Drought affects the competitive interactions between *Fagus sylvatica* seedlings and an early successional species, *Rubus fruticosus*: responses of growth, water status and $\delta^{13}C$ composition

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Summary

• Competitive interactions between European beech (*Fagus sylvatica* L.) seedlings and the early successional species *Rubus fruticosus*, and the role of water availability, are reported and discussed in relation to management practices and climatic changes in beech ecosystems of Central Europe.

• Responses of growth, water status, gas exchange and carbon isotope composition ($\delta^{13}C$) to two competition and three irrigation treatments were examined in a factorial-design glasshouse study.

• Under regular irrigation, coexistence with *R. fruticosus* did not significantly affect growth, water potential and gas exchange of beech seedlings. However, moderate water shortage caused a twofold reduction in beech biomass and changes in root : shoot ratios. Drought lowered transpiration rates and predawn water potentials (below the xylem embolism threshold) for *F. sylvatica*; $\delta^{13}C$ of leaves and fine roots increased (discrimination was reduced). By contrast, significantly lower $\delta^{13}C$ of *R. fruticosus* foliage indicated an improved water status. Competitive interference intensified the effects of reduced irrigation.

• Water availability regulates the competitive interactions between beech seedlings and *R. fruticosus*. Natural regeneration of beech seedlings may be inhibited by interference from a species such as *R. fruticosus*, especially during summer drought, as predicted by actual climate models.

Key words: *Fagus sylvatica*, competition, water availability, growth, water potential, carbon isotope composition, transpiration.

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Introduction

Throughout their life-cycle, trees interact with neighbouring plants composed of different life forms, physiology and resource requirements. For trees, coexistence with other species may have negative effects, such as soil water and nutrient depletion and competition for radiation, or positive effects such as nitrogen fixation (Flint & Childs, 1987; Messier & Kimmins, 1990; Neary *et al.*, 1990; Chang *et al.*, 1996b). Information on the ecophysiological basis of interactions between trees and neighbouring plants is required to understand, predict and manipulate regeneration and successional processes in forests. Moreover,

knowledge of the indirect effects of understorey vegetation on seedling recruitment patterns may have important silvicultural implications and economic benefits. Several cases have been reported of low productivity or even failure of plantations and of regeneration as a result of competition from understorey species (Brand, 1991; Morris *et al.*, 1993; Marino & Gross, 1998).

A number of management practices, including thinning, have focused on improving ecosystem productivity and are routinely used in forests, both to minimize competition between trees and to increase growth rates. Thinning frequently increases irradiance at the forest floor and may improve conditions for

the natural regeneration of trees. Conversely increasing light and temperature may promote growth not only of young trees but also of herbs and shrubs, leading to reduced growth of tree seedlings, by increasing competition.

In the past, coniferous trees have been the main focus of forest management in central Europe. More recently, management practices have changed and some now aim not only to transform uniform conifer monocultures into more structured, species-rich forests but also to improve natural regeneration by deciduous tree species (Schäfer, 1995). In particular, approaches to promote the natural regeneration of *Fagus sylvatica*, the most important deciduous tree species in central Europe (Ellenberg, 1992) are now supported by forest practitioners and governments (Dertz, 1996; Ministerium für Ländlichen Raum, Ernährung, Landwirtschaft und Forsten in Baden Württemberg, 1997).

European beech is capable of persisting as small trees for long periods in the forest understorey, but establishment can also be favoured by gap formation (Johnson *et al.*, 1997). Survival and growth of European beech at this stage of development will depend largely on its ability to coexist with highly competitive early successional species (Tognetti *et al.*, 1998). In particular, the consequences of competition for water is probably decisive for the growth and survival of young beech, which is drought intolerant and limited in distribution by water availability (Ellenberg, 1992).

Models of future climate for Central Europe not only predict an increase in temperature as a consequence of the anthropogenic climate change but also longer periods of drought during the growing season (Enquete-Kommision, 1994). Any decrease in soil water availability will exacerbate the competition between drought-sensitive beech seedlings and vigorous early successional species. Among the forests most affected by summer drought will be those on the quite common shallow rendzina soils of Southern Germany ('Schwäbische Alb', 'Frankische Alb') with low water storage capacity .

Rubus fruticosus, a fast growing species, establishes readily in the understorey following thinning of beech forests, on limestone soils. Many experiments highlight the negative effects of competition either on the survival and growth (Tesch *et al.*, 1993; Wang *et al.*, 1995; Newton & Jolliffe, 1998; Sauders & Puettmann, 1999), or on the water status of young tree seedlings (Petersen & Maxwell, 1987; Koukoura & Menke, 1995). However, studies of survival and growth do not explain the mechanism of competition and physiological studies alone seldom lead to a prediction of whole plant growth performance. The present study combines morphological and physiological studies in an assessment of competition between *R. fruticosus* and European beech. The aims of this study were to examine if, and to what degree, the presence of *R. fruticosus* promotes water depletion and restricts growth of 1-yr-old beech seedlings, and to test if different water availability regimes influence the patterns of competition between the two species. For this purpose we designed a glasshouse experiment consisting of microecosystems with defined species' composition and three different regimes of water availability.

Materials and Methods

Experimental design

Young European beech seedlings of similar biomass and structural characteristics, grown in a forest nursery in Freiburg (Germany; longitude: 48° N, latitude: 7°51′ E, 275 meters above sea level (masl)) and *R. fruticosus* plants, collected in winter from the field site 'Tuttlingen' in a low mountain range (Schwäbische Alb, Germany; longitude: 8°50′ E, latitude: 47°58′ N, 740–760 masl) were used for the experiment that was conducted in a glasshouse under controlled conditions. Beech seedlings were 1-yr-old as our main interest was to examine in more detail the early phases of seedling establishment – these being most critical for the patterns of survival and development of beech in forest (Madsen & Larsen, 1997).

Parts of *R. fruticosus* plants were selected and transferred from the field site to the glasshouse where they were left in tap water to develop new roots. Both species were transplanted into experimental basins (diameter 0.45 m; depth 0.35 m) simultaneously, to ensure the same degree of planting shock. For the experiments, soil from the upper 0.02 m of the profile at the field site 'Tuttlingen' was collected and used in a homogeneous mixture with quartz sand (1 : 1). Mixing soil with sand was used in order to minimize uncontrolled nitrogen release due to mineralization under glasshouse conditions and to maintain field pH (5.7–7.5). The soil from the field site is characterized as Terra fusca – Rendzina derived from limestone (Weißjura beta and gamma series). The mixture of top soil and quartz sand had a water holding capacity of 20%. All plants were well-watered during a 3-wk establishment period, in which leaf expansion of the beech seedlings took place.

The experiment consisted of a 2×3 factorial design, with two levels of competition and three levels of irrigation, resulting in six different treatment combinations. Two basins were used for each combination of treatments. The competition treatment was specified by the absence or presence of *R. fruticosus*. In the first case only beech seedlings were grown in each basin; in the second case beech seedlings and *R. fruticosus* were grown in the same basin. In the high irrigation treatment (HI) the plants were regularly watered, whereas in the intermediate irrigation treatment (II) the soil water potential was maintained in a range from -0.2 to -0.6 MPa by regulating irrigation. Finally, in the no irrigation treatment (NI), water was withheld after the establishment period. The treatments were conducted for a 52-d period.

Six beech seedlings and six *R. fruticosus* plants were arranged in rows, in each basin of the competition treatment, with a distance of 0.08 m between *R. fruticosus* and beech seedlings and of 0.12 m between plants of the same species. For the control treatment only six beech seedlings were planted in one

basin, 0.12 m apart from one another. In a similar study of competition, a 0.10-m radius around each seedling with crown diameter of 0.20 m was regarded as representative of the distance in which neighbouring plants compete for resources (Imo & Timmer, 1999). The beech seedlings used in the present study were of a maximum crown diameter of 0.20 m. Therefore, the planting design in each basin created competition between the interspecifics, but not between conspecifics. Similar experimental designs have been widely used for assessing the competitive ability of various species under given growth conditions (Gaudet & Keddy, 1988; Nernberg & Dale, 1997) and are intended to simulate neighbouring plant interactions in the field.

All basins were maintained under long-day conditions (16 h light/8 h dark) during both the establishment and treatment periods. Plants received natural daylight plus a daylight supplement provided by mercury lamps (SON-T AGRO 400, PHILIPS GmbH Eindhoven, The Netherlands). The photosynthetically active radiation (PAR) during the light period was a minimum of 200 μmol m^{-2} s^{-1} and 280 μmol m^{-2} s^{-1} at the surface of the basins and at the upper plant parts, respectively. Air temperatures were 20°C during the light and 15°C during the dark period. The rh was 35–40% during the light and 70–75% during the dark period.

Soil water potential

Soil water potential was regularly measured in all basins using gypsum blocks (5201F1 G-Blocks and 5910-A Soil Moisture Meter; Soil Moisture Equipment Corp., Santa Barbara, CA, USA). The G-Blocks were established before the beginning of the experiment at a depth of 0.20–0.25 m, representing 75–80% of the maximum rooting depth of plants.

Growth parameters

At the end of the experiment all plants were harvested, separated into stems, leaves and roots and oven-dried (2d, 75°C). In a number of previous studies (Brand & Janas, 1988; Brand & Magnussen, 1988; Morris *et al.*, 1990; Chang *et al.*, 1996a) the total dry biomass was found to be a reliable and sensitive estimate of competitive ability, since it consists of photosynthetic area (foliage weight), size of the root system (root weight), and structural dimensions (stem and branch weight).

Plant water potential

Predawn water potentials of the beech seedlings were measured at the bottom of the shoot at the end of the experiment using the 'Scholander Pressure Chamber' technique (Scholander *et al.*, 1965), as modified by Rennenberg *et al.* (1996). The seedlings were harvested at 04 : 00 AM and measurements were conducted on all 12 seedlings per treatment within 1 h of collection, during which they remained in plastic bags.

Carbon isotope composition

Carbon isotope composition ($\delta^{13}C$) was included for comparing the stomatal response of the two examined species to induced water shortage (Ehleringer & Cooper, 1988; Pate & Arthur, 1998).

$\delta^{13}C$ signatures were determined in the leaves and fine roots of beech seedlings and *R. fruticosus* plants at the end of the experiment. For both species, leaves developed during the period of the applied irrigation regimes were selected. The plant material was oven-dried for 3 d at 65°C and ground with a ball mill into a fine homogenous powder. 1–2 mg samples were transferred into tin capsules (Type A; Thermo Quest, Milan, Italy) and injected into an elemental analyser (NA 2500; CE Instruments, Milan, Italy) coupled to an isotope ratio mass spectrometer (Delta Plus; Finnigan MAT GmbH, Bremen, Germany). The $\delta^{13}C$ values were defined as: $\delta^{13}C$ (‰) = $[(R_{sample}/R_{PDB}) - 1] \times 1000$, where R_{sample} and R_{PDB} are the $^{13}C : ^{12}C$ ratios of sample and Pee Dee belemnite (PDB; Craig, 1957), respectively.

Transpiration

Transpiration was measured on two consecutive days per week for each set of treatments on six beech seedlings and on 12 *R. fruticosus* plants per treatment using a LI-1600 steady state porometer (Li-Cor. Inc., Lincoln, NB, USA). The measurements were conducted on three fully expanded leaves per plant and twice per day, at 09 : 00 AM and at 13 : 00 PM, in order to account for the variation caused by the different position of each leaf and internal diurnal rhythms of the test species.

Statistical analyses

All statistical analyses were carried out using SPSS 8.0 (SPSS, Inc., Chicago, IL, USA). No significant differences were observed between plants in different basins growing under the same combination of treatments. Therefore, only competition and irrigation and not replication had a significant effect on the measured parameters. The planting distance between conspecifics prevented their potential competition interactions. The careful maintenance of environmental conditions enabled us to use each plant as an experimental unit for the purpose of statistical analysis. A factorial ANOVA was applied for detecting significant differences between treatments. Where nonparametric methods were required, the Kolmogorov-Smirnov test was applied.

Results

Soil water potential (SWP)

The patterns of soil water potential of all treatments throughout the experiment are presented in Fig. 1. Application of the different water regimes was initiated on 27th March and differences

Fig. 1 Patterns of soil water potential during the experiment. The combination of three water supply levels (High Irrigation-HI, Intermediate Irrigation-II, and No Irrigation-NI) and two competition levels (beech and *Rubus*, where beech grew under competition from *R. fruticosus*, and beech without *Rubus*, where beech grew alone) resulted in six sets of treatments (NI-Beech and *Rubus*, closed squares; NI-Beech without *Rubus*, open circles; II-Beech and *Rubus*, closed triangles; II-Beech without *Rubus*, open triangles; HI-Beech and *Rubus*, multiplication signs; HI-Beech without *Rubus*, plus signs). The application of irrigation regimes was started on 27th March. The NI treatments were not watered at all after that point, whereas the irrigation of the II treatments was regulated in order to maintain soil water potential in a range of −0.2 to −0.6 MPa. The soil water potential of the HI treatments was maintained at its optimum by frequent irrigation. Transpiration was measured at different points of time during the experiment (Fig. 7). Both, beech seedlings and *R. fruticosus* plants were harvested on 15th May. Each value represents the mean soil water potential of two basins belonging to each set of treatments (See also Materials and methods for experimental design).

between the treatments were first observed about 3 wk later. Due to adequate water supply to the microecosystems of the HI treatment, the soil water potential never decreased, neither for HI-Beech with *Rubus*, nor for the HI-Beech without *Rubus*. In II treatments, soil water potential varied between −0.2 and −0.6 MPa. An effect of competition on soil water potential was exhibited for the NI treatments. Here, soil water potential decreased in parallel with and without *Rubus*, but was always more negative for the NI-Beech with *Rubus* treatment. For NI-Beech without *Rubus* treatment, soil water potential was maintained, for the last 3 wk, at approx. −0.6 MPa, whereas for NI-Beech with *Rubus*, soil water potential continued to decrease to values as negative as −1.2 MPa.

Total dry biomass, R : S ratio

Figs 2 and 3 show the total dry biomass and the root : shoot ratios of beech seedlings and of *R. fruticosus* for all six combinations of treatments, as measured at the end of the experiment. *R. fruticosus* biomass was independent of the rate of irrigation; only a slight and nonsignificant decrease was measured with decreasing water availability. The biomass of beech in II and NI treatments did not differ, but was significantly lower than in the HI treatment. Additionally, there was no significant difference among beech seedlings growing with and without competition, irrespective of irrigation regime.

An analogous response was documented for the root : shoot ratios of all studied plants (Fig. 3). Neither irrigation, nor

Fig. 2 Effects of water supply (High Irrigation, HI; Intermediate Irrigation, II; and No Irrigation, NI) and competition (Beech with *Rubus*, grey columns; Beech without *Rubus*, white columns; *Rubus* with Beech, black columns) on the total dry biomass of beech seedlings and *R. fruticosus* plants. Vertical bars indicate ± SE of the mean. Means are significantly different at a 95% level of significance, when they share no common letter. *n* = 12.

competition had a significant effect on the root : shoot ratio of *R. fruticosus*. There was a slight increase of its root mass with decreased water supply. The opposite was found for beech. Without competition, both II and NI regimes resulted in a significant reduction of the root : shoot ratio, when compared with the well-watered seedlings. Only under HI conditions was there a competition effect, as the root : shoot ratios of beech seedlings growing with *R. fruticosus* were significantly lower

than that without. Beech seedlings had generally greater root : shoot ratios than *R. fruticosus* when grown under HI conditions, but the difference between the species diminished at lower water availability.

Predawn plant water potential (Ψ) and correlation between Ψ and soil water potential

Fig. 4 shows the predawn, shoot water potential of beech seedlings for all treatment combinations at the end of the

Fig. 3 Effects of water supply (High Irrigation, HI; Intermediate Irrigation, II; and No Irrigation-NI) and competition (Beech with *Rubus*, grey columns; Beech without *Rubus*, white columns; *Rubus* with Beech, black columns) on the root : shoot ratio (R : S) of beech seedlings and *R. fruticosus* plants. Vertical bars indicate ± SE of the mean. Two means are significantly different at a 95% level of significance, when they share no common letter. *n* = 12.

experiment. The combined effects of irrigation and competition caused significant differences between almost all treatment combinations. Shoot water potential varied between irrigation regimes, and decreased sharply from the HI to the NI treatment. A strong linear correlation between soil and shoot predawn water potential emphasized the controlling role of soil water availability on the water status of beech seedlings ($R^2 = 0.963$, $P = 0.002$; data not shown). Furthermore, in II and NI treatments, the Ψ of beech seedlings competing with *R. fruticosus* were significantly lower than those of beech growing alone. As a consequence of reduced irrigation, predawn water potential of beech seedlings grown without competition decreased from −0.9 to −2.2 MPa. The respective range for beech seedlings grown with competition was −1.3 to −3.7 MPa.

Leaf and root δ13C and the correlation between Ψ and δ13C composition

The carbon isotope composition ($\delta^{13}C$) of foliage of beech seedlings and *R. fruticosus* at the end of the experiment are shown in Fig. 5. $\delta^{13}C$ of *R. fruticosus* varied little with varying irrigation. Moreover, $\delta^{13}C$ of *R. fruticosus* was consistently and significantly more negative than that of beech throughout the experiment. $\delta^{13}C$ of beech seedlings increased from the HI to the NI treatment and the differences between the irrigation treatments were significant. $\delta^{13}C$ of beech with *Rubus* was slightly increased, compared with beech without *Rubus*, but the difference between them was significant in the NI treatment only. Similar patterns were obtained for $\delta^{13}C$ of the fine roots but without significant differences between combinations of treatments (data not shown).

Fig. 4 Effects of water supply (High Irrigation, HI; Intermediate Irrigation, II; and No Irrigation, NI) and competition (Beech with *Rubus*, black columns; Beech without *Rubus*, grey columns) on predawn water potential (Ψ) of the beech seedlings. Xylem embolism threshold, after Hacke & Sauter (1995). Vertical bars indicate ± SE of the mean. Two means are significantly different at a 95% level of significance, when they share no common letter. *n* = 12.

Fig. 5 Effects of water supply (High Irrigation, HI; Intermediate Irrigation, II; and No Irrigation, NI) and competition (Beech with *Rubus*, grey columns; Beech without *Rubus*, white columns; *Rubus* with Beech, black columns) on leaf carbon isotope composition ($\delta^{13}C$) of the beech seedlings and *R. fruticosus* plants. Vertical bars indicate ± SE of the mean. Two means are significantly different at a 95% level of significance, when they share no common letter. *n* = 6.

Fig. 6 Relationship between predawn plant water potential (Ψ) and carbon isotope composition ($\delta^{13}C$) of the beech seedlings, measured in leaves (closed circles) and fine roots (open squares). For each treatment mean values of measurements with 6–12 measurements are displayed.

The $\delta^{13}C$ composition of leaves and fine roots and the predawn shoot water potentials for beech seedlings (Fig. 6) are highly correlated (R^2 values 0.973 and 0.875 for leaves and roots, respectively).

Transpiration rates and correlation between Ψ and transpiration

Rates of transpiration at 09 : 00 AM for all treatment combinations are shown in Fig. 7. The transpiration rates of both *R. fruticosus* and beech decreased under II and NI treatments compared with HI. Moreover, under all irrigation regimes beech without *Rubus* had slightly greater transpiration rates than beech with *Rubus* but the difference was significant in the NI treatment only. In most cases, transpiration of *R. fruticosus* was significantly higher than that of beech seedlings, growing with and without *Rubus* (45–70% and 35–60%, respectively). Under the NI treatment severe water shortage led to minimum transpiration rates during the last period of the experiment. That was the case not only for beech seedlings, growing with and without competition, but also for *R. fruticosus*.

Similar results were obtained for transpiration rates measured at midday (13 : 00 PM; data not shown), but transpiration was higher at that time of the day, as expected. Additionally, both morning- and midday-transpiration rates of beech seedlings correlated strongly with their predawn water potentials. Transpiration decreased linearly with a concurrent reduction of water potential ($R^2 = 0.895$, $P = 0.02$ and $R^2 = 0.875$, $P = 0.01$ for morning and midday, respectively; data not shown).

Discussion

The low soil water potential in basins where both *R. fruticosus* and beech seedlings were growing can be readily attributed to the limited amount of water ascribable for the two competitors.

Fig. 7 Effects of water supply (High Irrigation, HI; Intermediate Irrigation, II; and No Irrigation, NI) and competition (Beech with *Rubus*, grey columns; Beech without *Rubus*, white columns; *Rubus* with Beech, black columns) on the transpiration rates of beech seedlings and *R. fruticosus* plants, measured at 9 : 00 AM, at 2 consecutive days at three time points during the experiment. Vertical bars indicate ± SE of the mean. Means, included at the same level of irrigation, are significantly different at a 95% level of significance, when they share no common letter. $n = 6$ for the beech seedlings and $n = 12$ for *R. fruticosus* plants.

This situation corresponds well to natural conditions where neighbouring plants are forced to compete for finite resources. Comparison of soil water potential curves for the NI treatment with and without *R. fruticosus*, illustrates that extreme water depletion was due to the capacity of *R. fruticosus* to exploit and use more of the available soil moisture. Lüttschwager *et al.* (1999) also observed that understorey species used the water left by trees in Scots pine ecosystems in north-eastern Germany. Morris *et al.* (1993) reported that the intensity of drought for young pine seedlings was greater when growing in competition with species that rapidly depleted surface soil water. These findings are consistent with the present observation that soil water potential of the no competition-basins never declined below −0.6 MPa; one implication is that beech seedlings are capable of enduring water shortages for a period of about a month, with some limitations in growth, if the influence of neighbouring plants is eliminated. Comparable results were found in field studies (Petersen *et al.*, 1988; Pabst

et al., 1990; Jobidon *et al.*, 1998), where during a summer drought, soil water content was sufficient to maintain a high water status of Douglas-fir and *Picea mariana* (Mill.) seedlings, when no competing vegetation was present. Drought increased in presence of understorey vegetation.

The maintenance of the same biomass by *R. fruticosus*, irrespective of irrigation treatment, is indicative of its ability to regulate its water status independently of the water supply. However the reduced growth of beech seedlings exposed to soil water depletion, is almost certainly due to reduced plant water status (Fotelli *et al.*, 2000). The absence of significant differences in total biomass of beech seedlings between intermediate and no irrigation treatments suggests that a reduction in soil water potential of 0.4–0.6 MPa was sufficient to induce physiological changes that led to limitation of growth. Furthermore, water shortage alone probably accounted for the decreased growth of beech seedlings. This conclusion partially contradicts previous studies suggesting significant reductions in growth and total biomass of seedlings result from understorey competition (Eissenstat & Mitcell, 1983; Nilsson & Zackrisson, 1992; Smethurst *et al.*, 1993). However, in these studies, there was little evidence of a mechanism to account for the observed reduction in growth. This lack of specific knowledge has been pointed out previously. Many studies have been inadequate since they fail to confirm which components were involved in the competitive interactions (Koukoura & Menke, 1995; Imo & Timmer, 1999), and to discuss competition in light of the water depletion that maybe its consequence (Sands & Nambiar, 1984; White & Newton, 1989). By having independently studied the effect of water supply, we provide clear support for the argument that a shortage of soil moisture is the main factor accounting for reduced growth.

A general shift in biomass allocation with increasing shortage of water led to significantly reduced root : shoot ratio in beech seedlings. Reduced root : shoot ratios under water depletion are often attributed to an increase in carbon allocation to stem wood production (Britt *et al.*, 1991; Nilsson & Albrektson, 1993). In the present study, this strategy would not increase the 'competitive ability' of beech, as *R. fruticosus* exhibited a tendency to increase root growth, and thereby ability to exploit soil water. That competition was not solely responsible for the alteration of biomass allocation, was also found by Newton & Cole (1991), who also suggested that allocation of photosynthate to structural components above and below ground was constant over a wide range of competitive intensity. By contrast Landhäusser & Lieffers (1998) reported that in poplars competition increased root : shoot ratios. Since it is common for root : shoot ratios to change with tree size (Kozlowski *et al.*, 1991), it is not easy to reach safe conclusions about the responses of seedlings during short-term experiments.

The variation in water supply in the present study was clearly reflected by predawn shoot water potentials. The strong correlation between water potential in soil and beech seedlings supports this conclusion and another that lower water potentials in beech seedlings growing with *R. fruticosus*, compared with those growing alone, were competition-induced. Nevertheless, the NI treatment indicated that the competing vegetation depleted water noticeably only after Ψ of beech seedlings reached –2.0 MPa. A similar effect has been reported for other species growing with competition, for example *Pinus radiata*, *Robinia pseudoacacia* L. and Douglas fir (Nambiar & Zed, 1980; Eissenstat & Mitcell, 1983; Fredericksen *et al.*, 1993; Wang *et al.*, 1995). With an intermediate water supply, the presence of *R. fruticosus* lowered the water potential of beech to < −1.9 MPa; the threshold below which damage due to xylem embolism may occur in *Fagus sylvatica* (Hacke & Sauter, 1995). Beech seedlings growing alone did not approach this critical plant water potential. With no irrigation this impairment was unavoidable.

Negative effects of progressive drought on the physiological status of seedlings were also confirmed by $\delta^{13}C$ analysis. Shortages of water typically increase $\delta^{13}C$ signatures owing to the reduced internal CO_2 concentrations in leaves caused by stomatal closure (Farquhar *et al.*, 1989; Handley *et al.*, 1997; Gillon *et al.*, 1998). Many studies have shown that carbon isotope composition can be a reliable indicator of the water status of plants (Pate & Arthur, 1998; Robinson *et al.*, 2000). The increase in $\delta^{13}C$ signatures of beech leaves from –26.2 to –24.5‰ indicates their unfavourable water status as soil moisture availability declined. This assumption is supported by the strong correlations among $\delta^{13}C$, predawn water potential of beech seedlings and soil water potential. In comparison with beech, the significantly lower leaf $\delta^{13}C$ of *R. fruticosus* suggests that this species maintained its internal water status, even under drought. The greater ability to access water, and the greater competitive ability of *R. fruticosus* is emphasized by the even greater differences of $\delta^{13}C$ between beech and *R. fruticosus* as water shortages increased.

Drought tolerance mechanisms may explain the considerably higher transpiration rates of *R. fruticosus* in all irrigation treatments, as also described by Ni & Pallardy (1991) and Fotelli *et al.* (2000) for other species. The shade-tolerant beech usually exhibits lower gas exchange rates (Abrams *et al.*, 1994) consistent with lower rates of transpiration. The decrease in predawn water potential of beech seedlings may be a consequence of gradual stomata closure, as indicated by rates of transpiration in the three irrigation treatments. This interpretation is supported by the strong correlation between predawn water potential and transpiration, a finding also reported in previous studies with beech (Le Thiec *et al.*, 1994; Tognetti *et al.*, 1995; Rust & Hüttl, 1999), and interpreted as a response to avoid loss of water conductance.

Conclusion

The results of the present study illustrate the significance of soil water availability to the interactions between *F. sylvatica* seedlings and *R. fruticosus*. We demonstrated that with adequate

water, as induced by regular irrigation, beech seedlings can cope satisfactorily with competition from *R. fruticosus*, although the latter appears to maintain a more favourable water status. With even moderate shortages of water, the first signs of a limitation to growth are observed in beech seedlings. As drought increases, predawn water potentials fell to below the threshold for xylem embolism for European beech, thereby greatly increasing the inhibition of growth of beech by *R. fruticosus*. Low rates of transpiration by beech seedlings were consistent with these observations, as were carbon isotope signatures that clearly indicated the propitious water status of *R. fruticosus*. Competition may also limit the availability of other resources to beech and, induce nutrient deficiencies, which are also likely to play an important role in the growth of beech seedlings.

Acknowledgements

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