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Intensity and asymmetry of competition between plant pairs of different degrees of similarity: an experimental study on two guilds of wetland plants

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Using predictions from existing competition theory, we designed an experiment to test if competition intensity or asymmetry varied with the similarity of the interacting plants. Competition intensity and asymmetry were measured after one growing season for six species of plants grown in an additive pairwise design. Similarity was measured using a guild classification and was assigned to three levels: intraspecific, intra-guild and inter-guild interactions. The guild classification was based upon 27 ecological traits associated with both niche properties (e.g. rooting depth) and competitive ability (e.g. plant height). The six species represented two distinct guilds of wetland plants: obligate and facultative annuals.

The results confirmed two key predictions: The intensity of competition increased with increasing similarity between interacting plants, as predicted by the niche control paradigm. The asymmetry of competition decreased with increasing similarity, as predicted by the dominance control paradigm. Guild identity, as defined in our study, was not a good predictor of competitive ability.

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Introduction

The role of competition in structuring communities has for a long time been, and still is, one of the most important and sometimes divisive questions in plant ecology (e.g. Clements et al. 1929, Connell 1983, Schoener 1983, Keddy 1989). At least two distinctive views can be extracted from the vast literature on the subject (Yodzis 1986, Keddy 1989). The first view has borrowed concepts primarily from animal ecology, and emphasizes competition for resources, niche differentiation and resource partitioning as the mechanisms whereby competition and coexistence in plant communities can be described and explained (e.g. MacArthur and Levins 1967, May 1973, Werner 1979, Pianka 1983, Tilman 1982, 1988). The second view emphasizes com-

petition for space, dominance control and competitive herarchies as being the important features (Colwell and Fuentes 1975, Grime 1979, Yodzis 1986, Keddy 1989, 1990).

From both points of view, the degree of similarity between potentially competing species is important. Similarity can be divided into niche similarity and similarity in competitive abilities, which may vary independently (Aarssen 1984). This difference has been reflected in different views in coexistence theory. Classic competition theory suggests that if competition is strong, there is a limit to the niche similarity of the coexisting species (MacArthur and Levins 1967, MacArthur 1972). Others argue that similarity in competitive abilities, will increase the probability of coexistence (Aarssen 1983,

1989, Ågren and Fagerström 1984, Goldberg 1987, Fagerström 1988).

While these views are not mutually exclusive, they can be considered paradigms which emphasize different aspects of competition, and generate different testable predictions. The prediction from the first paradigm, niche control, would be that the intensity of competition between a pair of individuals should increase with increasing similarity between the competitors. While there are good theoretical reasons to expect this relationship, we know of no general experimental tests of this prediction. There are, however, numerous examples showing that intraspecific competition is more intense than interspecific (e.g. Weiner 1980, Fowler 1982, Berendse 1983). The second paradigm, dominance control, emphasizes another aspect of competition: the degree to which an interaction is asymmetric (Keddy 1989). Many studies indicate that this type of interaction is rule rather than exception in plant communities (see reviews in Connell 1983, Schoener 1983). Here the prediction is that the more different a pair of interacting individuals are, the more asymmetric the interaction will be. This is, however, not valid if the fundamental niches of the species are completely non-overlapping.

To be able to test these predictions we need to answer two questions: 1) How do we define and measure similarity between species? 2) How do we measure the two aspects of competition, intensity and asymmetry?

Measuring similarity

The first point could be solved by using the concept of guilds. The term guild has for a long time been used to designate a group of functionally similar organisms, but Root (1967) formalized the definition to "... a group of species that exploit the same class of resources in a similar way". The use of the guild as a unit for descriptive and experimental studies is well-established in animal ecology (e.g. Adams 1975, Cummins and Klug 1979, Terborgh and Robinson 1986), but has also become increasingly recognized in plant ecology (Platt and Weis 1977, 1985, Givnish 1987, Day et al. 1988, Keddy, in press). Classifying plants into different guilds is one way to be able to study patterns of competition between individuals representing different degrees of similarity. The guild classification should be constructed from traits associated with both niche property and competitive abilities of the species included. At the very least, similarity could be assigned to three levels: Intraspecific, intra-guild and inter-guild interactions.

Measuring competition intensity and asymmetry

For the second point we need to define intensity and asymmetry into measurable variables. For simplicity, consider a pairwise interaction between species i and species j. If Y_i is defined as the yield of one individual grown by itself, then the relative yield per plant (RYP) in interaction with j would be, $RYP_{ij} = Y_{ij}/Y_i$, and $RYP_{ji} = Y_{ji}/Y_j$. These expressions are based upon an additive design, where the number of plants per cell in monoculture (Y_i) is n_i, and in mixture (Y_{ij}), n_i+n_j.

From the above, a measure of intensity (I) of interaction can be defined as the sum of the relative reductions in yield of two interacting species: $I = (1-RYP_{ij})+(1-RYP_{ji})$. I can thus range from 0, where two interacting species are totally unaffected by each other, to 2, where competition leads to death of both individuals.

Similarly, asymmetry (A) can be defined as the absolute difference in the relative reductions in yield of two interacting species: $A = |(1-RYP_{ij}) - (1-RYP_{ji})| = |(RYP_{ij}-RYP_{ji})|$. A can range from 0, where the interacting species suppress each other equally, i.e. the interaction is symmetric, to 1, where one species totally suppresses the other, i.e. the interaction is highly asymmetric. This expression of asymmetry is similar to McGilchrist and Trenbath's (1971) definition of aggressiveness, which has been used in several competition studies (e.g. Mitchley and Grubb 1986; see also Wilson and Keddy 1986, Goldberg 1987, Goldberg and Fleetwood 1987).

The two measures are, however, interrelated, since both are derived from RYP. Asymmetry can thus never obtain a higher numerical value, than that of intensity (see marked boundaries in Fig. 2 below). One could also consider other types of interactions, e.g. mutualism and parasitism. These would yield other value-ranges of intensity and asymmetry, with less clear limits. In this study, however, we restrict ourselves to discussing competitive interactions.

Combining these two measures of competition gives us a tool to describe and compare the nature of interactions between plants of differing similarity. The objective of this study was to test for changes in these two components of competition with increasing degrees of similarity between the competitors.

Materials and methods
Choice of species

The plant species used in the experiment had to meet two conditions: 1) They had to provide a gradient of similarity, from very similar to very different species. 2) They had to possess the capacity to complete a full life-cycle in a short time-span.

Considering these two conditions six species representing two guilds of wetland plants were chosen, three obligate annuals, *Cyperus rivularis* Kunth, *Eleocharis obtusa* Roem. & Schult. and *Juncus bufonius* L., and three facultative annuals, *Lythrum salicaria* L., *Mimulus ringens* L. and *Verbena hastata* L. These are representatives of two of five distinct guilds recognized in a

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Table 1. The traits used for screening of 43 species of wetland plants with means for the two guilds used in the present study. Indicated with asterisks are the separating traits, which are significantly different between the two guilds (After Boutin and Keddy, unpubl.).

	Obligate annuals	Facultative annuals
Measured in garden		
Lifespan (yr)	1.1	2.4
% flowering	100.0	92.8
* Height (cm)	38.4	43.5
Rate of shoot extension (cm d^{-1})	0.04	0.06
* Total biomass (g)	23.8	12.2
* Above ground biomass (g)	15.8	5.3
* Below ground biomass (g)	8.1	6.9
Ratio below/above	0.54	1.37
* Photosynthetic area (cm^2)	709.0	501.9
* Photosynthetic area/ total biomass (cm^2 g^{-1})	36.9	37.8
* Photosynthetic area/ volume (cm^2 ml^{-1})	4.9	5.1
Dry weight/volume (g ml^{-1})	0.14	0.14
Number of shoots	98.4	1.0
* Crown area (cm^2)	0.13	0.03
Stem diameter (mm)	4.6	6.2
Rooting depth (cm)	1.2	2.8
* Diameter of main root (mm)	1.0	4.6
* Shortest distance between shoots or tillers (cm)	0.6	0.0
Longest distance between shoots or tillers	0.6	0.0
Measured in the field		
* Total height (cm)	31	78
Number of shoots	22.4	2.7
Stem diameter (cm)	0.3	0.6
Shortest distance between shoots or tillers (cm)	0.1	0.2
Longest distance between shoots or tillers (cm)	0.1	0.9
* Diameter of main root (cm)	0.0	0.7
* Rooting depth (cm)	0.7	1.9
Measured in greenhouse		
Relative growth rate (g g^{-1} d^{-1})	0.25	0.26

Experimental design

Three levels of similarity between the pair of interacting plants were designated: 1) intraspecific, 2) intra-guild and 3) inter-guild interactions. The plants were put in interaction in all possible pairwise combinations within and between the different levels/categories, which yielded six interspecific, six intra-guild and nine inter-guild interactions. The plants were grown in pots pair-wise and alone in a modified additive design with ten replicates.

Experimental conditions

Plants were germinated and grown from May to September in an outdoor compound at Carleton University, Ottawa, Canada. Seeds were sown on 2 May 1989 in trays with potting soil. Germination occurred within two weeks and the seedlings were transplanted on 1 June to pots with a diameter of 9 cm. A mixture of 1/3 commercial potting soil, 1/3 sand and 1/3 peat was used as substrate. Seedlings were kept under shade cloth until 15 June, when pots were placed in a randomized block design under full sunlight. The plants were watered daily and a complete hydroponic fertilizer (20 ml solution in each pot of 1/4 of the commercially recommended strength of the two mixtures: "7–11–27" and "15–0–0" (B & B Hydroponics, Ottawa, Canada)), was added every 15 d starting 20 June. Plants were harvested individually during one week starting 5 September and after that dried at 80°C for 72 h.

Data analysis

Total biomass of the plants was used as the measure of yield. The plants were, however, also separated into above- and below-ground biomass, but since both were strongly correlated to total biomass, these were not included further in the analyses.

A matrix was constructed from the obtained RYP-values. From this we calculated for each species, the mean response to and mean effect on other species, with corresponding rank orders. Response is defined as a species' ability to grow in the presence of another species, while effect is a species' ability to suppress another species (Goldberg and Werner 1983). Intensity and asymmetry were calculated, according to the formulas defined earlier.

ANOVA was used to test for differences in intensity and asymmetry between the three levels of similarity mentioned above, and Tukey's HSD was used to further test differences in means. A series of t-tests were used for comparing yields in mixture to yields in the respective monocultures. T-tests were also used for comparing RYP-values for the different species in the interspecific interactions. This was used to generate a competitive

recent study of 43 species of wetland plants (Boutin and Keddy, unpubl.). A method of screening for 27 morphological and functional traits was used to group the species into the different guilds (Table 1). The traits are associated with both niche properties (e.g. rooting depth) and competitive ability (e.g. canopy diameter, height) of the species. The two guilds used in this study were separated and described with the following most important characters: The obligate annuals (mud-flat annuals, sensu van der Valk 1981) had numerous short stems, a large crown area and a tendency to direct more growth towards above-ground structures. The facultative annuals were taller and had an erect, fast-growing main stem, topped by inflorescence. They also produced perennating organs at the base of the main stem (See also Table 1).
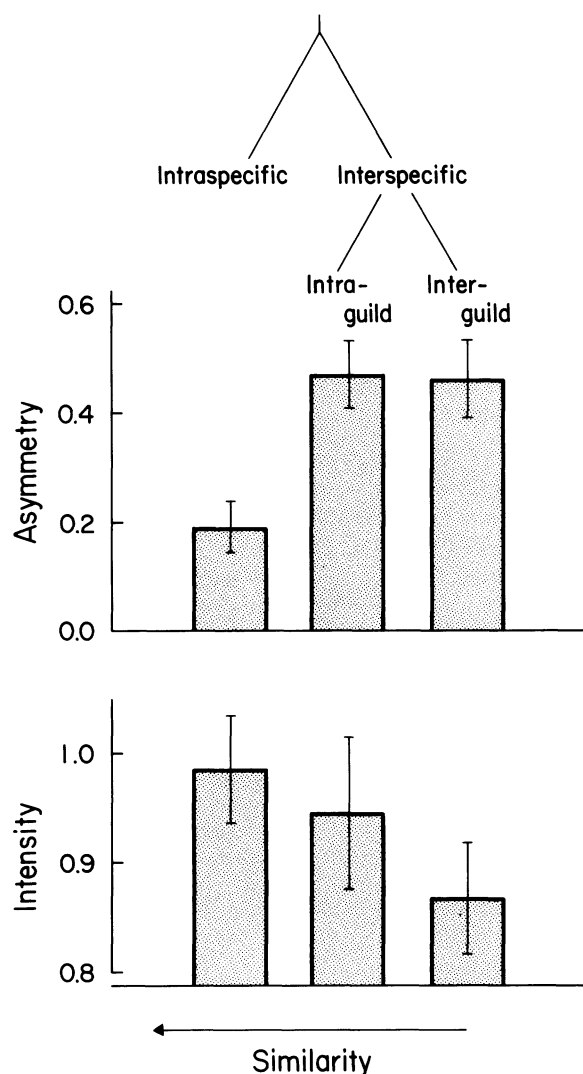
Fig. 1. The relationship between similarity and asymmetry (top) and intensity (bottom). Similarity is classified into three categories of interactions: Intraspecific, intra-guild and inter-guild, with a decreasing degree of similarity between the inter-acting individuals in the order mentioned. For definitions on asymmetry and intensity, see Introduction. Intensity increased with increasing similarity of the interacting plants (ANOVA, p < 0.01). Significant differences exist between the intraspecific and inter-guild interactions, as well as between intra-guild and inter-guild interactions (Tukey's HSD, p < 0.05). Asymmetry increased with decreasing similarity (ANOVA, p < 0.001). The interspecific interactions were significantly more asymmetrical than the intraspecific. No significant differences existed be-tween intra- and inter-guild interactions (Tukey's HSD, p > 0.05). Confidence intervals (95%) are indicated with vertical bars. Note that the scale for intensity has been cut and en-larged, since this measure is relative and highly dependent on the size of the interactive space (i.e. density of individuals), which in this experiment was minimized.

hierarchy among the species. Tukey's HSD was used to compare mean effects and mean responses between spe-cies. Where variances were nonhomogeneous, the anal-yses were made on log-transformed data.

Results

Main tests

As predicted, the intensity of competition increased with increased similarity of the interacting plants (ANOVA, p < 0.01) (Fig. 1 bottom). Although the variation of the means is largely overlapping, there are still significant differences between the intraspecific and inter-guild interactions, as well as between intra-guild and inter-guild interactions (Tukey's HSD, p < 0.05).

As predicted, asymmetry increased with decreasing similarity (ANOVA, p < 0.001): the interspecific inter-actions were more asymmetrical than the intraspecific (Fig. 1 top). No differences were, however, apparent between intra- and inter-guild interactions.

a) Intraspecific – interspecific. Looking at the results on intensity and asymmetry on a finer scale, they can be visualized in a phase-space diagram, where each pair of
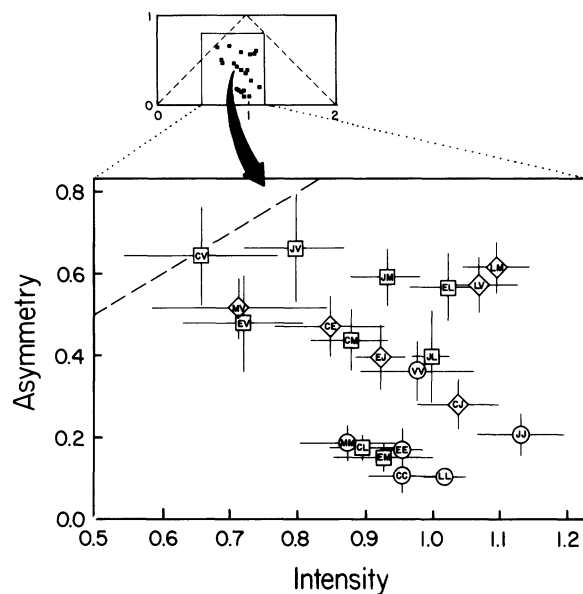

Fig. 2. Phase-space diagram on asymmetry and intensity for each interaction separately, where $\bigcirc$ = intraspecific, $\diamondsuit$ = intra-guild and $\square$ = inter-guild interactions. Species names are abbreviated as follows: C = *Cyperus rivularis*, E = *Eleocharis obtusa*, J = *Juncus bufonius*, L = *Lythrum salicaria*, M = *Mimulus ringens*, V = *Verbena hastata*. For clarity, the upper small diagram shows the whole area of possible value ranges for asymmetry and intensity in a competitive interaction, with the dashed lines indicating the theoretical limits. In the lower diagram the area, which covers intensity- and asymmetry-val-ues from this experiment, is enlarged. Note that, for visual expression, the intensity-axis is disproportionately enlarged.

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Table 2. Matrix on mean relative yield per plant. For each species is given the mean response to and mean effect on other species, with corresponding rank orders. Indicated with asterisks are results from t-test comparing mean yield values in mixture ($Y_{i(j)}$) and monoculture (Y_i). N.S. p > 0.05, * p < 0.05, ** p < 0.01, *** p < 0.001. Rank values from mean values on response and effect followed by the same letter are not significantly different (p > 0.05) according to Tukey's HSD.

	Cyperus	Elocharis	Juncus	Lythrum	Mimulus	Verbena	Mean response	Rank
Cyperus	0.52[1] ***	0.77 N.S.	0.55 ***	0.54 ***	0.77 N.S.	0.87 N.S.	0.70	1[a]
Eleocharis	0.33 ***	0.52[1] ***	0.35 ***	0.27 ***	0.53 ***	0.73 **	0.44	4[b]
Juncus	0.41 ***	0.73 *	0.43[1] ***	0.34 ***	0.76 N.S.	0.92 N.S.	0.63	3[a]
Lythrum	0.57 ***	0.67 *	0.64 **	0.49[1] ***	0.76 **	0.76 **	0.68	2[a]
Mimulus	0.32 ***	0.51 ***	0.31 ***	0.14 ***	0.56[1] ***	0.75 **	0.40	5[b]
Verbena	0.41 **	0.51 **	0.28 ***	0.17 ***	0.54 *	0.51[1] ***	0.38	6[b]
Mean effect	0.41	0.64	0.43	0.29	0.67	0.81		
Rank	2[a]	4[b]	3[a]	1[a]	5[bc]	6[c]		

1. Intraspecific interactions are included in the matrix, but not in the calculations on mean response and mean effect.

interaction is plotted according to its degree of intensity and asymmetry (Fig. 2). The intraspecific group is fairly homogeneous, with interactions high in intensity and low in asymmetry. The interspecific interactions, on the other hand, cover a broad range in both intensity and asymmetry.

b) Intra-guild. In the intra-guild group, intensity varies from relatively low, *Mimulus-Verbena,* to high in the *Lythrum*-interactions. Comparing the two guilds within this group, the degree of asymmetry is significantly lower (t-test; p < 0.001) among the obligate annuals.

c) Inter-guild. In the inter-guild group the interactions with *Verbena* show the lowest degree of intensity. Outliers with very low asymmetry are the interactions *Cyperus-Lythrum* and *Eleocharis-Mimulus,* i.e. these species are relatively equal in competitive ability.

Community matrices

The primary objective of this paper was to test the foregoing hypotheses. However, this experiment also yields a pairwise community matrix and a competitive hierarchy. Since there are comparatively few published matrices (Keddy and Shipley 1989), we briefly report on this aspect of our results.

In Table 2 a matrix of RYP-values for each interaction is presented. Here it is shown that yield in mixture in most cases is significantly lower than when grown singly, i.e. competition is present. It is also indicated that the plants utilize the space in the pot fully when grown singly. This is, according to Aarssen (1985), an important prerequisite to accurately compare the relative performance of two components in a mixture. For all species, the yield per pot does not differ significantly between plants grown singly or in intraspecific interaction (two plants per pot).

Table 3. T-test matrix on relative yield per plant. Below is given the resulting competitive hierarchy. Underlined species do not differ significantly. P-values are given for non-significant differences, asterisks denotes that the species in the row has a significantly higher RYP-value than the column-species in interaction with the same, ** p < 0.01, *** p < 0.001.

	Lythrum	Cyperus	Juncus	Eleocharis	Mimulus	Verbena
Lythrum	–	0.62	**	**	***	***
Cyperus	–	–	0.10	***	***	**
Juncus	–	–	–	***	***	***
Eleocharis	–	–	–	–	0.72	0.15
Mimulus	–	–	–	–	–	0.19
Verbena	–	–	–	–	–	–

Hierarchy: Lythrum > Cyperus > Juncus > Eleocharis > Mimulus > Verbena.

Goldberg (1987) and Goldberg and Fleetwood (1987) have emphasized the two components of competitive ability: effect and response. These can both be extracted from our data. Table 2 shows, that mean response separates the species into two groups, with *Cyperus*, *Lythrum* and *Juncus* being less affected by other species than *Eleocharis*, *Mimulus* and *Verbena*. The values of mean effect shows a similar pattern: *Lythrum*, *Cyperus* and *Juncus* have a stronger suppressive ability than the other species. Among these species competitive effect therefore appears to be correlated with competitive response, although the sample sizes are too small for a meaningful test.

When testing for differences in relative yield between species for each species mixture separately, a transitive competitive hierarchy could be constructed (Table 3). *Lythrum*, *Cyperus* and *Juncus* have a greater competitive ability than *Eleocharis*, *Mimulus* and *Verbena*.

Discussion

Main tests

The relationships between intensity, asymmetry and similarity obtained in this study (Fig. 1) are consistent with the widely held view that similar species interact more intensely and with the prediction that similar individuals have more symmetrical interactions. To the best of our knowledge, this is the first experimental test of these ideas, although there are several descriptive and indicative studies pointing in the same direction (eg. Connell and Keough 1984, Connell 1986).

The results can also be considered as experimental support for coexistence through competitive equivalence (e.g. Aarssen 1983). Species close in competitive abilities in our study show more symmetrical interactions (Table 3 and Fig. 2). As Keddy and Shipley (1989) put it: "Similar species will coexist because interspecific competition is approximately equal to intraspecific competition, thereby weakening differential interspecific interactions, which lead to exclusion." This has also been indicated in other studies (e.g. Hubbell and Foster 1986, Goldberg 1987).

There are two general aspects of our methods which we also wish to emphasize. The first point is that the two proposed measures of the nature of a competitive interaction, intensity and asymmetry, can be independently derived and meaningfully evaluated from a pairwise mixture experiment. They reflect two different aspects of competition: Intensity, although being a relative measure, highly dependent on the size of the interactive space (or density of the individuals), is a good measure of the total reduction in yield in a competitive situation. Asymmetry, on the other hand, gives a measure of the skewness of the interaction. The importance of deriving such measurable state variables for testing general theo-

ries has been emphasized elsewhere (Peters 1980, Rigler 1982, Keddy 1987).

The second point to be made is that similarity can be measured by categorizing the interactions according to the species they comprise. The results show that at least three obvious categories are valid: Intraspecific, intra-guild and inter-guild interactions.

Guilds

Our test depends upon being able to classify similarity into the three categories mentioned above. This in turn depends upon the accuracy of the guild classification used (Boutin and Keddy, unpubl.). An argument for its validity is the large number of traits measured in the study, including many that are generally believed to be closely linked to competitive ability, such as height, above- and below-ground biomass, photosynthetic area etc. As well, the resulting classification is consistent with other published studies (e.g. Grime 1977, Givnish 1987, Grubb 1986, Day et al. 1988).

Our two guilds, however, were similar in many ways. The species are all ruderals and behave like annuals. Clearer results might have been obtained by using more different guilds, for example contrasting clonal dominants against obligate annuals. Our results clearly show, however, that these guilds are not separated by competitive ability (Tables 2 and 3). Guild identity is thus, in this study, not a good predictor for relative competitive ability. Therefore, one can not rule out the possibility that some crucial plant traits are left out in the guild classification, and that this classification is not the best for testing the hypotheses. We therefore invite other tests of these hypotheses using other guild classifications.

Design constraints

There are some clear advantages with a simplified experimental design as the one we have used, but also a few constraints: Firstly, there is a time aspect. Although both guilds behave like ruderals and annuals, the facultative annuals are truly perennials and their possible superiority might not be expressed during only one growing season.

Second, the plants in this experiment were grown pairwise in pots rather than in stands. Canopy was thus not continuous and side lighting can be assumed to have been important. The experimental design may therefore have exaggerated below-ground competition. Below-ground competition for resources is assumed to be mostly symmetrical in its nature, while above-ground competition for light produces asymmetrical interactions (e.g. Weiner 1986, Weiner and Thomas 1986, Wilson 1988, Thomas and Weiner 1989, but see also Wilson 1989). Consequently, asymmetry could have been un-

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derestimated, especially in the inter-guild interactions, where there were the most pronounced differences in plant height, a trait known to be closely correlated with competitive ability (e.g. Givnish 1982, Gaudet and Keddy 1988).

Conclusion

Testing general ideas requires measurable properties. Here we have tried to combine two measurable properties of competition, intensity and asymmetry, with a novel measure of similarity. The results are in accordance with both the niche control paradigm and the dominance control paradigm. Intensity increases with an increased similarity between competing species, while asymmetry decreases with an increased similarity between the plants. The generality of our results and conclusions can only be tested by using similar approaches in other plant communities.

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