Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz
Journal of Plant Diseases and Protection 19, pp 345-351 (2004)
ISSN 0938-9938

Competitive ability of *Rumex obtusifolius* against native grassland species: above- and belowground allocation of biomass and nutrients

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Summary
Understanding the competitive ability of *Rumex obtusifolius* against grassland species is essential for developing efficient control strategies against docks. Here we present results from a greenhouse experiment where we tested shoot and root competition between *Rumex* regenerating from rhizome fragments and grassland species (grasses, herbaceous and leguminous species). Competitive ability was expressed as the relative above- and belowground biomass partitioning and, concentrations and allocation of carbon and nitrogen of the plant species studied. Regeneration of *Rumex* was significantly affected by competition through neighbouring native grassland species. *Rumex* responded to concurrent shoot and root competition of grassland species with 50% more investment in root biomass compared to shoot competition through those species alone. Aboveground biomass allocation of *Rumex* was unaffected by competition. Grassland species on the other hand responded to concurrent shoot and root competition through *Rumex* with 20% more shoot biomass compared to no competition treatment. Belowground biomass allocation of grassland species was unaffected by competition through *Rumex*. *Rumex* roots also showed a significantly higher C:N ratio when concurrent shoot and root competition through grassland species occurred compared to only shoot or no competition through grassland species. C:N ratios of *Rumex* shoots and of grassland shoots and roots remained unaffected by competition. Despite changes in biomass allocation of *Rumex* into the root system, this did not translate into changes in the amount of carbon and nitrogen stored in the biomass. However, grassland species allocated significantly more carbon into aboveground organs when only shoot competition and significantly more nitrogen when both shoot and root competition through *Rumex* occurred. Our data indicate that the competitive ability of *Rumex obtusifolius* regenerating from rhizome fragments could be significantly altered by management strategies focussing on improved grassland species performance.

Keywords: Broad-leaved dock, permanent grassland, herbaceous species, plant-plant interactions

Zusammenfassung
Konkurrenzfähigkeit von Rumex obtusifolius *gegenüber Grünland-Arten: oberirdische und unterirdische Allokation von Biomasse und Nährstoffen*
Kenntnisse über die Konkurrenzfähigkeit von *Rumex obtusifolius* gegenüber Grünland-Arten sind essentiell für die Entwicklung effizienter Kontrollstrategien gegen Ampfer. Wir präsentieren hier Resultate eines Gewächshaus-Experiments über die Auswirkungen von Spross- und Wurzelkonkurrenz zwischen sich aus Rhizomstücken regenerierendem *Rumex* und Grünlandarten (Gräser, Kräuter und Leguminosen). Die Konkurrenzfähigkeit der untersuchten Pflanzen wurde dabei ausgedrückt als die relative ober- und unterirdische Biomasse sowie die Konzentration und Allokation von Kohlenstoff und Stickstoff. Die Regeneration von *Rumex* war signifikant beeinflusst durch die Konkurrenz von benachbarten Grünlandarten. *Rumex* reagierte auf gleichzeitige Spross- und Wurzelkonkurrenz durch Grünlandarten mit einer um 50% höheren Investition in Wurzelbiomasse im Vergleich zur Behandlung mit alleiniger Sprosskonkurrenz. Die oberirdische Biomasse-Allokation von *Rumex* blieb von Konkurrenz

durch Grünlandarten unbeeinflusst. Grünlandarten reagierten auf gleichzeitige Spross- und Wurzelkonkurrenz durch *Rumex* mit einer um 20% höheren Sprossbiomasse verglichen mit der Behandlung, in der Konkurrenz ausgeschlossen wurde. Die unterirdische Biomasse-Allokation von Grünlandarten war unbeeinflusst von Konkurrenz durch *Rumex*. *Rumex*-Rhizome zeigten signifikant höhere C:N-Verhältnisse, wenn sowohl Spross- als auch Wurzelkonkurrenz durch Grünlandarten auftrat verglichen mit ausschließlicher Sprosskonkurrenz oder wenn keine Konkurrenz stattfand. Die C:N-Verhältnisse in *Rumex*-Sprossen sowie in Sprossen und Wurzeln der Grünlandarten blieben durch Konkurrenz unbeeinflusst. Trotz der Veränderungen der unterirdischen Biomasse-Allokation von *Rumex* konnte keine Veränderung des in der Biomasse gespeicherten Kohlenstoffs und Stickstoffs festgestellt werden. Die Grünlandarten jedoch verlagerten signifikant mehr Kohlenstoff in die Sprossmasse, wenn nur Spross-Konkurrenz und signifikant mehr Stickstoff, wenn sowohl Spross- als auch Wurzelkonkurrenz durch *Rumex* stattfand. Diese Ergebnisse geben einen Hinweis darauf, dass die Konkurrenzfähigkeit von sich aus Rhizomfragmenten regenerierenden *Rumex obtusifolius* durch Bewirtschaftungsstrategien, die auf einen konkurrenzkräftigen Grünlandbestand zielen, signifikant beeinflusst werden kann.
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Stichwörter: Stumpfblättriger Ampfer, Dauergrünland, krautige Arten, Interaktionen zwischen Pflanzen

Introduction

Competition occurs most commonly when plants utilise the same pool of growth-limiting resources or when one individual species produce chemicals that negatively affect the neighbours (Lambers *et al.* 1998). The competitive ability of a species depends on environmental conditions and its ability to capture resources such as light, water and nutrients (Tilman 1988). No species is competitively superior in all environments, rather, there are trade-offs among traits that are beneficial in some environments, but which cause plants to be poor competitors in other environments. For example, there is a trade-off between allocation to roots to acquire water and nutrients versus allocation to shoots to capture light and CO_2 (Tilman 1988). A high morphological plasticity allows a species to maintain dominance in spatially or temporally variable environments by enabling them to explore continuously new patches of resources that have not been depleted and thus maintaining fitness in the competition with surrounding plants (Grime *et al*. 1986).

In temperate regions, *Rumex obtusifolius* (broad-leaved dock) is a troublesome weed in grasslands and is increasing in dominance especially when cutting for silage and fertilising with slurry occurs (e.g., Stählin 1969, Nashiki 1995, Pekrun *et al.* 2002). The characteristics which make it such successful is its ability to establish quickly from seeds, to flower in the first year, and to produce large quantities of seeds which can remain viable in the soil for very long periods (Foster 1989). Due to its regeneration potential, *Rumex obtusifolius* can withstand close grazing and mowing and can quickly enter openings in the sward caused by gouging or by dung patches (Holm *et al.* 1977). The composition of the grassland plant community is closely linked to the balance of above- and below-ground resources, as well as differences in timing of resource use among plants (e.g. Tilman 1982, Aerts *et al.* 1991, Turner and Knapp 1996, Casper and Jackson 1997). Biomass allocation describes a plant's investment in organs and is ruled by direct trade-offs: biomass investment in a certain plant part can not be used elsewhere. Although *Rumex obtusifolius* is probably one of the best studied weed species world-wide, very few investigations have been conducted on the competitive ability of this species against native grassland species.

In the current study the competitive ability of broad-leaved dock regenerating from rhizome fragments against a grassland sward consisting of grasses, herbaceous and leguminous species was investigated. Therefore we manipulated shoot and root competition in the greenhouse by above- and below-ground trenching of pots. We hypothesised that the fast-growing *Rumex* is characterised by a high morphological plasticity both above- and belowground and follows a different strategy to invest nutrients into different plant organs than slow-growing grassland species and thus has a high ability to outcompete co-occurring grassland species.

Materials and Methods

Experimental design

The experiment was conducted in a greenhouse of the experimental farm „Wiesengut" in Hennef/Sieg near Bonn, Germany, using 4-litre pots (diameter 16 cm, height 20 cm) filled with homogenised sandy-loamy fluvisol obtained from the top 10 cm of an organically managed field of the experimental farm (C:N ratio 11.30, P = 6.2 mg/100g, K = 21.4 mg/100g). Plants were watered when needed using drip irrigation. Four different competition treatments were established by combinations of above- and belowground pot trenching: trenching with a glass panel above ground avoided shoot competition; trenching with a plastic panel below ground avoid root competition; no trenching allowed both shoot and root competition to occur concurrently. Of each pot, one half was planted with one rhizome of *Rumex obtusifolius* excavated from organically managed permanent grassland of the experimental farm. All rhizomes were cut to 4 cm length, horizontally embedded in the pots and covered with 1 cm of soil. The other half of the pot was planted with a grassland sward extracted from the same grassland. Ground cover of sward transplants consisted of similar proportions of grasses (e.g., *Agrostis capillaris, Holcus lanatus, Lolium multiflorum, Poa trivialis*), herbaceous (e.g., *Bellis perennis, Plantago lanceolata, Ranunculus repens, Taraxacum officinale*) and leguminous species (e.g., *Trifolium pratense, Trifolium repens*). Pots with different treatments were randomly distributed on a greenhouse table and rotated once per week to minimise location effects. Each treatment was replicated seven times. The experiment was established in August 2002 and lasted for 62 days (first regeneration of *Rumex obtusifolius* occured six days after starting the experiment).

Measurements

Allocation of biomass was determined after separating the side where *Rumex* was growing from the side where grassland species were growing by cutting the pots in half. Aboveground plant material was cut at the soil surface, oven-dried at 60°C and weighed. Below ground plant biomass was determined after rinsing roots free of soil using a fine water spray over a 1-mm mesh screen; afterwards roots were oven-dried at 60°C and weighed. To determine carbon and nitrogen concentration, oven-dried plant material was ground and analysed using a CHN-analyser (Carlo Erba, Rodano, Italy).

Statistical analysis

Statistical analyses were performed in SAS (version 8 for Windows, SAS Institute, Cary, NC, USA) by ANOVAs using the GLM procedure. Differences among *Rumex* and grassland species were determined using Tukey-Kramer HSD tests (ZAR 1996).

Results

Imposed competition treatments significantly affected shoot biomass allocation of studied grassland species. In treatments where competition between *Rumex obtusifolius* and grassland species was excluded, grassland shoot biomass was significantly lower than in pots where either shoot, root or both shoot and root competition was possible (Fig. 1). Competition treatments had no effect on shoot biomass allocation of *Rumex* (Fig. 1). Allocation to root biomass was significantly affected for *Rumex*, however remained unaffected for grassland species (Fig. 1). *Rumex* allocated significantly more biomass into roots when both shoot and root competition was allowed than when only shoot competition occurred (Fig. 1). Allocation to *Rumex* roots were similar for treatments where root, shoot and root or no competition took place (Fig. 1).

Total carbon and nitrogen concentration of *Rumex* roots was significantly affected by imposed competition treatments (Table 1). When competition was excluded or only shoot competition was allowed to occur carbon:nitrogen ratio of *Rumex* roots was significantly narrower than when either root competition or both shoot and root competition was allowed to occur. Carbon:nitrogen ratio of grassland shoots and roots and *Rumex* shoots were unaffected by imposed competition treatments (Table 1).

Competition treatments significantly affected the amount of carbon and nitrogen stored in aboveground parts of grassland species, however did not affect C and N allocation into *Rumex* shoots and roots or grassland roots (Fig. 2 A,B). When competition was excluded, significantly less carbon was allocated to grassland aboveground material than when shoot competition occurred (Fig. 2A). Similar amounts of carbon were stored in grassland shoots when shoot or shoot and root competition occurred (Fig. 2A). When competition was excluded, significantly less nitrogen was stored in shoot biomass of grassland species than when both shoot and root competition took place (Fig. 2B). Nitrogen allocation in grassland shoot biomass was similar regardless if shoot, root or both shoot and root competition was allowed to occur (Fig. 2B).

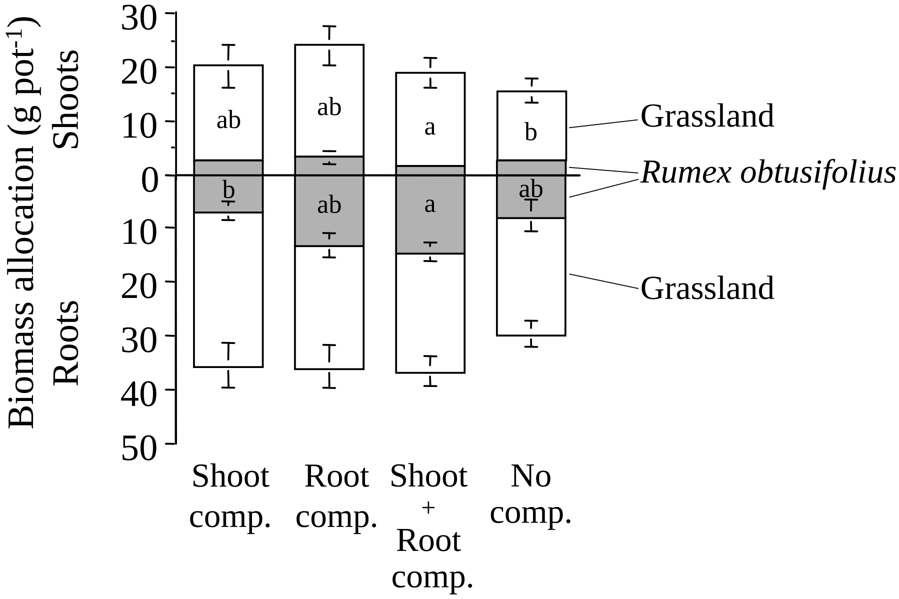

Fig. 1: Biomass allocation of *Rumex obtusifolius* and grassland species (grasses, herbaceous and leguminous species) at different competition treatments (means ± SE, n = 7). Different letters within *Rumex* or grassland indicate significant differences at α = 0.05 (Tukey-Kramer HSD test).

Abb. 1: Biomasse-Allokation von Rumex obtusifolius *und Grünlandarten (Gräser, Kräuter und Leguminosen) bei unterschiedlichen Konkurrenzbedingungen (Mittelwerte ± SE, n = 7). Unterschiedliche Buchstaben innerhalb einer Artengruppe weisen auf signifikante Unterschiede hin (α = 0.05, Tukey-Kramer HSD Test).*

Tab. 1: Carbon:nitrogen ratio in shoots and roots of *Rumex obtusifolius* and grassland species (grasses, herbs and legumes) at different competition treatments (means ± SE, n = 7). Different letters within a row indicate significant differences at α = 0.05 (Tukey-Kramer HSD test).

Tab. 1: Kohlenstoff:Stickstoff-Verhältnis in Sprossen und Wurzeln von Rumex obtusifolius *und Grünlandarten (Gräser, Kräuter und Leguminosen) bei unterschiedlichen Konkurrenzbedingungen (Mittelwerte ± SE, n = 7). Unterschiedliche Buchstaben innerhalb einer Zeile weisen auf signifikante Unterschiede hin (α = 0.05, Tukey-Kramer HSD Test).*

Species group	**Plant part**	**Competition treatments**			
		Shoot comp.	**Root comp.**	**Shoot + root comp.**	**No comp.**
Rumex	shoots	2.31 ± 0.75 a	2.79 ± 1.17 a	1.24 ± 0.52 a	2.36 ± 0.97 a
Grassland	shoots	17.05 ± 3.94 a	16.79 ± 2.76 a	20.25 ± 3.60 a	12.47 ± 2.21 a
Rumex	roots	6.81 ± 1.82 b	13.08 ± 2.28 a	14.42 ± 1.75 a	7.73 ± 2.94 b
Grassland	roots	28.62 ± 4.26 a	22.65 ± 3.93 a	22.05 ± 2.82 a	21.76 ± 2.51 a

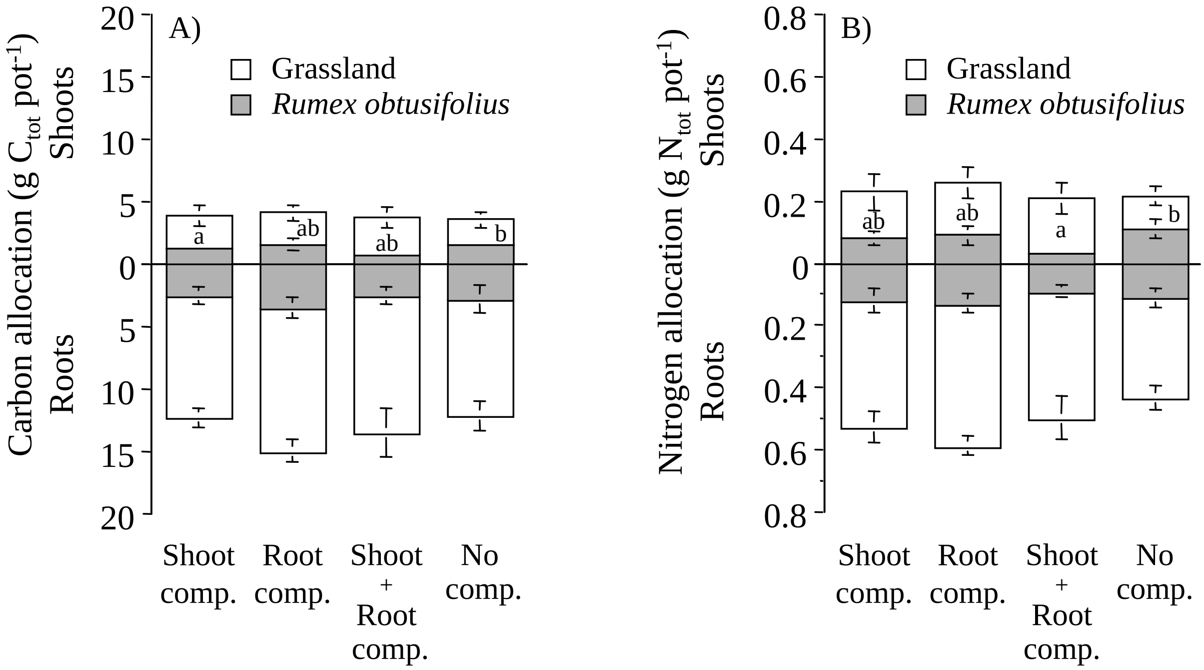

Fig. 2: Allocation of carbon (A) and nitrogen (B) in biomass of *Rumex obtusifolius* and grassland species (grasses, herbs and legumes) at different competition treatments (means ± SE, n = 7). Different letters within *Rumex* or grassland indicate significant differences at $\alpha = 0.05$ (Tukey-Kramer HSD test).

Abb. 2: Allokation von Kohlenstoff (A) und Stickstoff (B) in der Biomasse von Rumex obtusifolius *und Grünlandarten (Gräser, Kräuter und Leguminosen) bei unterschiedlichen Konkurrenzbedingungen (Mittelwerte ± SE, n = 7). Unterschiedliche Buchstaben innerhalb einer Artengruppe weisen auf signifikante Unterschiede hin (α = 0.05, Tukey-Kramer HSD Test).*

Discussion

Our results showed that the regeneration of *Rumex obtusifolius* from rhizome fragments was significantly affected by competition of neighbouring native grassland species. *Rumex* responded to concurrent shoot and root competition of grassland species with 50% more investment in root biomass compared to shoot competition through grassland species alone. This is in line with findings where *Rumex* seedlings have been grown together with seedlings of *Lolium perenne* in a pot experiment (NASHIKI *et al.* 1992). In contrast, when *Rumex* seedlings have been planted in gaps of a *Lolium perenne* sward, *Rumex* was much more affected by root competition than by shoot competition (JEANGROS and NÖSBERGER 1990, 1992). An explanation for this contrasting result might be that the competitive ability does not only vary between species (CAHILL 2002) but can also vary between developmental stages of the same species. Thus, *Rumex* seedlings can be sensitive to shading, while *Rumex* regenerating from rhizomes is more sensitive to both root and shoot competition of neighbouring species. Since we studied effects of competition on the regeneration of *Rumex* from buried rhizome fragments, this could mean that the time lag *Rumex* needs to regenerate from rhizomes (in our experiment some individuals regenerated already within six days) is crucial for grassland species to outcompete *Rumex*. While *Rumex* invested into root biomass when both shoot and root competition was allowed to occur, grassland species responded with 20% more shoot biomass compared to no competition. Obviously, clonal and tussock-forming morphology of grasses showed a higher plasticity in allocating biomass above ground in response to competition (e.g., LAMBERS *et al.* 1998).

While *Rumex* predominantly allocated biomass into roots when both shoot and root competition through grassland species occurred, these roots showed a significantly higher C:N ratio than roots grown when either shoot or no competition occurred. This could be attributed to an investment of carbon in secondary plant compounds with impacts on decomposition rates of *Rumex* roots since higher C:N ratios are commonly associated with lower decomposition rates (LAMBERS and POORTER 1992).

Despite changes in biomass allocation of *Rumex* into the root system, this did not translate into changes in the amount of carbon and nitrogen stored in the biomass. However, grassland species allocated significantly more carbon and nitrogen aboveground when competition through *Rumex* occurred. Nitrogen in grassland shoots was highest when root and shoot competition through *Rumex* occurred concurrently. This plasticity to store and remobilize carbon and nitrogen could provide a mechanism for growth in the spring when the availability of soil nutrients is low (BAUSENWEIN *et al.* 2001).

Taken together, our results demonstrate that the fast-growing *Rumex obtusifolius* showed morphological and chemical plasticity only below ground, however was unresponsive regarding above-ground allocation of biomass and nutrients. Grassland species, on the other hand, only responded above ground to competition with *Rumex* by altered biomass and nutrient allocation. Thus, we assume the success of *Rumex* in a competitive environment is based on the investment into an extensive root system which ensures a rapid regeneration when conditions are more favourable (e.g., when grassland has been mowed). If the aim is to define control strategies against *Rumex obtusifolius* in grassland based on the findings of the current experiment it is important to note that interactions between *Rumex* and grassland species are not only based on competition for resources but also through direct interaction like allelopathy of the competing partners (CARBALLEIRA *et al.* 1988). There is evidence that a dense sward can limit the growth and establishment of *Rumex obtusifolius* from seedlings (e.g., JEANGROS and NÖSBERGER 1990). In the current experiment it could additionally be shown that the competitive ability of *Rumex obtusifolius* regenerating from rhizome fragments could also be significantly altered by management strategies focussing on improved grassland species performance.

Acknowledgements

I am grateful to Ulrich Köpke for comments on the manuscript. Thanks to Christina Günther, Harriet Leese, Ute Reinhold, Birgit Stöcker, Sonja Reinhardt and Dieter Zedow for technical assistance and conducting laboratory analyses.

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