The role of growth form and correlated traits in competitive ranking of six perennial ruderal plant species grown in unbalanced mixtures

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Abstract – The competitive abilities of six perennial ruderal plants of three different growth forms were compared via yield measures using an additive diallel experimental design with unbalanced mixtures (9:3 or 3:9 plants per pot, respectively). Thus, in a given mixture species A was grown in two configurations: three individuals in centre position of the pot together with nine plants of species B in border position and vice versa. Effect competitive abilities as well as response competitive abilities of the species were significantly related to canopy height and plant biomass. The species with lower rosette growth form and smaller biomasses were weaker competitors than the species possessing elevated canopies along with higher biomasses, whereas total leaf area was not significantly correlated with competitive ability between species. Species differences in competitive ability were stronger between the plants grown in the central position than between those grown in the border position. Furthermore, interactions between species-specific traits and configuration could be observed, indicating the importance of species proportions and arrangement patterns for evaluation of competitive outcome in the field. The degree of complete transitivity of the competitive network of the six ruderal species, which was significantly higher than expected under the null model in our experimental design, also seemed to depend on species proportions in mixture. Shifts in root:shoot ratio of the centre plants when faced with competition by the border plants were in the direction of higher shoot allocation for the weak competitors with rosette growth form irrespective of the neighbour species, except for *Bunias orientalis*, which showed a more plastic response. The stronger competitors showed higher root allocation (*Urtica dioica*) or were hardly affected at all. Consistent with the results of our experiment, the weaker competitors occur at rather frequently disturbed and therefore transient field sites whereas the stronger comp

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1. INTRODUCTION

Recent studies of competition within groups of naturally or potentially co-occurring plant species have led to the hypothesis that competitive hierarchies are common in herbaceous plant communities [19, 25]. There is also empirical evidence that major plant traits implicated in the occupation of space (e.g. height, total biomass) underly the competitive relationships [e.g. 7, 11, 23]. The findings have reopened the discussion on the predictability of species abundance in plant communities.

The hitherto existing studies on competitive hierarchies have been performed with species from ephemeral communities (annuals), crops or metastable plant communities (wetland communities, [chalk] grassland, pastures), but to our knowledge none of these have dealt with species from ruderal plant communities dominated by perennials. In nutrient rich ruderal habitats plant communities combine high productivity and variation in the competitive relationships due to continual or occasional disturbance and rapid successional changes [5]. The results of short-term competition experiments, therefore, may be more closely related to performance in the field for species occupying such sites than for species from metastable plant communities. Additionally, in most studies a more intense competition is hypothesized or has been found experimentally under conditions of high soil resource availability [e.g. 1, 2, 4, 13, 16, 29], particularly for light resources [e.g. 9, 27; see also 1]. Consequently, fast growing ruderal species which may prevail through several successional stages are well suited for comparative competition studies. A number of such species are increasing in abundance concomitantly with the expansion of anthropogenic disturbance [8, 15], thus enabling a comparison between experimentally obtained competitive hierarchies and observations of species performance in the field.

In this study we investigate competitive rankings, the transitivity of the competitive hierarchy and correlated plant traits of six perennial ruderal plant species. We also analysed changes in root:shoot ratios indicating shifts in competitive pressure [18]. The species we used experimentally are widespread (and expansive) in Europe and are often recorded as dominant in seral plant communities of disturbed sites [e.g. 5]. They were selected with respect to differences in growth form and in habitat preference concerning disturbance intensity in order to investigate whether there are interrelations between these differences and competitive rankings.

An additive diallel experimental design was chosen with unbalanced species ratios in the mixtures designed to reflect differing proportions of co-occurring species in plant communities and to compare the competitive abilities for each species when infrequent and when frequent. For that purpose, the species assigned to be infrequent was planted in the centre of a pot (three plants per pot) and was surrounded by a ring of nine plants of the species assigned to be the frequent species. In this way, the common field situation with patches of infrequent species situated in a matrix of frequent species should be simulated. For determination of competitive ability we distinguished between the effect and the response component [10, 11, 22], i.e. between the ability of plants to affect performance of neighbouring plants and their ability to tolerate competitive effects of neighbouring plants.

2. MATERIAL AND METHODS

2.1. Study species

The selected six species are similar with respect to general habitat preferences [6], but represent the most important morphological types of ruderal perennials: (i) dense rosette plants with sessile leaves (*Bunias orientalis* L. [Brassicaceae], *Cirsium vulgare* (Savi) Ten. [Asteraceae]), (ii) open rosette plants with long petiolate leaves (*Arctium tomentosum* Mill.[Asteraceae],

Rumex obtusifolius L. [Polygonaceae]) and (iii) multistemmed erect plants without rosettes (*Urtica dioica* L. [Urticaceae], *Artemisia vulgaris* L. [Asteraceae]). All species are 'nitrophilous', i.e. nutrient-demanding [5] with 'competitive - ruderal' or 'competitive' (*U. dioica*) life strategies according to Grime et al. [15].

2.2. Experimental

The experiment was run from March to August 1994. Fruits of *B. orientalis* had been collected from a single stand near Würzburg in September 1993. Seeds of the other species were obtained commercially (Bornträger GmbH, Offstein, Germany).

Seeds were germinated in a growth cabinet in mid March. The seedlings were grown on vegetable mould in a glasshouse (20 °C/10 °C day/night) for 3 weeks and then moved outside for an additional two weeks for adaptation to ambient weather conditions. After this pretreatment the juveniles of all species were well developed with similar sizes: rosette diameters of *B. orientalis, C. vulgare, A. tomentosum* and *R. obtusifolius* 7-10 cm and shoot lengths of *U. dioica* or *A. vulgaris* 5-8 cm. Thus problems with the use of yield measures for competition analysis due to initial size bias between competing plants in mixtures [12] were reduced.

On May 3 juveniles selected for healthiness and size homogeneity were planted in plastic pots. The species were arranged in three different configurations (I-III) as shown in *figure 1*. Configuration I denotes three individuals of a given species as 'centre' plants, whereas in II nine individuals of one species are arranged as 'border' plants (controls for additive aspects of the design). Configuration III is a combination of I and II with the centre and the border plants being different species. The contiguous neighbours of configurations II and III were spaced equally (7-8 cm). The distances between the centre plants were 12 cm. Each species was planted in configuration I and II (centre and border controls, respectively). Additionally, each species as the centre plant was combined



Figure 1. Plant configurations in the two monoculture controls (1 and II) and in the unbalanced mixture treatment (III). C, central plants; B, border plants.

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with each other species as the border plant (five treatments, configuration III). Thus, as six species were used in the diallel design, there was a total of 42 treatments. Each treatment was replicated three times, resulting in a total of 126 pots. The treatments were arranged as a randomized complete block design.

The plastic pots with a volume of 60 L (height 70 cm, diameter 36 cm; drain holes at the bottom sides) and filled with a bottom layer (10 cm) of gravel topped by a homogenous mixture (1:1) of loamy soil and quartz sand, were set up at a plain, sunlight exposed area in the Botanical Garden of Würzburg. Spacing between the pots was adjusted to avoid mutual shading between plants of adjacent pots.

The pots were watered daily except for periods with sufficient rainfall. Within the first two weeks a few fading juveniles were replaced. There was no additional mortality during the rest of the experiment. Two weeks after planting the pots were fertilized once with a solution (Wuxal NPK 12-4-6 [12 vol % N, 4 vol % P, 6 vol % K]; 2 mL per pot). At the end of May a depot fertilizer was added (Multicote N-P-K-Ca [12 % N, 12 % P₂O₅, 12 % K₂O, 8 % CaO w/w]; 40 g per pot). In order to prevent damage by pests (aphids) the plants were treated once with the systemic insecticide Metasystox in mid June.

The plants were harvested after a three month growth period at the beginning of August. Although the plants had already reached large sizes by this time, no roots penetrated through the perforations at the bottom sides of the pots. For the border plants only aboveground biomass was harvested, whereas total biomass was harvested for the centre plants (fine roots omitted). Total leaf area of the centre plants was measured with a leaf area meter (Li Cor 3100, Nebrasca, USA). Dry mass of plant shoot or root material was determined after oven-drying (70 °C, 72 h).

2.3. Analysis

Effect competitive abilities can be compared between neighbour species when effects of these species on the same target species are measured, whereas comparison of response competitive abilities of different target species requires the measurement of their response to the same neighbour species [see 11, 22]. Mean effect competitive ability C_{ej} of neighbour species j was calculated for every species (n=6) using the following equation:

$$\bar{C}_{ej} = 1 - \frac{1}{n} \left(\sum_{i=1}^{n} \frac{y_{ij}}{y_{i0}} \right)$$
(1)

where y_{ij} is the mean aboveground dry mass (per individual) of the target species *i* grown with neighbour species *j* and y_{i0} is the mean aboveground dry mass

(per individual) of target species i in the control treatment without neighbour plants, both measured at harvest time. The quotient of y_{ij} and y_{io} will therefore be termed 'proportional yield' in the following text. Due to our unequal mixture design both possible proportions of the two species in mixture (species *i* in central position, species *j* in border position and vice versa) were separately calculated.

The mean response competitive ability C_{ri} of target species i was calculated analogously:

$$\bar{C}_{ri} = \frac{1}{n} \sum_{i=1}^{n} \frac{y_{ij}}{y_{i0}}$$
(2)

again for both possible proportions of the two species in mixture in separate analyses. For comparative reasons, i.e. for an identical calculation of mean competitive effect and mean competitive response based on the same set of (six) competing species including the species under consideration, the results from the 12:0 monoculture treatment were needed for each species. Unfortunately, this set of data was missing. Therefore, the y_{ii} values for *i* and *j* being the same species A (12:0 monoculture) were approximated as follows: the differences between the y_{ij} values of species A when grown in mixture with the other species and the mean (experimentally obtained) y_{ii} values of all other species grown in the same respective mixtures were averaged and the so-obtained mean difference value added to the mean y_{ii} value of all other species grown in mixture with species A. The resulting y_{ii} value therefore represents the amount of reduction of the aboveground biomass of species A when grown in mixture with itself estimated by derivation from all other experimentally found values. As this procedure can only estimate the true values which would have been obtained by analysis of the 12:0 monocultures a certain degree of inaccuracy is necessarily introduced in the mean response and effect competitive abilities. However, both parameters were calculated from five true and only one estimated y_{ij} values. Therefore, the reliability of the obtained mean competitive abilities should not be severely affected.

The Kruskal-Wallis test was used to test for global differences between the species concerning mean competitive effect and mean competitive response, respectively. Randomization tests [21] were performed to determine whether the mean competitive effect or the mean competitive response of a single species departed significantly from the average value of all species. For that purpose six values were randomly drawn from the population of effect or response competitive ability values from all species 4 999 times. The mean of each set of six values was then calculated yielding a distribution of 5 000 means (including the observed value). The number of means with equal or

greater absolute value than the observed mean within the random distribution was then determined and the error probability of rejecting the null hypothesis calculated by dividing this number by 5 000. Application of 5 000 permutations results in estimated significance levels of 0.042 < P < 0.058 in 99 % of the time when the true significance level of the observed value is 0.05 [21] and is therefore highly accurate.

Significance of differences between root:shoot ratio of the central plants grown in monoculture and root:shoot ratio of the central plants grown in mixture with the border plants was tested with a two-sample randomization test [21] again performing 4 999 randomization runs. For the clonal species *U. dioica* rhizomes were subsumed under 'roots'.

Statistica for Windows (Statsoft, Inc. 1995, Tulsa, OK) was used for all analyses with values of P < 0.1 regarded as marginally significant and values of P < 0.05 accepted as significant.

The transitivity of the competitive hierarchy between the six species was analysed according to Shipley [24]. The rationale of transitivity analysis is to investigate the extent of consistent competitive hierarchies between the species included in a diallel competition experiment or within subsets of these species. For that purpose a quadratic binary matrix is constructed with row and column number being equal to the number of species. Thus, for each pairwise species mixture (AB) there are two values in the matrix (species A in row head, species B in column head = ABand vice versa = BA). The outcome of the competition experiment for each pairwise species mixture is then coded for the matrix as follows: if species A performs better when grown with species B than when grown in monoculture, AB is set to 1, otherwise it is set to 0. Likewise, if species B performs better in mixture with species A then when grown with itself, BA is set to 1, otherwise it is set to 0. In this way, there are four possible competitive relationships between two species AB: 1,1; 1,0; 0,1 and 0,0. In essence, after construction of the binary matrix, transitivity analysis determines how many completely transitive paths of different lengths exist in the binary matrix and whether the obtained numbers deviate significantly from the null hypothesis. Completely transitive paths (networks) of different length are consistent competitive hierarchies in species subsamples of different size. For example, if AB = 1 and BA = 0, then this represents a completely transitive path of length 1. If, in addition, BC = 1; CB = 0; AC = 1 and CA = 0 this would be an example for a completely transitive path of length 2. The criterion for the existence of a completely transitive path of a given length is that there is a competitive dominant and a competitive subordinate species in all pairwise competitive relationships and that there are no reversals in rank structure between the species

included in the path. The rank structure may be depicted graphically (e.g. *figure 6*). The null model involves the calculation of the number of completely transitive paths from random distributions of the 0's and 1's in the binary matrix. For further explanation of the parameters determined in transitivity analysis see *table 1*. Details on the method are given in Shipley [24].

Shipley [24] used a comparison between even mixtures of two species and the respective monocultures (replacement designs). We based the analysis on the species mixtures of configuration III (figure 1), treating the higher intensity of interspecific competition for a species grown in central position (C) as 'mixture' and the higher intensity of intraspecific competition for a species grown in border position (B) as 'monoculture'. Therefore, if average performance (per individual aboveground biomass at harvest time) of a species in central position of a given mixture was better than in border position, the corresponding coefficient in the binary matrix was set to 1, otherwise it was set to 0. The binary matrix was then analysed with the help of a computer program which identifies all completely transitive paths and calculates the relevant probabilities given the null hypothesis [24].

3. RESULTS

3.1. Competitive ability and correlated traits

The mean competitive effects and responses of the six species (*figures 2* and 3) differed significantly between species (P<0.05) for the border plants and highly significantly (P<0.01) for the central plants. Average competitive ability was higher for the border plants due to the fact that nine border plants affected only three central plants whereas the reversed proportion holds for central plant competitive ability.

The results shown in *figures 2* and *3* demonstrate a significant positive correlation of mean effect and response competitive ability with plant species height ranking at harvest time for central plants (Spearmans r = 0.89 in each case, P < 0.02). For the border plants this correlation is only marginally significant for effect competitive ability (r = 0.72, P < 0.08) and not significant for response competitive ability (r = 0.66, P > 0.15).

The low-growing rosette plants generally showed reduced competitive abilities when compared to the average. Whereas *C. vulgare* showed significantly or marginally significant lower competitive abilities only in the central position (P<0.02 and P<0.07, respectively), *B. orientalis* was a below-average competitor when grown as a border plant (P<0.02) but not significantly so when grown as a central plant (P>0.2). In contrast to *A. tomentosum*, which likewise showed a



Figure 2. Mean effect competitive ability of the six ruderal plant species as (subordinate) central plants (A) or as (dominant) border plants (B). Plant species are ordered from left to the right according to canopy height. White bars, dense rosette plants; light gray bars, open rosette plants; dark gray bars, erect plants. Species abbreviations (range of canopy heights): Cv, C. vulgare (10-20 cm); Bo, B. orientalis (20-40 cm); At, A. tomentosum (25-40 cm); Ro, R. obtusifolius (30-50 cm); Ud, U. dioica (50-90 cm); Av, A. vulgaris (100-170 cm). Asterises denote significantly positive or negative deviation from the average effect competitive ability of the six species represented by the dashed line; m denotes marginal significance. Error bars indicate the range of effect competitive ability values.



Figure 3. Mean response competitive ability of the six ruderal plant species as (subordinate) central plants (A) or as (dominant) border plants (B). The dashed line denotes the average response competitive ability of the six species. Other parameters as in *figure 2*.

trend for below-average competitive ability, the other petiolate leaved rosette plant, *R. obtusifolius*, showed strong competitive ability, though only marginally significant for effect competitive ability in the border position and response competitive ability in the central position (P<0.09). The two erect plants both showed above-average competitive ability. Whereas *U. dioica* was a marginally significant stronger competitor only for response competition as a border plant (P<0.07), *A. vulgaris* proved to be a superior competitor (P<0.05) except for an only average response competition performance in the border position (P>0.7).

Proportional yield (above-ground biomass) of the species in the border position is shown in relation to mean species-specific biomass of the central plants (*figure 4*) and in relation to mean species-specific total leaf area of the central plants (*figure 5*). The species as border plants showed exponentially decreasing proportional yield with increasing central plant biomass.

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A. vulgaris consistently showed stronger competitive ability than would have been expected by regression on its mean leaf area values (*figure 5*). R. obtusifolius exhibited opposite departures from the regression lines for leaf area but per biomass effects were uniformly stronger than predicted by the respective regressions. Thus, species-specific traits added to the explanation of competitive ability.

Between 81 and 98 % of the variances of the log-trans-

formed proportional yield of the border plants grown

in mixture were explained by linear regression on spe-

Proportional yield of the border plants also

decreased linearly with species-specific total leaf area

cies-specific central plant biomass.



Figure 4. Proportional yield of the border plants in dependence on species-specific mean total biomass of the central plants. Symbols for the central plant species are: triangle, C. vulgare; filled circle, B. orientalis; diamond, A. tomentosum; open circle, U. dioica; square, R. obtusifolius; cross, A. vulgaris. Error bars indicate \pm S.E.

3.2. Transitivity

The analysis of the binary matrix for complete transitivities comparing plant performance in the border position (higher intraspecific competition) with plant performance in the centre position (higher interspecific competition) yielded more asymmetric and completely transitive paths than expected by the null model (*table I, figure 6*). The occurrence of six completely transitive paths of length L = 2 was significantly greater than the corresponding expected value. The occurrence of a transitive path of length L = 3 is marginally significant (P = 0.060). Of a possible 15 pairwise interactions (L = 1), 10 were asymmetric, although this number was not significantly different from the expected one. A. vulgaris was involved in 3 out of the 5 interactions which were not asymmetric (figure 6). Although A. vulgaris was generally a superior competitor (see the results for competitive effects and responses) in all of these interactions either species involved showed higher performance in the central position. B. orientalis and A. tomentosum as competitors of similar strength also showed mutually higher performance in mixture when grown in the centre position. Contrastingly, A. tomentosum and C. vulgare, which had similar competitive ability both showed weaker performance in the centre position when grown in mixture.

3.3. Effects of competition on root:shoot ratio

The weak competitors, C. vulgare and A. tomentosum, had a considerably lower root:shoot ratio



Figure 5. Proportional yield of the border plants in dependence on species-specific mean total leaf area of the central plants. Symbols for the central plants as in *figure 4*. Error bars indicate \pm S.E.

Table I. Results of the transitivity analysis.

L	δ(L)	T(L)	μ(L)	m(L)	$P(\geq m(L))$
1	0.48	15	7.231	10	0.117
2	0.083	20	1.692	6	0.035
3	0.005	15	0.073	I	0.060

According to Shipley [24] L denotes completely transitive paths of various lengths, $\delta(L)$ is the probability of a completely transitive path of length L occurring under the null hypothesis, T(L) is the maximum number of completely transitive paths of length L in the binary matrix, $\mu(L)$ is the expected number of completely transitive paths of length L given the null hypothesis, m(L) denotes the corresponding observed number of the respective paths and $P(\ge m(L))$ is the probability of a contract of a tleast m(L) completely transitive paths given the null hypothesis. The probability of a randomly chosen species A performing better as a central plant when in mixture with a randomly chosen species B than as a border plant (Θ) = 18/30.

(25-60 % of the control ratios) in almost all of the different mixtures with border plants (*figure 7*). B. orientalis, on the other hand, showed a marginally significant lower root allocation (P < 0.07) only when grown in mixture with the strong competitor *R. obtusifolius*. Competition with the weak competitor *C. vulgare* and



Figure 6. The signed directed graph of interactions between the six species. When species A shows higher performance as the (subordinate) central plant in a given pairwise mixture with species B than it does in the (dominant) border position, a solid arrow points from species A to species B. In the reversed case (species A showing weaker performance as the central plant than it does in border position), a dashed arrow points from species A to species A to species B. Species abbreviations as in *figure 2*.

with A. vulgaris caused a proportionately higher root growth for this species (P<0.05). The more intermediate competitors A. tomentosum and U. dioica hardly changed the root:shoot ratio of B. orientalis.

Root:shoot ratio of the strong competitors R. obtusifolius and A. vulgaris were at most weakly, though not significantly, affected by border plant competition. Both showed a slight tendency for a higher root allocation when faced with the weak competitors. Due to high variation between individuals of U. dioica only differences in root:shoot ratio when grown together with the strong competitors R. obtusifolius and A. vulgaris (by about + 75 to 100 % of the control ratios) were significant or marginally significant (P<0.04 and P<0.08, respectively). Even so, the average competitor U. dioica exhibited a consistent trend for higher root:shoot ratios in all pairings with border plant species.

4. DISCUSSION

The results show clearly that both competitive effect and response rankings of the species are linked to plant biomass and canopy height (*figures 2, 3* and 4), i.e. the weaker competitors consistently were the species with the (lower) rosette growth form along with smaller biomasses whereas the stronger competitors showed elevated canopies together with higher biomass values. These findings conform with results from other studies showing clear relationships between shoot height and/or biomass and competitive ability [3, 7, 32], irrespective of the neighbour species.

Leaf area, on the other hand, was more loosely related to competitive ability mainly because of the greatly differing shoot morphologies of the species and because of the species-specific ratios of above- to belowground competition. This was best seen when the two strongest competitors, *R. obtusifolius* and *A. vulgaris*, were considered. Except for the mixture with the overtopping species *A. vulgaris* as a border plant, the particularly high leaf-area to biomass ratio of *R. obtusifolius* coupled with its relatively low canopy height apparently led to additional ability for light competition when grown in mixture with species of lower or comparable canopy height.

On the other hand, A. vulgaris showed strikingly stronger competitive ability as would have been expected by its comparatively low total leaf area along with its elongated and elevated canopy allowing relatively high light access to the lower canopies of the

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other species in mixture. Thus, it can be assumed that *A. vulgaris* was a belowground competitor in the first hand. The weaker competitors *C. vulgare*, *B. orientalis* and *A. tomentosum* in most cases showed slightly less competitive ability than would have been predicted from their total leaf area values, a finding that can be explained with their low canopy height.

4.1. Effect and response competitive ability

Species differences in effect and response competitive ability between weak and strong competitors were more pronounced in the central position (i.e. when subordinate) than in the border position (figures 2 and 3). This was most likely due to the higher degree of 3intraspecific competition among the border plants (due to higher plant density per pot as compared to the central plants), partly buffering the differences in competitive ability between the species. For response competitive ability in border plant position this effect seemed to be so strong that there were no differences between C. vulgare and A. vulgaris although these species showed profound differences in the central plant position. In addition, an edge effect of increased light availability for the border plants may have contributed to the weaker differences in competitive ability among the border plants, whereas for belowground competition similar edge effects were largely eliminated by the intensely mixed root systems of the species irrespective of planting position. The relatively high competitive ability of *C. vulgare* in the border plant position could have been caused by such configuration effects, which are confounded with plant density in our design: the low growing rosette leaves of this species when grown in the centre position specifically suffered from light competition by the surrounding ring of neighbours contrasting to the improved light conditions experienced by this species when grown in border position. The other two weak competitors, A. tomentosum and B. orientalis, which showed no such distinct competitive ability in dependence on the configuration, produced long petiolate leaves or reacted with increased leaf angles, respectively. When grown in the centre position they therefore partly escaped inhibiting competition. Thus, differences in competitive abilities between species may vary considerably with species dominance and arrangement patterns in the field. Especially in ruderal plant communities, which are generally patchy and locally disturbed, configuration and edge effects may be important determinants of competitive interactions between species.

The striking similarity of competitive effects and responses of the same species in the same position and density, especially for the centre plants (*figures 2A* and 3A) implies strong size-symmetrical competition. This means that resource preemption by the central (target)

plants clearly was more important for response competitive ability than tolerance of depleted resources by the border (neighbour) plants [11]. The latter component could have been crucial for response competitive ability had the target species been smaller than the neighbour species at the onset of the experiment [9]. Other studies have found positive relationships between effect and response competitive ability [e.g. 10, 22] or no significant correlation between those two components [11, 20] as is assumed for size-asymmetrical competition [11]. In our design all species in mixture were approximately evenly sized at the beginning. Thus, species that grew faster initially or that had already developed growth form characteristics conferring competitive advantages (e.g. elevated canopies) before resource competition became intense, had the chance to pre-empt resources more efficiently leading to the observed concordant rankings in response and effect competitive abilities.

4.2. Transitivity

Despite the considerable weaker contrast between the 3:9 and 9:3 mixtures (centre:border plants in a given two-species mixture) as compared to the usual monoculture:mixture contrast applied in transitivity studies there was still evidence for complete transitivity in the competitive network of the six ruderal species. This is consistent with the pronounced differences in competitive ability between most of the species and confirms the hypothesis that (morphologically) dissimilar species tend to predominantly form completely transitive networks [19].

Hence, it was not surprising that non-asymmetric interactions in the network were restricted to the morphologically or competitively similar species pairs B. orientalis/A. tomentosum, C. vulgare/A. tomentosum and A. vulgaris/R. obtusifolius. More striking was the double occurrence of a non-asymmetric interaction between the potent competitor A. vulgaris and the inferior competitors A. tomentosum or B. orientalis, respectively. The fact that the latter species performed better when grown together with nine border plants of the strong competitor than when only three of them were present was probably caused by the apparent ability of A. vulgaris plants to efficiently deplete water or nutrient resources. If true, there was little additional negative effect of further six individuals of A. vulgaris, in fact, partial relief could occur from intraspecific competition for the other species in mixture. This assumption is strengthened by the observation that A. vulgaris individuals grown in border position were substantially reduced in size as compared to individuals grown in centre position. Therefore, these non-asymmetric interactions may in a sense be artefacts due to capacity limitations of the pots used in the experiment.



Figure 7. Differences in root:shoot ratio between the central plants of the controls and the central plants of the same species grown in mixture with the border plants of the other species. The differences are shown as % values of the controls. Abbreviations for the border plants as in *figure 2*. The error bars indicate \pm S.E. of differences from the mean value of the control plants.

A comparison between the high density monoculture treatment and the 3:9 mixture would have yielded a considerably stronger completely transitive network: if one estimates aboveground performance of the six species in the hypothetical 12:0 monoculture treatments from the known values of all mixture treatments (data not shown), the resulting transitive network between the six species would include 13 completely transitive paths of length 1, 10 completely transitive paths of length 2 and 4 completely transitive paths of length 3 when compared with the 3:9 mixtures (the species under consideration being the central plant). On the other hand, distinct configurations with the proportions of plants in mixture held constant might also have an effect on the transitivity of the competitive network (see the discussion for *C. vulgare* above). Future investigations of the consequences of varying proportions and configurations of plants in mixture in diallel experiments for the transitivity of competitive networks could further improve our ability to predict the outcome of competitive interactions between co-occurring species in the field.

4.3. Root:shoot ratio

For the centre plants shifts towards higher root allocation clearly was related to elevated canopies, i.e. to reduced light competition, but also varied with the intensity of interspecific competition. Thus, among the species with erect stems or elevated canopies only *U*. *dioica* showed a considerably higher root:shoot ratio indicating that this species was more affected by interspecific competition in mixture than *A. vulgaris* and *R. obtusifolius*, which showed only a slight tendency for higher root allocation. Conversely, the weak competitors with low canopy height except for *B. orientalis* reacted with higher shoot allocation indicating prevalent aboveground competition [10].

Shifts in root:shoot ratio were more consistent among the centre (target) plants than within the neighbour plants. C. vulgare, for instance, showed a relatively constant allocation pattern even when mixtures with the strong belowground competitor A. vulgaris were compared with those of the strong aboveground competitor R. obtusifolus. This target species-specific allocation pattern towards shoot allocation may partly be explained by the low rosette growth form of C. vulgare, which particularly suffers from light competition. Another argument may hold for the rhizomatous species U. dioica, which was relatively invariable in higher allocation to roots, irrespective of the neighbour species. Besides being partially relieved from light competition by its erect stems, U. dioica might generally allocate more resources to rhizomatous growth to escape local crowding. At the other extreme, B. orientalis represented the species which was most prominently neighbour-specific in allocation pattern. The profound plasticity of *B. orientalis* leaf growth with respect to leaf length and leaf angle may explain its proportionately higher shoot allocation when mixed with the potent light-competitor R. obtusifolius as opposed to the (relatively) weak light competitors C. vulgare and A. vulgaris. R. obtusifolius and A. vulgaris, though only weakly affected, possibly also had the tendency for an allocation pattern following the relative intensities of aboveground competition.

Thus, although relative allocation to roots or shoots seemed to depend upon the proportion of above- to belowground competition in the first hand [see also 10, 17, 30 and references therein], inconsistencies within neighbour plant species must be considered that may be related to species-specific plant traits and to habitat-adaption of the target plants.

In occasionally disturbed ruderal habitats competitive dominance may typically be only partly realized [14]. Furthermore, our results suggest that competitive relationships between species may respond considerably to variations in configuration and density proportions of the species which are particularly important in ruderal habitats due to their generally pronounced spatial heterogeneity of vegetation structure. For these reasons the question arises as to what extent experimentally found largely consistent competitive hierarchies, as obtained for the species in our study, can contribute to the explanation of species abundancy in the field. To date there are few data available which are relevant to this question [c.f. 23]. In our case field observations of variation of species frequency in dependence on habitat disturbance correspond with species ranking in our experiment. Consistent with their weak competitive ability and their short life-span as monocarpic perennials, A. tomentosum and C. vulgare most frequently occur in disturbed and transient habitats as pioneer species. Within the CSR model of plant strategies [14] these two species therefore mainly represent the ruderal strategy. However, as both species are most frequent in habitats with high nutrient availability, the observed higher shoot allocation when affected by competition may be crucial for assuring the capture of sufficient energy for reproductive success even in the early stages of succession. The pronounced plasticity of root:shoot allocation together with a comparatively high growth rate [26] lends B. orientalis some traits of the competitor strategy. These traits may in part compensate for its lack of competitive strength resulting from its low canopy height and may contribute to explain its persistency as a polycarpic perennial even in less disturbed sites [26, 28]. The other three long-lived species are most widespread in occasionally disturbed habitats, where all of them can dominate during several phases of succession. This agrees well with the observed competitive strength. In contrast to the other species all of them show one of the most important characteristics of the competitor strategy, i.e. high and/or dense leaf canopies [14]. In addition, U. dioica features lateral spread by clonal growth which, together with high competitive ability, may explain its potential to form large dominance stands even in late successional herbaceous plant communities.

5. CONCLUSIONS

The results of our study support the propositions of Keddy and Shipley [19] on general patterns in both transitivity of the competitive network and relations between competitive ranking and plant traits. They also suggest changes in the performance of the competing species with variation in proportion or configuration of the competitors. Although the outcome of the competition between a given set of interacting plants depends upon a variety of additional factors not addressed in this study [see 31] the results may directly pertain to evaluation of competition in the field. The competitive ranking obtained for our set of species agrees well with their performance in widespread ruderal plant communities. The competitively subordinate species generally occur at rather frequently disturbed sites in early secondary succession, whereas the competitively superior species predominate at occasionally disturbed sites in both longer lasting and later phases of ruderal succession.

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