INFLUENCE OF WATER AVAILABILITY ON COMPETITIVE INTERACTIONS BETWEEN PLANT SPECIES ON SANDY SOILS

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Abstract: The gravimetric soil water content of four different successional stages of inland dune vegetation revealed pronounced seasonal changes and particularly a major drought period in the late summer. In order to analyze the effect of these seasonal water changes on the competitive interactions of two dominant species (*Carex arenaria* and *Deschampsia flexuosa*) in one of these stages root development was compared under experimentally manipulated water conditions in a minirhizotron experiment. Under well-watered conditions, the root growth of *C. arenaria* and *D. flexuosa* was not influenced by competition, but was significantly reduced for *C. arenaria* at low water availability. Accordingly, the relative yield based on total biomass was significantly lower under water shortage than under well-watered conditions for *C. arenaria*, indicating higher interspecific competition compared to intraspecific competitive interactions. These results indicate (i) that soil water status is an important factor for belowground competitive interactions and (ii) that seasonal changes in soil water content may have a pronounced effect on the outcome of competition and, in consequence, on the structure of the respective plant communities.

INTRODUCTION

In terms of community dynamics, competition is one of the most important factors for the formation of different successional stages (BAZZAZ 1996). Competitive relationships are known to depend on water (MARTENS et al. 1997, BERTILLER et al. 1996), light (BEYSCHLAG et al. 1990, 1992, DEAR et al. 1998, JOHNSON et al. 1998) and nutrients (LANDHAUSSER & LIEFFERS 1998, CALDWELL et al. 1996) as well as the species and growth form of neighbouring plants (BAZZAZ & GARBUTT 1988, BAZZAZ 1990, TREMMEL & BAZZAZ 1993). Under nutrient-limited conditions, however, competition between plant species is known to occur predominantly belowground (KLIMEŠ & KLIMEŠOVÁ 1994, VILA 1997, BONIS et al. 1997, CASPER 1997).

Previous studies on sandy soils indicate that water availability plays an important role in the outcome of competition between plant species (BERTILLER et al. 1996, COLLET et al. 1996, SINGH et al. 1998). Plant communities on these nutrient-poor sandy soils of inland dunes often form characteristic successional stages on a rather small spatial scale. Patches of bare soil are initially covered by pioneer plants able to fix the sand before mosses and mainly

grasses take over as dominant species (*Polytrichum piliferum* SCHREB. ex HEDW., *Carex arenaria* L., *Deschampsia flexuosa* (L.) TRIN., *Agrostis capillaris* L., *Festuca ovina* L.).

On inland dunes we observed a high mortality of one dominant species (*Carex arenaria*) during the late summer in 1996 and 1997 in an early successional stage while other plants were not obviously influenced. NOBLE et al. (1979) also noticed a high mortality of *C. arenaria* in the summer. As a rule we observed that ramets of *C. arenaria* died while the genet survived and spread out again in the following spring. In contrast *D. flexuosa*, another common plant on inland dunes, seemed capable to extend its cover more constantly, showing the highest mortality in winter. These growth patterns resulted in a rather patchy distribution of both species on a very small spatial scale in the field. So the dominance of a species is restricted to a grid of about 1 m and at the edge of a clonal patch the other species becomes dominant.

For a better understanding of the processes leading to the observed vegetation patterns, we analyzed the influence of water availability on the belowground competition of two dominating grass species *Deschampsia flexuosa* and *Carex arenaria* in one of the occurring successional stages, a species-poor dry grassland. We hypothesize that short-term seasonal changes in soil water content strongly influence competitive relationships and therefore the structure of these grassland communities.

METHODS

Study site

The study area is located 20 km south-east of Bielefeld (Northern Germany) in an inland dune area called "Senne" (08° 41' E, 51° 55' N). This ecosystem is predominantly afforested with pines, but open areas are covered with different successional stages of plant communities typical for sandy soils.

Soil water content

Besides sampling in a dry grassland (with *Carex arenaria* L., and *Deschampsia flexuosa* (L.) TRIN.) we determined the gravimetric water content in bare sandy soil, a pioneer plant community dominated by *Corynephorus canescens* (L.) P. BEAUV. and *Spergula morisonii* BOREAU, and a heathland community with *Calluna vulgaris* (L.) HULL and *Molinia caerulea* (L.) MOENCH to test for seasonal similarities in water content between different stages. Samples were taken monthly and always in the first week of the month from July 1997 to May 1998 (except for November 1997). Composite samples from 5 individual cores were taken at predawn from 5 sites per stage with a ground auger (diameter 5 cm, length 30 cm).

The species

Two dominant species of early successional stages on inland dunes were used for the minirhizotron experiments: (1) *Carex arenaria* (*Cyperaceae*), the sand sedge, is a sympodial rhizomatous plant and forms an extensive perennial rhizome system with deep roots of about two and more meters. (2) *Deschampsia flexuosa* (*Poaceae*), the wavy hair-grass, is a perennial thicket grass with a rooting depth of about 30 cm. Both species are common on inland dunes in Northern Germany.

Minirhizotron experiment

Belowground competition between *C. arenaria* and *D. flexuosa* was experimentally assessed in minirhizotrons (height: 30 cm, width: 50 cm, depth: 3.5 cm) filled with 5.25 dm^3 sand. The experiment lasted one month. The total nitrogen content of the substrate was similar to the field situation (< 0.005% N).

Experimental plants for the present investigation were obtained through vegetative multiplication from one genet of both species originating from the inland dunes near Bielefeld (geographical co-ordinates: 08° 41' 17" E, 51° 55' 04" N). The clonal fragments used consisted of one ramet (*C. arenaria*) and respectively five ramets (*D. flexuosa*) with a rooted rhizome of 10 cm in length and a fresh weight of 1g. A replacement design was used for the experiment. For the mixture treatment one ramet of *C. arenaria* and one ramet of *D. flexuosa* were planted in a minirhizotron. For the monoculture each minirhizotron contained two ramets of each species. Plants were grown under two different water treatments: (1) high water: plants were watered every second day up to field capacity and (2) low water: plants were watered up to field capacity only once at the beginning of the experiment (1st July 1997). Consequently the water availability in the low water treatment decreased steadily and was the limiting resource for plant growth. The use of deionized water for irrigation made sure no further mineral nutrients were added and measurements of the nitrogen content of the substrate showed no difference between the high and low water treatment. We used four replicates in each treatment. The minirhizotrons were kept in a growth chamber under an angle of 30° so that roots could hit the glass wall. The plants were grown under the following conditions: temperature: day 20 °C and night 15 °C; dewpoint of the air: day 12 °C and night 12 °C; light intensity (12 hours a day): 550 ± 50 µmol PAR $*m^{-2}*s^{-1}$. Root growth was analyzed every third day by means of image analysis with the software Adobe Photoshop[TM] 3.0 (Adobe Systems, Inc., 1994, U.S.A.). For this purpose the root system was photographed at a distance of 50 cm with a piece of a graph paper fixed at the glass-disk of the minirhizotron. All roots of a plant and therefore the summarized root-length values from the resulting digital images were expressed in cm relative to the grid of the attached graph paper. The different colours of roots of *C. arenaria* (white) and *D. flexuosa* (brown) made it easy to differentiate between the two species. After 30 days, plants were harvested. The measurement of the total root length of harvested plants showed no significant difference when compared to root length measured by means of image analysis from photos taken immediately before harvesting. Apart from determining total root length by means of a scanner (Scan Jet Iicx, Hewlett Packard, U.S.A.) and a root analyzing program (DIAS, Delta-T Devices Ltd., England), the above- and belowground biomass of harvested plants was measured.

Data analysis

By using a replacement design with one plant of each species in a mixture and two plants of a species in a monoculture, we compared the ratio of intraspecific to interspecific competition. According to HARPER (1977) the appropriate analysis is to calculate relative yield (RY) per plant for each species:

$$RY_{ij} = Y_{ij} / (Y_i)$$

and the relative yield total (RYT) for the mixture:

$$RYT = RY_{ij} + RY_{ji}$$

where Y_{ij} is the average summarized root length of one plant from species i grown in a mixture with one individual of species j and Y_i is the average summarized root length of two plants of species i in a monoculture. Hence the RY for a species will equal 0.5, if there is either absolutely no competition or if intra- and interspecific competition have precisely the same effect.

Statistical analyses were carried out with STATISTICA for Windows (Version 5.0, StatSoft, Tulsa, U.S.A.). Differences between the biomass data of the treatments in the minirhizotron experiments were tested with an ANOVA. The non-destructive measurements of root length over time in the minirhizotrons were tested with a one-way within-subjects (repeated measures) ANOVA (within factor: date). Differences in the water availability between the 4 successional stages were tested with an ANOVA and changes in water availability in time were tested with a one-way within-subjects (repeated measures) ANOVA (within factor: date). Post hoc comparisons of means were generally done by means of an LSD-test. To test for significant differences between RY/RYT and the fixed theoretical values of 0.5/1.0 we calculated the probabilities of deviations for small samples (PARKER 1979, BORTZ 1999). If assumptions of normality and homogeneity of variances were not satisfied, we used log transformed data for the analysis.

RESULTS

Soil water content

Measurements of soil water content showed pronounced seasonal changes within four different successional stages (open sand, pioneer plant community, dry grassland, heathland community) in the field (Fig. 1). In all stages less precipitation and continuously high temperatures resulted in a period of water shortage during the late summer. This seasonal course was most obvious in the heathland community where dense vegetation additionally led to high transpiration (Fig. 1). Moreover the average soil water content was significantly different between these stages (ANOVA, $F = 69.82$, $\text{d.f.}_{effect} = 3$, $\text{d.f.}_{error} = 148$, $P < 0.001$) and rose continuously with increasing vegetation cover from the bare sandy soil to the pioneer plant community, the dry grassland and finally the heathland community.

In the dry grassland, where *C. arenaria* and *D. flexuosa* predominantly occur, the soil water content was significantly lower in August, September and October (ANOVA; $F = 33.72$, $\text{d.f.}_{effect} = 9$, $\text{d.f.}_{error} = 18$, post hoc $P < 0.05$) as compared to the rest of the year (Fig. 1). After the beginning of September the soil water content rose again and strongly increased during the winter months. Hence, for at least 2 months this plant community experienced a significant drought period.

Root length

In general the minirhizotron experiments revealed a considerable effect of water shortage on both species. In *C. arenaria* as well as *D. flexuosa* water deficiency caused a significant reduction of root length when compared to well-watered plants for both the mixture treatment and the monoculture (ANOVA, $F = 15.84$, $\text{d.f.}_{effect} = 1$, $\text{d.f.}_{error} = 24$, $P < 0.001$, Fig. 2). After 30 days at low water, root length was reduced to approximately one third of that of the watered plants (Fig. 2).

Under well-watered conditions, root growth of *C. arenaria* and *D. flexuosa* was not different between monocultures and mixtures (Fig. 2A and C).
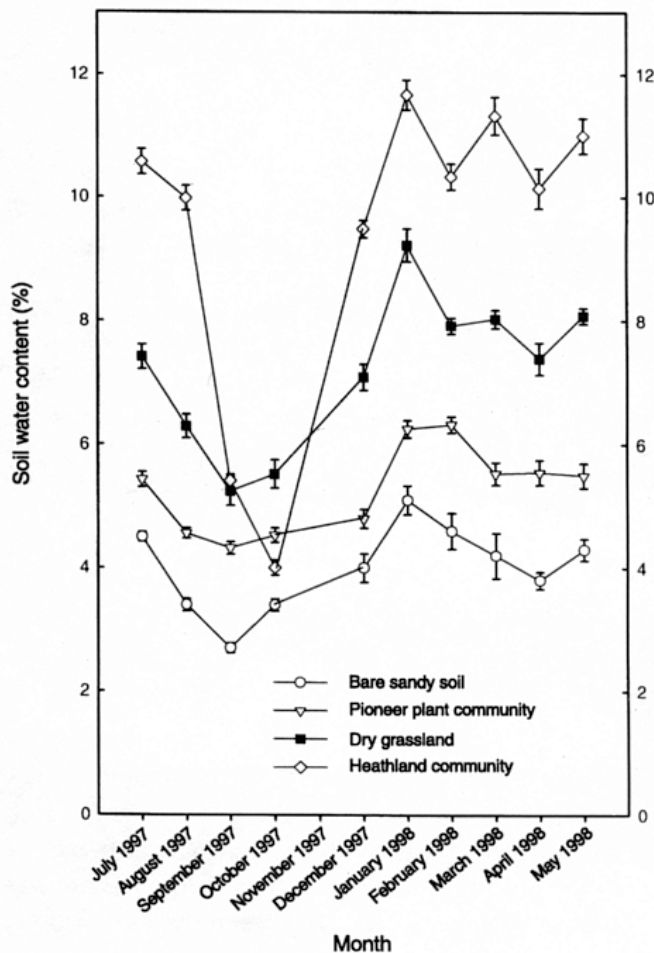
At the end of the experiment, under low-water conditions in the mixture, the root length of *C. arenaria* reached only 50% of the monoculture (Fig. 2B). In *D. flexuosa* the reduction of root length in the mixture as compared to the monoculture was not as pronounced at the end of the experiment (Fig. 2D). Here, however, the extremely low values of root length might have highly increased the influence of methodical constraints.

Root/shoot ratio and biomass

The results of the root-biomass measurements generally redraw the picture gathered by means of root length measurements. The root biomass of *C. arenaria* was significantly higher than that of *D. flexuosa* for both the control and mixture treatments (ANOVA, $d.f._{effect} = 1$, $d.f._{error} = 24$, $F = 30.28$, $P < 0.001$). There was one exception if treatments were directly compared: under low water availability and in competition the root biomass of *C. arenaria* was significantly reduced when compared to the control (ANOVA, post hoc, $P < 0.05$, Fig. 4). Moreover, the root biomass of *C. arenaria* was significantly lower under low water availability in the mixture compared to the corresponding high water treatment (ANOVA, post hoc, $P < 0.01$, Fig. 4). Hence, the root growth of *C. arenaria* seemed to react more sensible to drought in a competitive situation. In addition to this the variability in total biomass of *C. arenaria* in this treatment was much higher and one of the replicates was almost dead at harvesting time (0.07 g total dry weight). For *D. flexuosa* no significant differences of root biomass between any of the treatments could be detected (Fig. 4).

Aboveground, the situation is quite different: a significant reduction of aboveground biomass of *C. arenaria* (ANOVA, post hoc, $P < 0.01$, Fig. 3) and *D. flexuosa* (ANOVA, post hoc, $P < 0.05$, Fig. 3) was measured in competition under high as compared to low water availability. The overall effect of shoot biomass, however, was comparable with the results for root biomass and showed a significant difference between the two species (ANOVA, $d.f._{effect} = 1$, $d.f._{error} = 24$, $F = 6.26$, $P < 0.05$).

Fig. 1. Time course of soil water content in four successional stages on inland dunes (bare sandy soil, pioneer plant community, dry grassland, heathland community) between July 1997 and May 1998. Shown are $\bar{x} \pm$ s.e. ($n = 5$ (July – November), $n = 3$ (December – May), d.f. = 8).
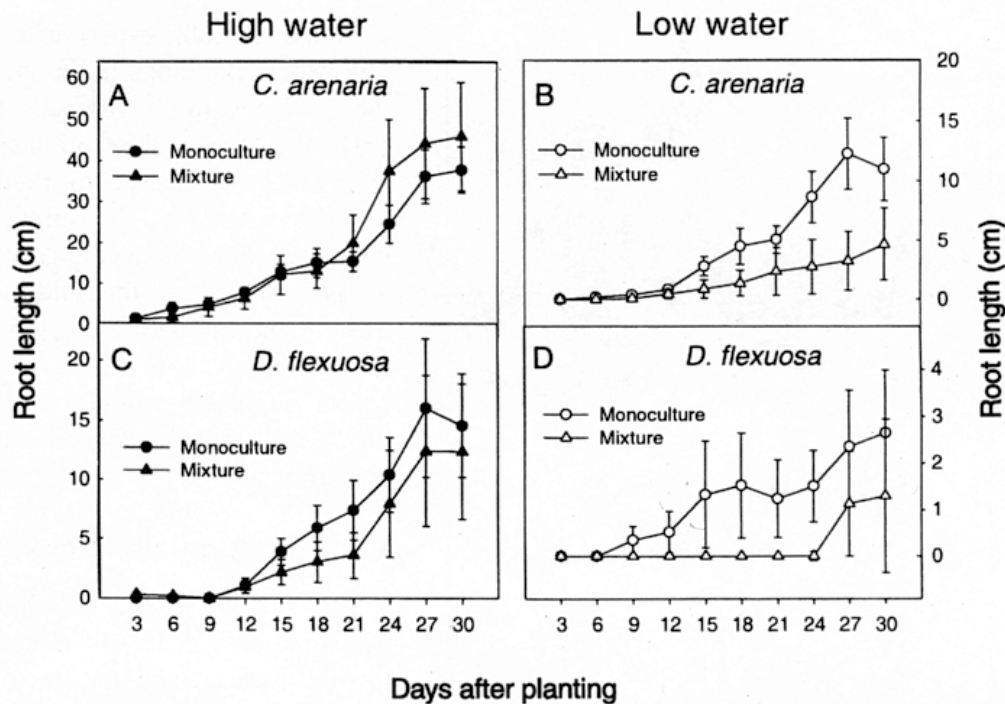
Fig. 2. Root length per single plant of *C. arenaria* (A, B) and *D. flexuosa* (C, D) in a minirhizotron experiment under high and low water availability in monoculture as well as in mixture ($\bar{x} \pm$ s.e., $n = 4$, d.f. = 8).

These different influences of water supply on the allocation patterns of the studied species have also been observed for the root/shoot ratios. While the root/shoot ratio of *D. flexuosa* considerably declined under low water availability there was no obvious change of root/shoot ratio in *C. arenaria* (Fig. 5). Under drought conditions, the growth of *C. arenaria* was significantly reduced above- and belowground, whereas for *D. flexuosa* only aboveground biomass was affected leading to lower root/shoot ratios.

Relative yield

Based on the observed changes in the total biomass of the harvested plants, relative yields (RY) were calculated to standardize the competition level for the two species concerned (Tab. 1). Under high water availability the RY of both species equalled 0.5 indicating that there was no difference in the biomass of individual plants depending on whether they grow together with another plant of the same or different species. Under drought conditions, however, the RY of *C. arenaria* was significantly lower than 0.5 ($P < 0.01$) which implies that interspecific competition had a greater effect on individuals of *C. arenaria* than intraspecific competition. For *D. flexuosa* no significant changes in RY depending on the water treatment could be detected.

The relative yield total (RYT) measures the degree to which two components of a mixture make demands on the same resource units, which means for a RYT > 1 that a certain degree of niche differentiation occurs. According to our data, RYT for high water availability equalled unity while there was a marginal reduction of RYT for plants growing under drought conditions (Tab. 1). This means that the studied species were not complementary in their resource use and under low water availability interspecific competition for resources seemed to be important.

Table 1. Relative yields of C. arenaria and D. flexuosa in mixture with high and low water availability and relative yield totals for these treatments based on total biomass of single plants ($\bar{x}$ ± s.e., $n = 4$). Significant deviations from 0.5 (RY) or 1.0 (RYT) were determined using probabilities of deviations for small samples. + = $P < 0.10$; ** = $P < 0.01$.

Treatment	Total biomass relative yields		Total biomass relative yield totals
	C. arenaria	D. flexuosa	
High water	0.508 ± 0.12	0.520 ± 0.23	1.028 ± 0.31
Low water	0.223 ± 0.10**	0.362 ± 0.39	0.529 ± 0.37+

DISCUSSION

Measurements of soil water content showed significant seasonal changes with a pronounced late summer drought period of about 2 months (Fig. 1). During this time changes in the vegetation patterns of C. arenaria could be observed in the field, while D. flexuosa did not seem to be influenced at the same time (RÖTTGERMANN 1998). In fact, C. arenaria showed a strong decrease in vegetation cover and aboveground biomass due to water shortage, whereas the vegetation cover and biomass of D. flexuosa were not affected (RÖTTGERMANN 1998). Measurements of vegetation cover of D. flexuosa in 1995, 1996 and 1997 constantly showed about 5% cover throughout the year. However, the vegetation cover of C. arenaria declined from about 10% in 1995 to about 2.5% in 1997, with pronounced changes caused by the high mortality of ramets in the summer months (RÖTTGERMANN 1998). In the present minirhizotron experiment significant and considerable belowground competition between D. flexuosa and C. arenaria could be detected under nutrient- and water-limited conditions, corresponding well to Tilman's hypothesis that belowground competition is more important in resource-poor environments (TILMAN 1988).

The water content in the minirhizotrons, which was similar to the soil water content measured in the field, had a considerable influence on the outcome of competition. This effect was especially obvious for the competitive effect of D. flexuosa on C. arenaria leading to a significant reduction of root and shoot biomass of C. arenaria under drought as compared to well-watered conditions (Figs. 3, 4). Moreover, the calculation of relative yields (RY) for C. arenaria also showed a significant reduction under low water availability which implied that interspecific competition had a greater effect on individuals of C. arenaria than intraspecific competition. For D. flexuosa, however, no significant influence of water availability on the biomass production of individual plants growing in the mixture or the monoculture could be detected. According to this, relative yield totals (RYT) were not significantly different from unity under high water availability, although a marginal reduction was found for the low-water treatment. Hence, the studied species were not complementary in their resource use and under low-water availability interspecific competition seemed to be rather limiting for growth of C. arenaria. Moreover, the variability of total biomass in competition and under drought conditions was much higher and the low total biomass data measured after one month made the competitive exclusion of C. arenaria on a longer time scale highly probable. Thus, both species were sensitive to water shortage, but while C. arenaria did not suffer from interspecific competition at high water supply it might become an inferior competitor after a period of drought. In the field, C. arenaria was often found in rather moist downhill sites of a dune slope while D. flexuosa seemed to be established at drier spots (WILLIS & JEFFERIES 1963, WATT 1936).
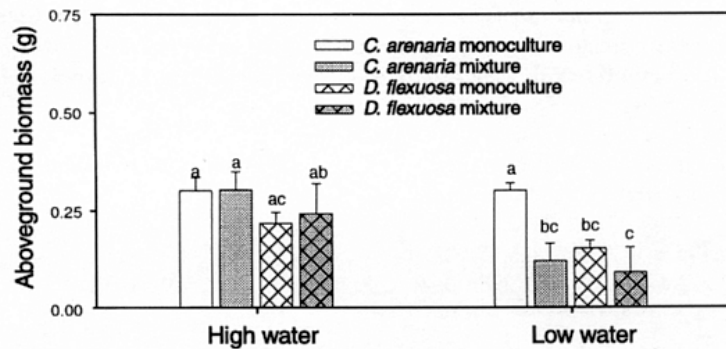
Fig. 3. Aboveground biomass per single plant of *C. arenaria* and *D. flexuosa* in a minirhizotron experiment under high and low water availability in monoculture as well as in mixture ($\bar{x} \pm$ s.e., $n = 4$, d.f. = 24). Significant differences between aboveground biomass of plants grown in monoculture versus mixture are shown by different letters above bars.
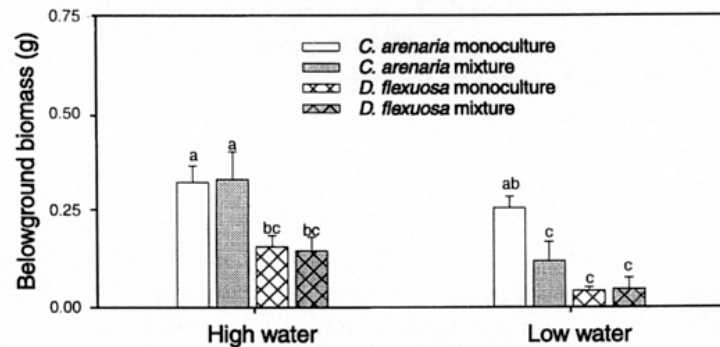

Fig. 4. Belowground biomass per single plant of *C. arenaria* and *D. flexuosa* in a minirhizotron experiment under high and low water availability in monoculture as well as in mixture ($\bar{x} \pm$ s.e., $n = 4$, d.f. = 24). Significant differences between belowground biomass of plants grown in monoculture versus mixture are shown by different letters above bars.

According to the calculations of relative yield (RY), competition for *C. arenaria* was predominantly interspecific under low water availability. So far few experimental studies have investigated the importance of intra- versus interspecific competition in pairwise interactions. While KEDDY & SHIPLEY (1989) found 7 of 8 data sets on plant competition showing asymmetric relationships, with higher interspecific competition for one of the competing individuals, HENRY et al. (1999) revealed the overwhelming influence of density rather than interspecific effects. However, asymmetric competition seemed not to be important in clonal plants (HARA 1994, SILVERTOWN et al. 1992). In total, pairwise competitive interactions seemed to be rather species specific, depending on the relative competitive strength of the two species.

Although these results refer to an experimental data set from a highly artificial environment in comparison to the situation in the field, field measurements on the development of vegetation cover of *C. arenaria* and *D. flexuosa* often showed situations of small clonal fragments similar to the experimental situation, resulting from damaged and/or dead ramet connections, interacting on a small spatial scale (RÖTTGERMANN 1998). Particularly in these patches, where single ramets try to establish, the rooting depth of both *C. arenaria* and *D. flexuosa* did not exceed 30 cm, similar to the minirhizotrons. Field observations supported the investigation of water as an important factor on plant interactions in this resource-limited environment. However, nutrient availability also might be a constraint for both the field situation and the
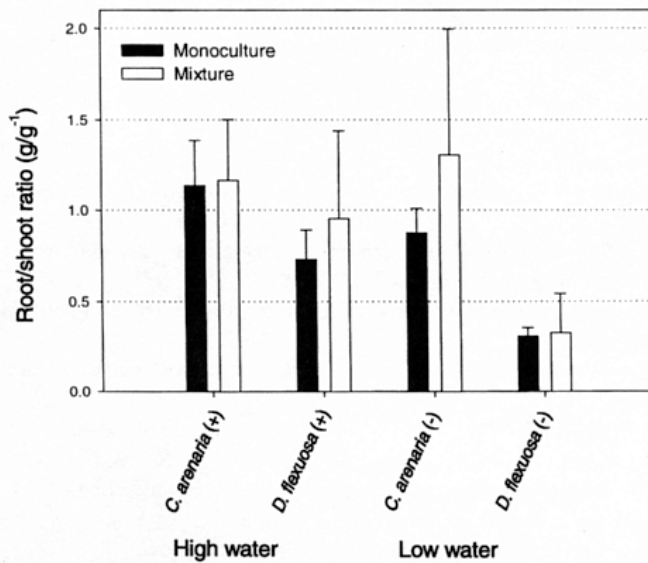
Fig. 5. Root/shoot ratio per plant of *C. arenaria* and *D. flexuosa* in a minirhizotron experiment under high (+) and low (-) water availability in monoculture as well as in mixture ($\bar{x}$ ± s.e., $n = 4$). Significant differences between root/shoot ratios of plants grown in monoculture versus mixture could not be detected.

experiment. The low nutrient content of the substrate, combined with no addition of mineral nutrients and the comparatively short experimental period makes the combined effect of water and nutrients improbable in the experimental design. In the field, however, the effect of competition for nutrients might be much more pronounced.

In summary, the late summer drought period measured for a dry grassland in the field could reduce the competitive effect of *C. arenaria* within this successional stage, and, in consequence, effect the competitive balances throughout the entire year. In conclusion, not only the absolute values of soil water content effected the belowground competitive relationships, but, above all, the relative changes in water availability could be important for the plant community structure. We assume similar mechanisms for the other early successional stages (e.g. pioneer plant community and heathland community) and it would be interesting to study these processes on a community level to get a better insight into the importance of competition for the whole inland dune system.

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