).

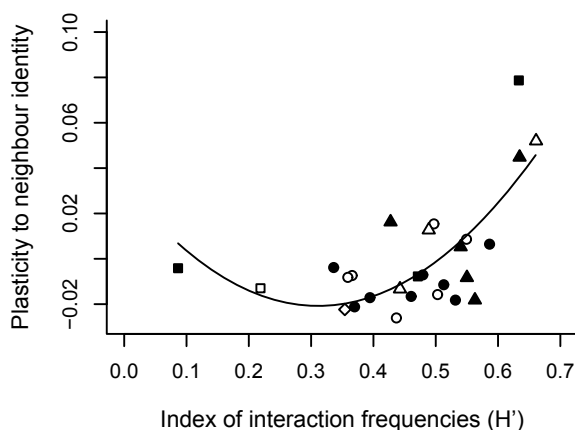


Fig. 3. Relationship between the degree of plasticity to neighbour species identity (conspecific *versus* heterospecific) and the index of interaction frequencies H' ($F_{2,24} = 15.3$, $P < 0.0001$, $R^2 = 0.56$). The index is more positive as encounters with both neighbour types become more common and even in frequency. Plasticity was calculated based on five aboveground traits and is represented by residual plasticity after accounting for differences in focal plant biomass (see Methods for further details). Study sites are highlighted with different symbols: Site 1 – open circle; Site 2 – closed circle; Site 3 – closed triangle; Site 4 – open triangle; Site 5 – open rhombus; Site 6 – closed square; Site 7 – open square. See site description in Table 1. Modified from Fig. S5 in I.

The relationships were strongest for plasticity in allocation to supportive structures and leaf area. There were significant positive correlations between plasticity in leaf area and vegetative height ($r = 0.50$, $P = 0.008$), and between plasticity in allocation to supportive structures and SLA ($r = 0.59$, $P = 0.001$).

The relative abundance of a focal species in its home community and the degree of spatial association with neighbour species in the field did not affect the degree of plasticity, whereas more abundant heterospecific neighbours elicited a greater plastic response in focal plants (Fig. 6). There was no significant correlation between H' and the abundance of the neighbour species.

Table 3. The results of models assessing the relationship between plasticity to neighbour identity (conspecific *versus* heterospecific) and the index of interaction frequencies (H'). The differences in focal and neighbour mass between conspecific and heterospecific treatments were included as covariates. Model coefficients (\pm SE) and their significance (** – $P < 0.01$; *** – $P < 0.001$) are presented. Two models were fitted for each relationship: a) a model assuming phylogenetic independence ($\lambda = 0$; No phyl. signal); and b) a model with a correlation structure that takes into account phylogenetic dependencies between species based on the observed Pagel’s λ (With phyl. signal). Akaike information criteria (AIC), likelihood ratio (LR) and the statistical significance of the test are shown. Redrawn from Table 2 in I.

	No phyl. signal	With phyl. signal	LR	P
H'	–0.34 (0.12)**	–0.34 (0.11)**		
$H' \times H'$	0.54 (0.14)**	0.52 (0.13)***		
Dif. focal mass	0.38 (0.06)***	0.38 (0.05)***		
Dif. neighbour mass	–0.001 (0.003)	–0.001 (0.002)		
AIC	–135.2	–133.2	0.002	0.968

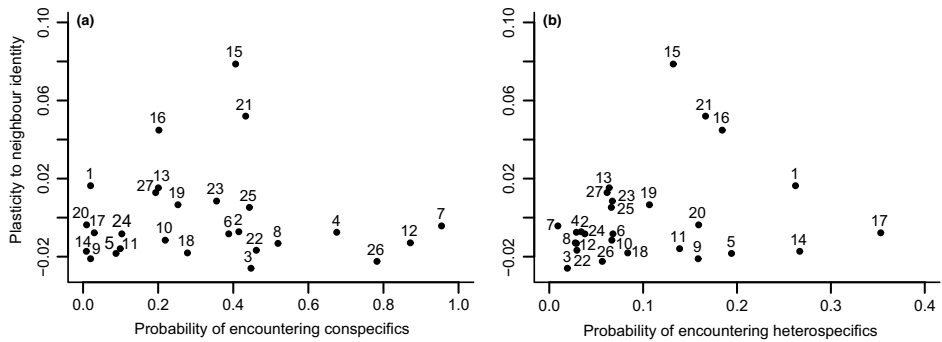


Fig. 4. Relationship between the degree of plasticity to neighbour species identity (conspecific *versus* heterospecific) and (a) probability of encountering conspecific neighbours (polynomial model: $F_{2,24} = 1.1$, $P = 0.351$, $R^2 = 0.08$), (b) probability of encountering the species used as the neighbour in the heterospecific treatment (polynomial model: $F_{2,24} = 2.5$, $P = 0.108$, $R^2 = 0.17$). Plasticity was calculated based on five aboveground traits and is represented by residuals after accounting for differences in focal plant biomass (see Methods for further details). Numbers on the graph represent different focal species in Table 2. Modified from Fig. 3 in I.

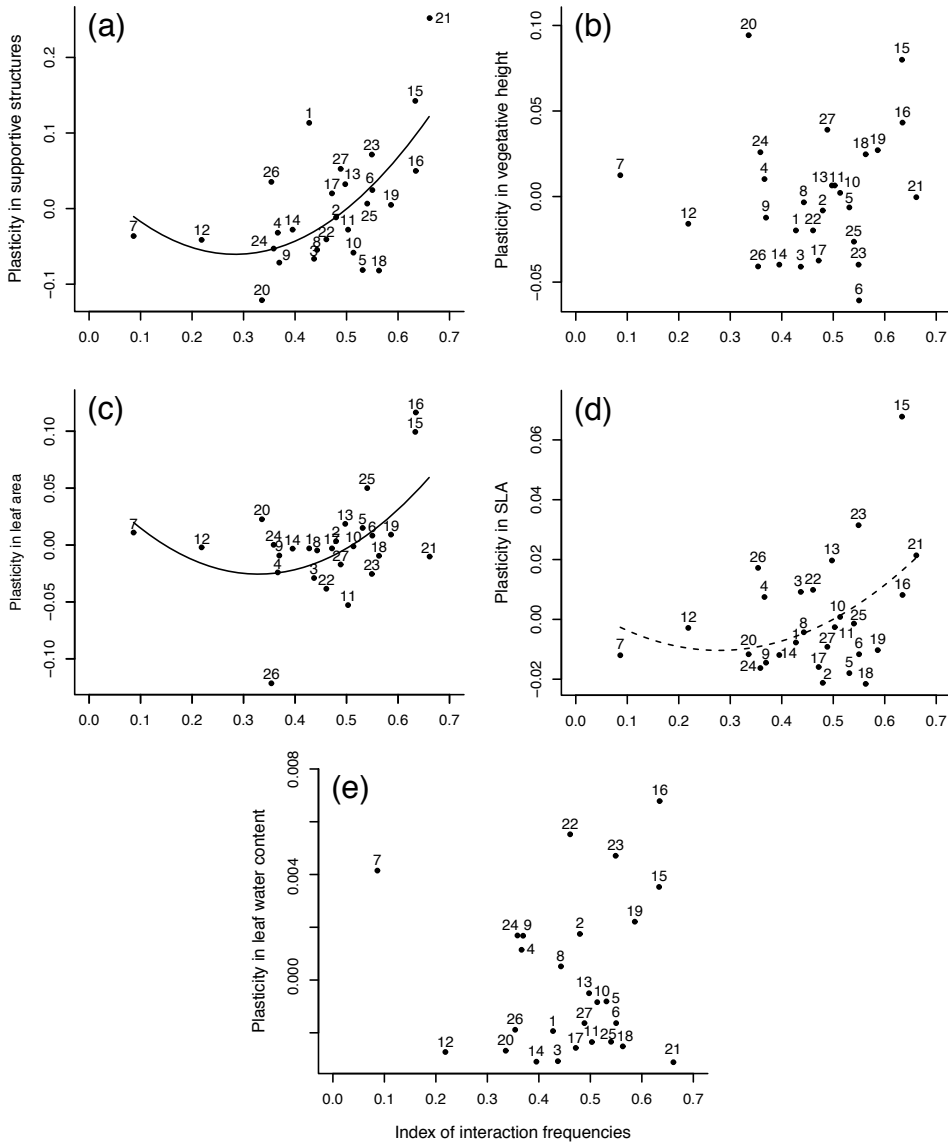


Fig. 5. Relationship between the degree of plasticity in five aboveground traits and the index of interaction frequencies (H'). The index is more positive as encounters with both neighbour types become more common and even in frequency. Plasticity is represented by residuals after accounting for differences in focal plant biomass. Numbers on the graph represent different focal species in Table 2. Redrawn from Fig. S8 in I.

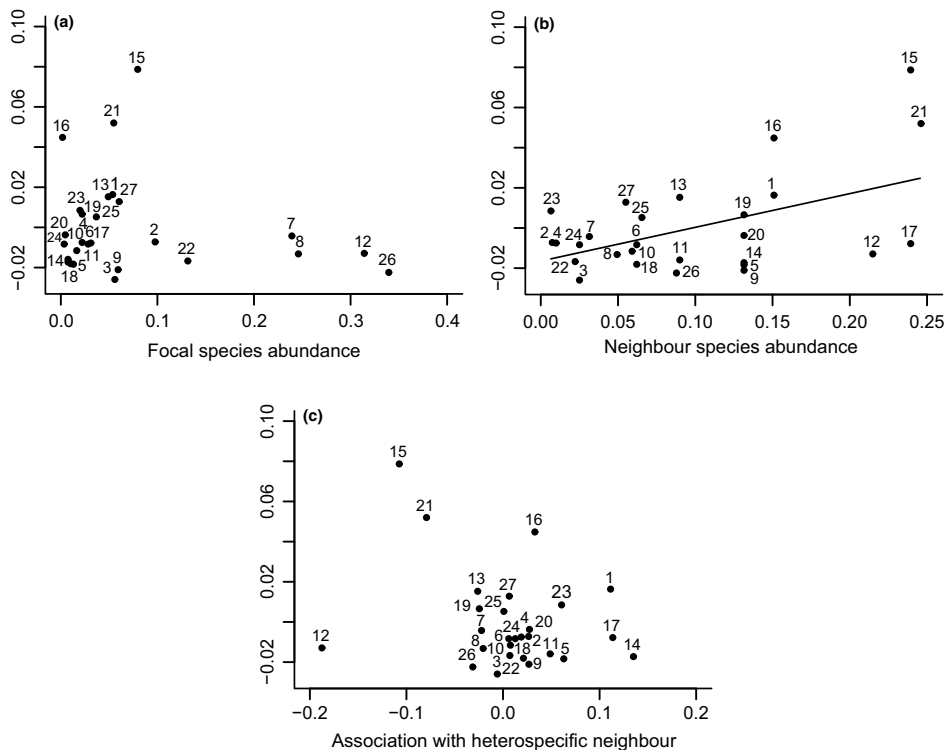


Fig. 6. Relationship between the degree of plasticity to neighbour species identity (conspecific *versus* heterospecific) and (a) focal species abundance (linear relationship: $F_{1,25} = 0.83$; $P = 0.371$; $R^2 = 0.03$), (b) neighbour species abundance (linear relationship: $F_{1,25} = 8.6$; $P = 0.007$; $R^2 = 0.26$), and (c) association of focal species with the species used as the heterospecific neighbour (calculated as the difference between the observed and expected frequencies of encountering the neighbour species; linear relationship: $F_{1,25} = 2.4$; $P = 0.132$; $R^2 = 0.09$). Plasticity was calculated based on five aboveground traits and is represented by residuals after accounting for differences in focal plant biomass (see Methods for further details). Numbers on the graph represent different focal species in Table 2. Redrawn from Fig. 4 in I.

3.2 Paper II (competitive ability study)

The effects of neighbour density and identity on focal plant mass were dependent on the degree of conspecific aggregation recorded in the field (Fig. 7a). Species with a low degree of conspecific aggregation achieved greater growth with heterospecifics than with conspecifics. On the contrary, species with a high degree of conspecific aggregation, exhibited greater growth with conspecifics. Similarly, the species used in the heterospecific treatment had a significant effect on the way focal plant mass was affected by neighbour density and identity (Fig. 7b). Focal species that frequently encountered heterospecific

neighbour in the field were more suppressed by conspecific competition, and species that rarely encountered the heterospecific neighbour were more suppressed by heterospecific competition.

At sites where clonal dispersal data were available (Sites 1 and 2), the degree of conspecific aggregation was negatively correlated with the mean distance between adjacent, clonally propagated ramets or adjacent conspecifics if clonal propagation was very rare (Fig. 7c). Species that placed clonal offspring at a very short distance achieved greater growth with conspecific neighbours, while species with greater distances between adjacent ramets were less suppressed by heterospecific competition.

The strength and direction of the relationship between the competitive response and the degree of conspecific aggregation differed between the groups of species representing different study communities. The most pronounced dependence was detected in plants representing Site 1 and Site 2 (Fig. 7a), while a similar but marginally non-significant relationship was found in Site 4. The opposite trend – the more aggregated a species was, the more successful it was in competition with heterospecifics – was observed in Site 6, although the effect was not significant.

The degree of intraspecific aggregation and competitive response to the density and identity of neighbours were significantly affected by species growth form. Graminoids were characterised by the highest intraspecific aggregation; forbs and legumes exhibited a similar degree of intraspecific aggregation, which was lower than that of graminoids (Fig. 8a). Graminoids tended to be suppressed by competition with heterospecifics as much as or more than by competition with conspecifics, while forbs exhibited the opposite trend and legumes always achieved greater growth with heterospecific neighbours (Fig. 8b).

To ascertain whether the results obtained for above-ground mass were representative of the whole plants, competitive response was also calculated using root density data, which was available for Site 2. The relationships between conspecific aggregation, frequency of heterospecific encounters and competitive response were very similar to those observed in the analysis of above-ground biomass (Fig. 9).

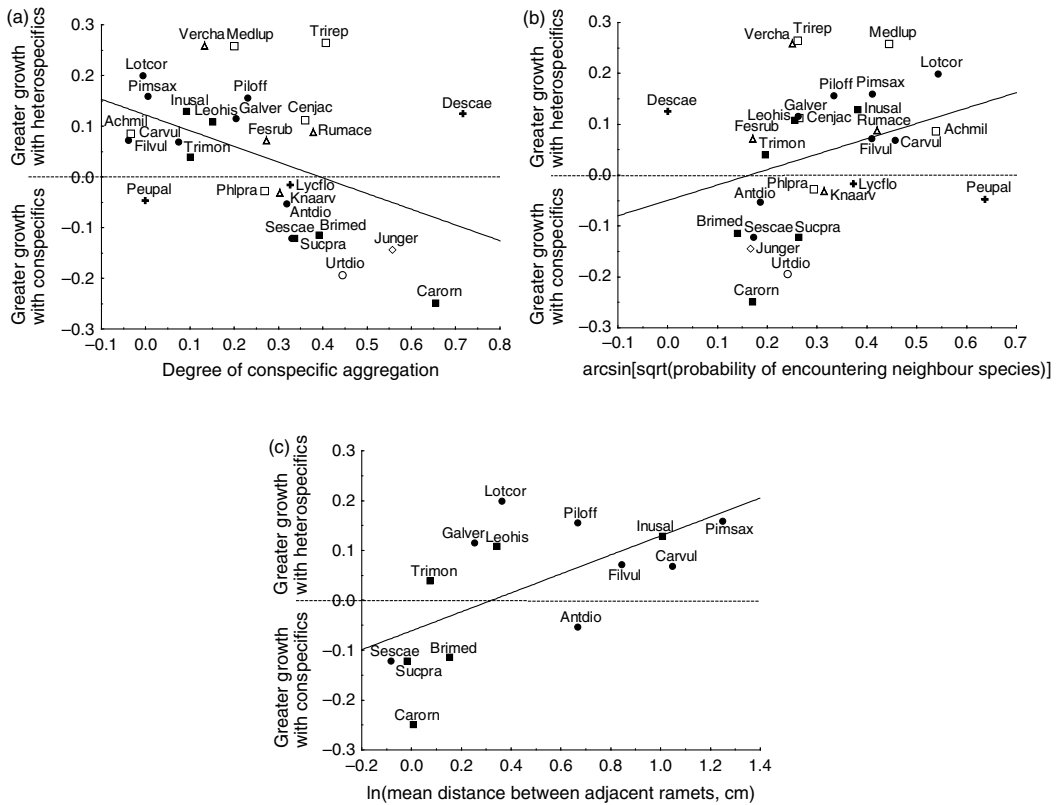


Fig. 7. Relationship between the difference in competitive response to conspecific and heterospecific neighbours and (a) the degree of intraspecific aggregation ($n = 28$), (b) the probability of encountering the species used in the heterospecific treatment ($n = 28$), and (c) the mean distance between adjacent ramets ($n = 14$). The difference in competitive response was calculated as the difference in slopes of the regression lines between neighbour density and $\ln(\text{focal plant mass})$ in the heterospecific and conspecific treatments (see Fig. 2 for details). Different symbols are used to highlight different sampled communities: filled squares, Site 1; filled circles, Site 2; open squares, Site 3; open triangles, Site 4; open circle, Site 5; crosses, Site 6; open diamond, Site 7 (descriptions in Table 1). Abbreviations of focal species are provided in Table 2. Redrawn from Fig. 2 in II.

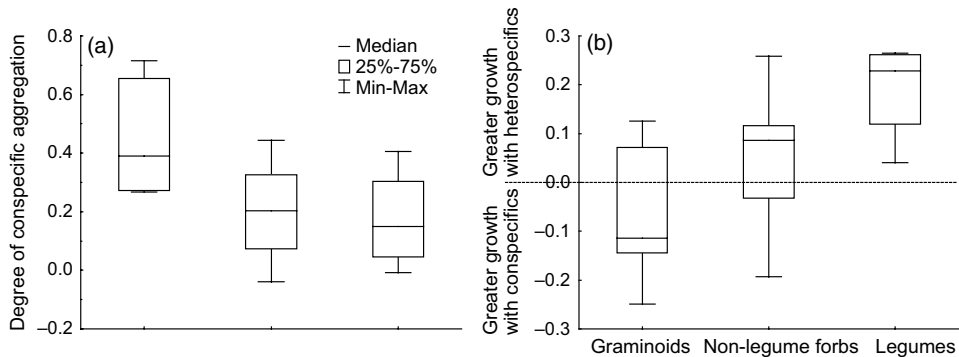


Fig. 8. The relationship between species growth form and (a) the degree of conspecific aggregation ($n = 28$) and (b) the difference in competitive response to heterospecifics *versus* conspecifics ($n = 28$). The difference in competitive response was calculated as the difference in slopes of the regression lines between neighbour density and $\ln(\text{focal plant mass})$ in the heterospecific and conspecific treatments. Redrawn from Fig. 3 in **II**.

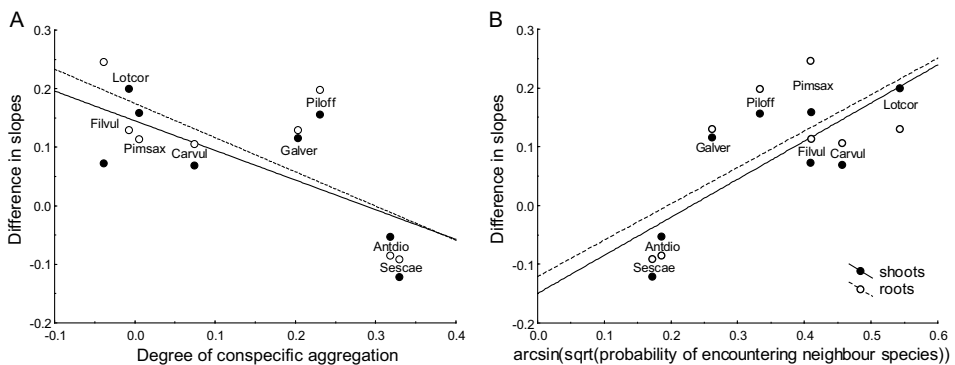


Fig. 9. Relationship between the difference in competitive response to conspecific *versus* heterospecific neighbours and (a) the degree of conspecific aggregation, and (b) the probability of encountering the species used in the heterospecific treatment for eight plant species from an alvar grassland (Site 2). The difference in competitive response was calculated as the difference in the slopes of the regression lines between neighbour density and $\ln(\text{focal plant shoot mass})$, shown with filled circles and solid line, or between neighbour density and $\ln(\text{focal plant root density})$, shown with unfilled circles and dashed line. Positive values indicate focal species that achieved greater shoot mass or root density with increasing densities of heterospecific than conspecific neighbours, while negative values indicate focal species that achieved greater shoot mass or root density with conspecifics than with heterospecifics. Abbreviations of focal species: Antdio, *Antennaria dioica*; Carvul, *Carlina vulgaris*; Filvul, *Filipendula vulgaris*; Galver, *Galium verum*; Lotcor, *Lotus corniculatus*; Pilooff, *Pilosella officinarum*; Pimsax, *Pimpinella saxifraga*; Sescac, *Sesleria caerulea*. Redrawn from Fig. S2 in **II**.

3.3 Paper III (kin recognition study)

Marginally non-significant effects of genetic relatedness on plant shoot mass were detected in two species (Table 4). Focal plants of *Deschampsia cespitosa* attained on average 22% greater shoot mass when grown among siblings than when grown among non-siblings. Conversely, focal plants of *Leontodon hispidus* attained 24% lower shoot mass when grown among siblings compared with non-sibling groups.

Clear differences in biomass allocation and leaf morphology in response to neighbour relatedness and density were only observed in one species. *Trifolium repens* grown among siblings significantly increased allocation to seed reproduction at high neighbour density, whereas plants grown among unrelated individuals exhibited an intermediate level of allocation to inflorescence production and limited response to neighbour density (Table 4; Fig. 10a). Similarly, plants grown with siblings increased SLA and exhibited no significant change in petiole elongation in response to increasing neighbour density, while plants from non-sibling groups increased petiole elongation and showed little change in SLA (Table 4; Fig. 10b,c).

A significant interaction between the effects of neighbour relatedness and density was also detected in the SLA of *Lychnis flos-cuculi* (Table 4). In this case, at low neighbour density, plants grown with siblings had significantly smaller SLA than plants grown with non-siblings (Fig. 11). No significant differences in SLA between plants grown with siblings and non-siblings were observed at high plant density.

Other species examined in this study did not show any significant responses to neighbour relatedness in any measured trait at either neighbour density (Table 4).

Table 4. 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. \$ $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Redrawn from Table 1 in **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	
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	

	Shoot mass		Inflorescence mass		Elongation		SLA		Root density	
	X ²		X ²		X ²		X ²		X ²	
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	**

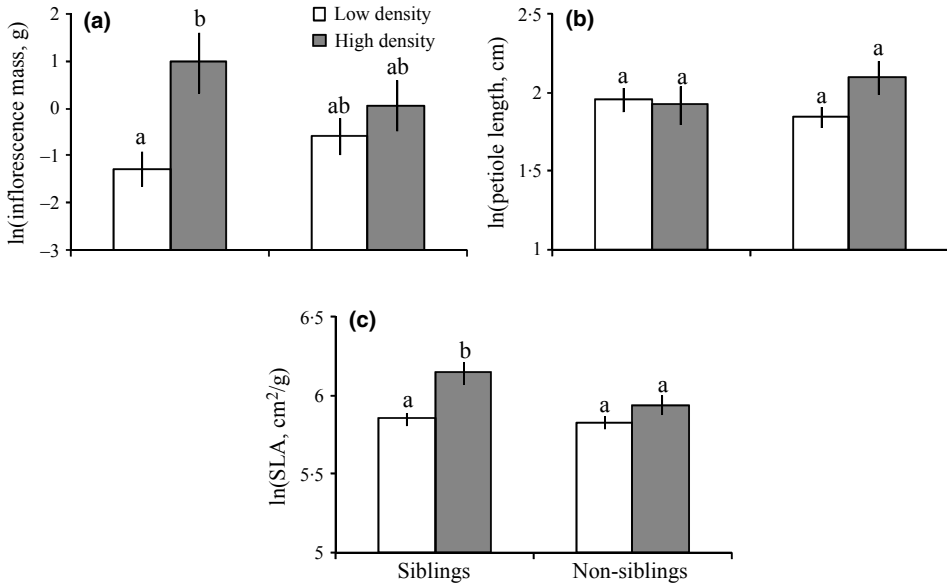


Fig. 10. The effects of neighbour density and genetic relatedness on the a) allocation of biomass to inflorescences, b) petiole elongation, and c) specific leaf area of *Trifolium repens*. Predicted trait means \pm SE derived from models containing plant shoot mass as a covariate are presented. Therefore, 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 test). Redrawn from Fig. 1 in III.

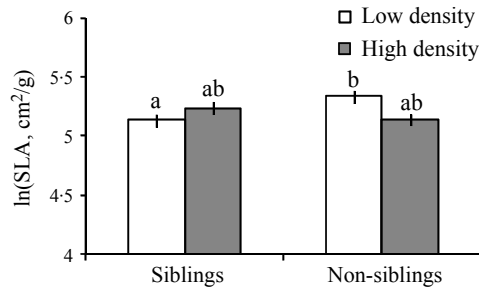


Fig. 11. The effects of neighbour density and genetic relatedness on specific leaf area of *Lychnis flos-cuculi*. Predicted trait means \pm SE are presented and are derived from models containing plant shoot mass as a covariate. Therefore, the graph demonstrates differences in trait means that could not be attributed to corresponding differences in plant shoot size. Different letters indicate significant differences between means ($P < 0.05$, Tukey test). Redrawn from Fig. 2 in III.

4. DISCUSSION

4.1 Paper I (plasticity in response to neighbours' frequency)

The results of the experiment examining morphological plasticity to neighbour identity demonstrate that a significant proportion of interspecific variation in plasticity to neighbour identity could be explained by how frequently different neighbours are encountered by a focal species in its natural environment. The degree of plasticity was highest for focal species that encountered both conspecific and heterospecific neighbours with high and comparable frequency (Fig. 3). In species exhibiting low frequencies of interactions with one or both of the neighbour species, low levels of plasticity were detected, in accordance with theoretical predictions (Moran, 1992; Alpert & Simms, 2002). The relationship between plasticity and the index of interaction frequency remained significant when phylogenetic dependences between the studied species were taken into account. The index explained considerably more variance in plasticity than the frequencies of conspecific and heterospecific encounters separately confirming the importance of the *evenness* of encounters with different neighbours in shaping plasticity to neighbour identity.

We also found that plants exhibited a greater plastic response to neighbour identity when the focal species was coupled with a heterospecific neighbour that was overall more abundant in the field. This suggests that plants may experience a stronger selective pressure to respond plastically to species that dominate their home communities. In the grassland communities that were examined in this study, the dominant species tended to be graminoids. In the community context, dominant or keystone species are essential and determine the function and structure of the whole community (Wade, 2007). Therefore, graminoids may play an important role in plant community structuring despite being weak competitors (Cahill *et al.*, 2008; **II**).

Our study was not designed to establish environmental factors that triggered plasticity to neighbour identity. It has been shown that competitive ability can be strongly influenced by plant size (Keddy *et al.*, 2002; Wang *et al.*, 2010), with larger individuals exerting a stronger negative impact on the growth of their neighbours. We found that differences in neighbour mass could not explain variation in morphological plasticity, suggesting that size-mediated resource competition was not the mechanism underlying the differential response to neighbours (Table 3). This is to be expected as plasticity was estimated as a change in plant morphology and biomass allocation that could not be explained by changes in total biomass. Therefore, it is likely that plasticity to the species identity of neighbours was triggered by signal other than resource depletion by neighbours of different size. Such signals may include root exudates and volatiles (Semchenko *et al.*, 2014; Karban *et al.*, 2016).

Depending on the identity and strategy of the neighbours, plastic responses in plant functional traits in response to neighbour identity may result in trait

divergence between neighbouring plants and, possibly, improved coexistence if this leads to niche differentiation (Zuppinger-Dingley *et al.*, 2014; Lipowsky *et al.*, 2015). In our study, we only measured traits of focal plants and used a single population from each species. Future research should examine the adaptive value of plasticity to neighbour identity and its consequences for niche differentiation and species coexistence. Nonetheless, our findings highlight the importance of plant–plant interactions for intraspecific trait variation, which should be considered in studies attempting to predict community and ecosystem processes based on species traits (Burns & Strauss, 2012; Zhu *et al.*, 2015).

Although we found a strong positive relationship between plasticity to neighbour identity and the relative frequency of interactions with different neighbours, other factors are known to be important for the evolution of plasticity. Some focal species may not benefit from morphological plasticity to neighbour identity if the same phenotype is equally effective in competition with both neighbour species. The evolution of phenotypic plasticity may also be constrained by factors such as deficient sensory capabilities, the maintenance costs of the genetic and cellular machinery required for a plastic response, the lag-time between environmental and phenotypic change or a lack of genetic variability (DeWitt *et al.*, 1998; Pigliucci, 2001). Furthermore, competition with neighbours of different identities may have triggered physiological adjustments or changes in belowground traits, which were not measured in this study.

Studies on invasive plant species and biodiversity manipulation experiments show potential for fast local adaptation to abiotic and biotic components of the ecosystem (Callaway *et al.*, 2005; Lankau, 2012; Ravenscroft *et al.*, 2014; Zuppinger-Dingley *et al.*, 2014). Our study shows a similar pattern in natural grassland systems, where variability in species composition of immediate neighbours results in an enhanced ability to modify morphology in response to neighbour identity.

4.2 Paper II (competitive ability study)

We found a significant relationship between the frequency with which plants encounter conspecific and heterospecific neighbours in the field and the competitive ability measured in a common garden experiment. The more aggregated species maintained greater growth when surrounded by conspecifics compared to when surrounded by heterospecifics, indicating weaker competitive ability. Species with a low degree of conspecific aggregation revealed greater growth with heterospecific than conspecific neighbours, reflecting higher-than-average competitive ability. In other words, plants grew better with the neighbour type that they encountered most frequently in nature.

Most species in temperate grasslands possess an ability to reproduce clonally (Rusch & van der Maarel, 1992; Klimeš *et al.*, 1997). We found a significant correlation between the distance of clonal dispersal and competitive ability: species that placed clonal offspring at a very short distance exhibited lower compe-

titive ability against heterospecifics than species with longer dispersal distances. This finding supports the hypothesis that a high degree of conspecific aggregation due to limited dispersal can be associated with a weaker competitive ability. Spatial aggregation of conspecifics and the relative intensity of intra- and interspecific competition have both been central to the theories explaining species coexistence (Bolker *et al.*, 2003; Silvertown, 2004). Theoretical models show that, if dispersal distance and investment in altruism are allowed to co-evolve, altruists maintain short dispersal distances while individuals adopting a selfish strategy evolve towards greater dispersal ability (van Baalen & Rand, 1998; Koella, 2000). The significant relationship between conspecific aggregation and competitive response to conspecifics *versus* heterospecifics observed in this study suggests that competitive restraint and dispersal ability might be co-evolved in temperate grassland plants.

Although we detected a significant overall relationship between the degree of conspecific aggregation and competitive response to neighbours, the strength and direction of the relationship varied between different study communities. The dependence of competitive response on conspecific aggregation was most pronounced in plants from calcareous grasslands, where the least-aggregated species were the strongest competitors against heterospecifics. The opposite trend (presumably competition-dispersal trade-off), although statistically not significant, was observed in plants from a flooded meadow community (Site 6): the dominant grass in this community (*Deschampsia cespitosa*) exhibited the highest degree of spatial aggregation and the strongest competitive ability against subdominant forbs. Calcareous grasslands are characterised by high species richness and a long history of continuous management by grazing or mowing (Poska & Saarse, 2002; Pärtel *et al.*, 2007). The flooded meadow is younger, species-poor and subject to frequent disturbance due to flooding. It is possible that age and disturbance of communities influence dispersal ability and its relationship with competitive ability. In disturbed communities, competition-dispersal trade-off might prevail (Fakheran *et al.*, 2010). In older, species-rich communities, where species and ramet density is high and competition is intense, other selective forces may prevail. Competition and disturbance can select for fundamentally different traits.

Stoll and Prati (2001) pointed out that aggregation of weak competitors is advantageous, especially at high densities and in the presence of strong competitors. It has been shown that competition may lead to an increase of the spacer length in stoloniferous plants (Schmid, 1986) and to a decrease in rhizomatous plants (Cheplick, 1997). Therefore, plant response to competition may depend on clonal growth strategy. We found that the shortest distance between adjacent ramets in the field conditions was detected in rhizomatous plants (e.g., *Sesleria caerulea*, *Carex ornithopoda*), which were weak competitors as indicated by better growth with conspecifics. Stoloniferous plants, such as *Pilosella officinarum* and *Antennaria dioica*, demonstrated intermediate distances between ramets. Finally, *Pimpinella saxifraga* and *Carlina vulgaris* propagate only with seeds and had the longest distance between adjacent individuals.

We found that species growth form had a significant impact on both conspecific aggregation in the field and competitive response in the common-garden experiment. The degree of conspecific aggregation was on average significantly higher in graminoids. The growth of graminoids was suppressed by competition with heterospecifics as much as or more than by competition with conspecifics, while non-leguminous forbs exhibited the opposite trend, and legumes always achieved greater growth with heterospecific neighbours. Therefore, species characteristics examined in this study were significantly influenced by phylogenetic provenance. Similar results were obtained in a study examining the effect of phylogenetic distance on the strength of interspecific competition where monocots were weaker competitors against forbs and forbs were stronger competitors against monocots (Cahill *et al.*, 2008). Significant differences between growth forms have also been identified in studies examining the strength of microbial feedbacks (Bartelt-Ryser *et al.*, 2005; de Kroon *et al.*, 2012), the effects of grazing (Deleglise *et al.*, 2011), patterns of colonisation and extinction in experimentally established plant communities (Cadotte & Strauss, 2011) and the ability of legumes to invade communities containing different growth forms (Turnbull *et al.*, 2005).

Our results show that weaker competitors tend to form highly aggregated spatial distribution patterns in the field, probably aiding their persistence in the community, but stronger competitors seem to avoid frequent conspecific interactions (Fig. 12). At the same time, all plants tended to grow better with the neighbour type that they encountered most frequently in nature. Further investigation of the importance of community age and productivity, disturbance and management history, and the costs and benefits of different competitive and dispersal strategies in different habitats, is needed to improve our understanding of the mechanisms promoting species coexistence.

4.3 Paper III (kin recognition study)

In this study, one out of eight species (*Trifolium repens*) exhibited significant differences in multiple measured traits in response to the presence of siblings *vs.* non-siblings. The only other significant effect of neighbour relatedness was detected in the SLA of *Lychnis flos-cuculi*. Therefore, our results indicate that kin recognition may not be a common phenomenon in temperate grasslands, with only a small proportion of plants likely to alter their morphology and biomass allocation when growing next to kin. Moreover, kin recognition might be difficult to detect in experimental studies as it may depend, among other factors, on plant density and can elicit species-specific responses that vary in magnitude and direction.

While fitness consequences of sibling competition have previously been examined in many studies (Cheplick, 1992; File *et al.*, 2012), few have considered morphological responses to kin *vs.* nonkin, and each study encompassed only one focal species at a time (Dudley & File, 2007; Murphy & Dudley, 2009; Biedrzycki *et al.*, 2010; Bhatt *et al.*, 2011; Biernaskie, 2011). The fact that many studies published to date have reported significant phenotypic changes may reflect

the difficulty of publishing negative results or may be due to the careful selection of study species with life histories that could be predicted to promote kin selection (e.g., formation of monospecific stands and high rates of selfing, S. Dudley, pers. comm.). Our study is the first to address the generality of kin recognition in plants by including multiple species that were not chosen on the basis of their biology but as a representative sample of a community.

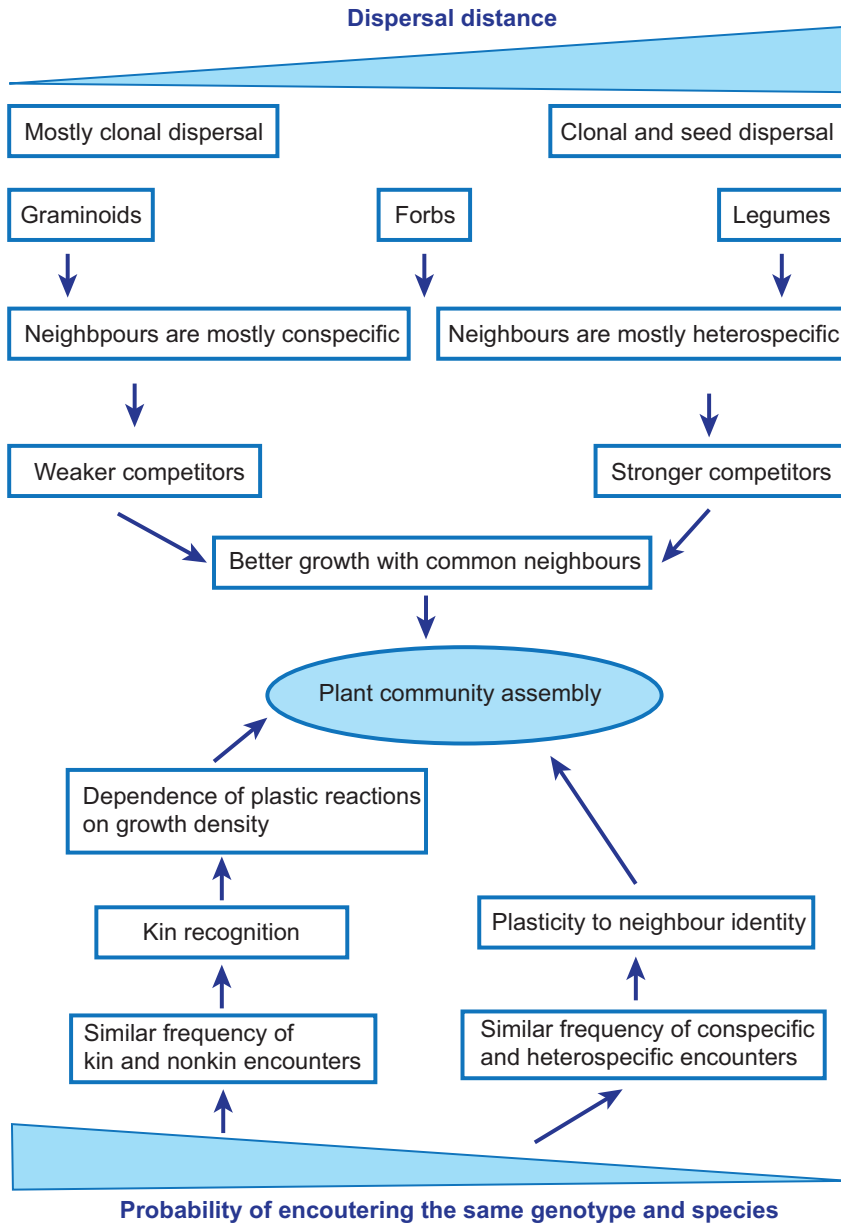


Fig. 12. Presumable relationships between plant dispersal ability, probability of encountering the same genotype and species, competitive ability and plasticity in response to neighbours' identity based on the results of the thesis.

We predicted that species exhibiting the ability to discriminate between kin and nonkin should reduce investment into competitive traits and increase resource use efficiency as the density of sibling neighbours increased. The phenotypic plasticity observed in *Trifolium repens* in response to the density and identity of neighbours supports this prediction. This species significantly increased investment to inflorescence mass and, consequently, to seed production when grown among siblings at high neighbour density. Clonal plants may respond to unfavourable growth conditions (e.g., shading) with higher seed reproduction at the expense of vegetative growth (Watson, 1984; Geber *et al.*, 1992; Newton *et al.*, 1992). Such a reaction can be explained as an escape of offspring to more favourable growth conditions. In addition, *T. repens* revealed greater SLA when grown with siblings at high neighbour density. Previous studies have shown that an increase in SLA improves shade tolerance as it enables more efficient light capture (Ballaré *et al.*, 1994; Griffith & Sultan, 2005) and, in our case, it enables higher photosynthetic rates to fuel increased seed production. It is possible that the increase in SLA also reduces kin competition in dense growth conditions by shading the soil surface and precluding the germination of additional seeds. Escaping conspecific competition is in accordance with our competitive ability study, where legumes always achieved greater growth with heterospecific neighbours (II). No change in petiole elongation was recorded when *T. repens* was grown with siblings, while enhanced elongation was observed in plants competing with unrelated neighbours. Shading by neighbours usually triggers an increase in elongation and is known as a means of overtopping competitors (Schmitt *et al.*, 1995; Leeflang *et al.*, 1998; Weijschedé *et al.*, 2006). To summarize, *T. repens* exhibited reduced allocation to competitive organs and increased allocation to seed production coupled with increased SLA when grown among siblings. Increased biomass allocation to seed reproduction in sibling groups has been documented in *Ipomoea hederacea* (Biernaskie, 2011), but no previous studies reported changes in elongation and SLA in response to sibling presence.

In our study, one further species (*Lychnis flos-cuculi*) modified SLA in response to neighbour relatedness. However, the benefit associated with this response is hard to interpret, as SLA changed in the opposite direction: it was significantly higher at low density and with non-sibling neighbours. A different response observed in *L. flos-cuculi* might be related to species growth form. During the first growing season, plants form a primary rosette and several side rosettes that require low neighbor density with sufficient light for successful growth (Bowman *et al.*, 2008). If *L. flos-cuculi* can discriminate between neighbours of different relatedness, plants can suppress the growth of non-siblings at low plant density by shading them with larger leaves and greater SLA. Among relatives at low density, *L. flos-cuculi* did not elicit such a response, which may indicate reduced horizontal leaf spread. No significant changes in root/shoot allocation were detected in any species. As root mass was not measured directly, some responses in biomass allocation may have been overlooked. We found that the way plants reacted to increasing neighbour density differed between relatedness treatments. As a result, alternative conclusions might have been reached if

only a single neighbour density had been chosen. It is important to recognize that kin recognition may trigger a different response depending on whether a plant experiences little competition or intense competition with its neighbours.

It can be predicted that the evolution of an ability to recognize kin will be most strongly favoured if both kin and nonkin neighbours are encountered at similar frequencies (Moran, 1992). The probability of kin interactions is collectively determined by species life-history traits, particularly those related to offspring dispersal (Lovett Doust, 1981; Cheplick, 1992), but also by community properties, such as species richness and evenness. Field measurements in the community where the seeds were collected show that the nearest neighbouring ramet to *T. repens* plants often belongs to the same species (44%) implying a potential for frequent interactions between genetically closely related neighbours (unpublished data). Besides *T. repens*, a high frequency of conspecific encounters was also observed in *L. flos-cuculi* (41%). Species that demonstrated marginally nonsignificant effects of genetic relatedness on plant shoot mass (*Deschampsia cespitosa* and *Leontodon hispidus*) attained 22% greater shoot mass and 24% lower shoot mass when grown among siblings compared with non-siblings, respectively. For *D. cespitosa*, high frequency of conspecific encounters was observed in the field (95%); for *L. hispidus*, frequency of conspecifics was 20%. Further measurements of genetic relatedness are needed to ascertain how often conspecific encounters represent sibling interactions in the studied species. However, based on the frequency of conspecific encounters, it is likely that *D. cespitosa* experiences frequent interactions with genetically identical or closely related individuals, while such interactions are less frequent in *L. hispidus*. Besides the effects of kin recognition, plant biomass may be influenced by niche partitioning whereby plants achieve higher productivity among genetically diverse individuals due to differences in resource requirements and uptake (File *et al.*, 2012). It is likely that kin recognition and niche partitioning affect plant biomass accumulation simultaneously and the outcome depends on the strength of each process. Lower biomass of *L. hispidus* in sibling groups may indicate the absence of kin recognition and may be due to niche partitioning. Further studies focussing on the fitness consequences of growing among kin *versus* nonkin are required to disentangle the relative contribution of kin recognition and niche partitioning to the outcome of plant interactions.

CONCLUSIONS

The studies reported in this thesis demonstrate that the frequency and identity of neighbours influence evolutionary processes and functional traits in plant communities. The ability of plants to discriminate between neighbours can result in morphological plasticity to neighbour identity, avoidance of competition with siblings and greater growth with the neighbour type that is encountered most frequently in nature. Aggregation of weak competitors and segregation of strong competitors, at least in some types of communities, may create community spatial patterns that promote species co-existence.

The results of this study show that plasticity to neighbour identity is the highest when conspecific and heterospecific neighbours are common and encountered at similar frequencies by a focal species in its home community. This relationship was not affected by size-mediated competition with neighbours and remained significant when phylogenetic dependencies between species were taken into account.

Our results suggest that kin recognition may not be a common phenomenon in temperate grasslands. Morphological plasticity to genetic relatedness varied depending on plant density, and the magnitude and direction of responses varied between studied species. In addition, it can be conditional upon the same conditions as plasticity to species identity of neighbours: plasticity to neighbours' genetic relatedness should be promoted when kin and nonkin neighbours are common and encountered at similar frequencies by a focal species in its home community. Further genetic analyses of plants in the field conditions are required to improve our understanding of conditions in which kin recognition is likely to evolve.

Our results also demonstrate that species with a low degree of conspecific aggregation are on average stronger competitors than species with a high degree of conspecific aggregation. Temperate grasslands are predominantly composed of perennial species possessing an ability to reproduce clonally, and our results confirm the observations that conspecific aggregation is strongly related to clonal dispersal distance. Our results reveal that the shortest distance was detected between rhizomatous plants, while stoloniferous plants demonstrated intermediate distance between ramets, and species that propagate only with seeds had the longest distance between adjacent conspecific individuals. These results were more pronounced for old and species-rich communities. The opposite trend (presumably a competition-dispersal trade-off), was observed in plants from a flooded meadow community, which is frequently disturbed by floods and characterised by high productivity. It is therefore possible that different disturbance regimes and productivity levels may modify selection on plant competitive and dispersal abilities.

Contrary to the pattern of plasticity to neighbour identity, we found that competitive ability and spatial aggregation of plants were significantly influenced by phylogenetic provenance. The degree of conspecific aggregation was on

average significantly higher, and competitive ability lower, in graminoids, while legumes achieved greater growth with heterospecific neighbours and exhibited longer dispersal distances. Investigating the importance of community productivity, age and management history, as well as plasticity of clonal growth, could give further insight into the processes determining the relationship between spatial patterns and competitive ability, as well as improve our understanding of the processes underlying species coexistence.

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SUMMARY IN ESTONIAN

Evolutsioonilised seosed taimede konkureerimiskäitumise ning naabrite identiteedi ja esinemissageduse vahel parasvöötme niidukooslustes

Taimed on paikse eluviisiga ja võivad reageerida välistingimuste muutustele morfoloogilise plastilisuse abil, s.t muutes oma fenotüüpi. Plastilised reaktsioonid võivad ilmneda mitte ainult abiootiliste, vaid ka biootilistele tegurite varieerumisele, sealhulgas vastusena naabertaimedele. Taimed on võimelised ära tundma oma lähinaabreid, kes võivad olla liigikaaslased või teiste liikide esindajad, lähisugulased või kauged sugulased. See, kes satub olema taime naaber, sõltub paljudest teguritest, sealhulgas liikide eripärast, levimisvõimest ja kogu koosluse tunnustest.

Fokaaltaim võib olla ümbritsetud lähisugulastest kui liigile on iseloomulik piiratud ulatusega seemneline või vegetatiivne levimine. Vastavalt evolutsioonilisele mänguteooriale, peaksid lähisugulased omavahelistes interaktsioonides panustama vähem ressursse konkureerivasse käitumisse ning rohkem paljunemisse võrreldes olukorraga, kus naabriteks on kauged sugulased. Teoreetilised mudelid on näidanud, et „altruistid“ (kooperatiivse käitumisega isendid) peaksid kasvama üksteisele lähemal, sel ajal kui „isekad“ (tugevad konkurendid) peaksid levima üksteisest kaugemale. Teisalt on võimalik ka konkurentsi- ja levimisvõime lõivsuhe, mille puhul liigid ei saa olla samaaegselt head konkurendid ja head levijad.

Vaatamata järjest ulatuslikumale naabrite äratundmisvõime uurimisele, jääb ikkagi selgusetuks selle nähtuse esinemissagedus taimekooslustes. Enamus katseid on läbi viidud kunstlikes tingimustes, keskendudes üksikutele liikidele ja seejuures uurimata kasvutiheduse mõju taimede vahelisele konkurentsile. Erinevaid naaberliike või taimeliigile erineva sugulusastmega naabreid võib vaadelda alternatiivsete biootiliste keskkondadena ja evolutsioonilised tegurid, mis soodustavad naabrite äratundmise kujunemist, peaksid olema samad kui mistahes adaptiivse plastilisuse puhul. Teoreetilised mudelid ja piiratud empiirilised andmed on näidanud, et plastilisuse evolutsioonis mängib olulist osa eri keskkondade esinemissagedus, kus sarnase sagedusega keskkondade esinemine paljude põlvkondade jooksul peaks soosima plastilisuse evolutsiooni. Seega plastilisus võiks olla maksimaalne, kui taimed kogeavad kahte alternatiivset keskkonda 50% tõenäosusega. Kui aga üks keskkond domineerib sageduselt teiste üle, saavutatakse suurim kohasus fikseeritud arengustrateegia kujunemisega.

Käesolevas doktoritöös uuriti fokaalliigi morfoloogilise plastilisuse sõltuvust liigikaaslaste ja teise sagedase naaberliigiga kokkupuutumise sagedusest. Samuti uuriti, kas plastilisus on seotud taimeliigi levikuga koosluses, oletades, et koosluse dominant omab suuremat plastilisust või kutsub seda esile naaberliikides. Vaatluse all oli ka seos erinevate liikide konkurentsivõime ja liigisisese ruumilise agregeerumise vahel.

Töö eksperimentaalse osa eripäraks oli asjaolu, et pandi kokku välivaatlustest saadud koosluste andmed (liikide esinemissagedused ja iga fokaalliigi naaber-

liikidega kokkupuutumise sagedus) ning potikatse plastilisuse hinnangud. Kõik eksperimendis kasutatud taimed kasvatati oma kodukoosluste seemnetest. Mullasegud valmistati võimalikult originaalmuldade lähedastena, tuginedes mulla-proovide keemilisele analüüsile ja lisades iga koosluse mikroobset inokulumit. Plastilisuse uurimisel kasutati 27 liiki (I) ja konkurentsi katses 28 liiki (II) seitsmest Eesti niidukooslusest, kasvatades fokaalliike koos liigikaaslastega ja teise koosluses sagedase naaberliigiga. Kõik liigid olid mitmeaastased ja esindasid võimalikult erinevaid kasvuvorme: nende hulgas oli seitse graminoidi (*Poaceae*, *Cyperaceae*, *Juncaceae*), neli liblikõielist (*Fabaceae*) ja 17 mitte-liblikõielist rohundit. Erinevalt katsete tavapraktikast kasvatati taimi naabrite erineva tiheduse juures (0, 1, 2, 3, 4, 6 või 8 naabrit). Sugulaste äratundmise katses (III) kasvatati kaheksat fokaalliiki koos lähisugulastega (sama emataime järglased) või sama koosluse juhusliku päritoluga liigikaaslastega, rakendades kahte kasvutihedust (kaks või neliteist isendit poti kohta). Taimi kasvatati 2009. aasta vegetatsiooniperioodil Tartus, välitingimustes. Kasvuperioodi lõpus mõõdeti kõigi taimeosade massid, juurte ohtrus ja ruumiline jaotus mullas ning määrati taimede plastilisus naabrite suhtes, kasutades viit maapealset tunnust (tugistruktuuride kuiv biomass, maksimaalne vegetatiivne kõrgus, lehtede üldpindala, lehe eripind ja lehtede veesisaldus).

Statistiline analüüs näitas, et plastilisus naabrite identiteedile on suurim, kui fokaalliigi kokkusaamine liigikaaslastega ja teise koosluses tavalise naaberliigiga esineb enam-vähem võrdse sagedusega, seega kinnitades plastilisuse tekke teoreetilisi aluseid. Plastilisus ei sõltunud naabrite biomassist, taimeliikide fülogeneetilisest päritolust ega koosluse eripärast. Katsetulemused näitasid, et taimed reageerisid suurema plastilisusega liikidele, kes olid koosluses sagedasemad (dominandid). Järelikult graminoidid, keda peetakse nõrkadeks konkurentideks, kuid kes on kooslustes sageli dominandid, kutsuvad esile naabrite suuremat plastilisust.

Suguluse rolli uurivas katses vaadeldi nii maapealse biomassi sõltuvust naabrite identiteedist ja kasvutihedusest, kui ka õisikute kuivmassi, lehepikkuse, lehe eripinna, leherootsu pikkuse ja juurte tiheduse sõltuvust maapealse biomassi allokatsioonist. Kaheksast liigist ühe, valge ristiku (*Trifolium repens*) puhul, eristus plastilisus selgelt teistest liikidest: kasvades suure kasvutiheduse juures koos sugulastega, investeerisid selle liigi isendid rohkem seemnelisse paljunemisse ja suuremasse lehe eripinda pikkuskasvu arvelt. Suuremat investeerimist seemnelisse paljunemisse võib käsitleda põgenemisena tihedast lähisugulaste grupist soodsamatesse kasvutingimustesse. See on kooskõlas konkurentsi katsetulemustega, kus liblikõielised näitasid paremat kasvu oma liigikaaslastest eemal. Teine liik, käokann (*Lychis flos-cuculi*), käitus vastupidi: tema lehe eripind oli suurem väikese kasvutiheduse juures ja koos mittersugulastega. Võimalik, et see liik püüab varjutada mittersugulasi, jättes sugulaste puhul lehe eripinna muutmata.

Tuginedes töö tulemustele võib väita, et parasvöötme niidukooslustes ei ole sugulaste äratundmist lihtne tuvastada. Lisaks mitmetele teistele tingimustele, sõltub morfoloogilise plastilisuse ilming taimede kasvutihedusest. Plastilised reaktsioonid varieeruvad oma ulatuse ja suuna poolest, mis teeb nende inter-

preteerimise keeruliseks. Plastilisus lähisugulastele võib sõltuda samadest tingimustest nagu plastilisus naabrite liigilisele identiteedile: plastilisus peaks olema kõrgeim, kui fokaalliigi sugulastest ja mittesugulastest naabrid esinevad võrdsete sageduste juures. Edaspidised täpsemad geneetilised uuringud peaksid tooma enam selgust sugulaste äratundmise ja selleks vajalike tingimuste kohta.

Meie tulemused näitasid üldist tendentsi, et potikatses kasvavad taimed paremini koos naabritega, kellega nad sageli kohtuvad looduslikus koosluses. Vähem agregeerunud liigid olid enamasti tugevama konkurentsivõimega ja kasvasid paremini teiste liikide naabruses; enam agregeerunud liigid olid aga nõrgema konkurentsivõimega ja kasvasid paremini koos liigikaaslastega. Need seosed väljendusid kõige tugevamalt kahe vanema liigirikka koosluse puhul (Lääne-Eesti loopealsed). Vastupidine trend, s.t konkurentsi- ja levimisvõime lõivusuhe, kuigi statistiliselt mitteoluline, esines liigivaesel üleujutataval luhaniidul. Võimalik, et koosluse vanus, häirituse aste, liigirikkus, konkurentsi tugevus ja veel teisedki tegurid mõjutavad taimede kasvamise ja levimise strateegiaid. Vastavalt teoreetilistele seisukohtadele ja vähestele empiirilistele andmetele, võivad näiteks koosluse häirituse aste ja konkurentsi tugevus mõjutada evolutsioonilisi protsesse erinevates suundades. Meie katsetulemused kinnitasid seda väidet.

Kahes eelpool mainitud liigirikkas koosluses uurisime veel ka seost taimede levimiskauguse ja potikatses kasvamise edukuse vahel. Levimiskauguse mõttmisel selgus, et kõige lühem vahemaa kлонаalselt paljunevate isendite vahel esines risoomide abil levivatel liikidel (näiteks *Sesleria caerulea*, *Carex ornithopoda*), järgnesid maapealsete stoolonitega liigid (näiteks *Pilosella officinarum*, *Antennaria dioica*) ja kõige kaugem vahemaa oli ainult seemnetega levivatel liikidel (*Pimpinella saxifraga*, *Carlina vulgaris*). Selles järjekorras kahanes edukam kasv koos liigikaaslastega ja suurenes kasvu edukus teiste liikide esindajatega, saavutades maksimumi seemneliselt paljunevate liikide puhul. Katse tulemused näitasid, et liikide konkurentsivõime ja ruumiline agregeerumine olid oluliselt mõjutatud fülogeneetilisest päritolust. Nõrgemat konkurentsivõimet omavad graminoidid olid enamasti rohkem liigisiselt agregeerunud, samal ajal kui liblikõielised taimed kasvasid paremini koos teiste liikide taimedega ja levisid suurematele vahemaadele.

Antud töö tulemused näitavad, et taimeliigi konkurentsivõime ja fenotüübiline varieeruvus ei sõltu üksnes abiootilisest keskkonnast, vaid ka taimede levimise strateegiast ja ruumilisest paigutusest koosluses, mis määravad konkureerimise tõenäosuse samast liigist lähi- ja kaugsugulastega ning teiste liikide esindajatega. Kuigi mõned liigid näitasid selget plastilisust naabrite geneetilise suguluse ja liigikuuluvuse suhtes, siis enamus liike näitas vähest plastilisust ja eri liigid reageerisid naabritele eri moel. Seega spetsiifiliste naabrite äratundmine ei pruugi olla looduses laialt levinud ja võib sõltuda paljudest populatsiooni ja koosluse aspektidest. Samuti vajavad edasist uurimist taimede koöperatiivset käitumist soodustavad tegurid. Tuleviku uuringud peaksid pöörama suuremat tähelepanu taimekoosluste eri aspektidele nagu vanusele, liigirikkusele, häirituse tasemele ning majandamise ajaloole, selgitamaks nende mõju liikide kooseksisteerimisele.

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