



Regeneration growth of the invasive clonal forb *Rorippa austriaca* (Brassicaceae) in relation to fertilization and interspecific competition

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Abstract

A special type of clonal growth, spread by lateral roots, is hypothesized to be a favourable trait of invasive, opportunistic plant species of disturbed habitats. We tested this hypothesis for the invasive forb *Rorippa austriaca* (Brassicaceae). Regeneration from root fragments, subsequent vegetative spread and allocation patterns in relation to varied nutrient supply and intensity and pattern of interspecific competition were analyzed in container experiments. Regeneration success from root fragments was 100% and clonal spread was rapid but vegetative performance was strongly reduced under unfertilized conditions and, particularly, when interspecific competition was present. While the ratio of above- to belowground bio-mass did not differ considerably between treatments, *R. austriaca* allocated a high amount of resources to belowground growth resulting in low aboveground but high belowground biomass at harvest time relative to the matrix vegetation. Differences in shoot number or biomass between simulated gaps and densely vegetated quadrants in the containers were (relatively) weak. Reproductive effort was less reduced under low resource levels, and the clones did not set seed at all, irrespective of the treatment. Our results show that clonal growth by lateral roots and plasticity in clonal growth patterns in *R. austriaca* promote both exploitation of gaps and nutrient-rich microsites and resistance to competitors. Such plasticity, combined with its ability to regenerate from widely-dispersed root fragments, contribute to the ability of the species to invade and persist within disturbed and spatially heterogeneous habitats.

Introduction

Clonal growth is a widely successful characteristic that has been found in 66.5% of 2760 surveyed central European plants (Klimeš et al. 1997). However, clonal plants generally seem to be at least somewhat underrepresented among alien invasive plants (Klimeš et al. 1997; Pyšek 1997). A possible explanation is mostly poor sexual reproduction of clonal plants. Seedlings have seldom or never been observed in the field for many species (Harper and White 1974; Grubb 1977; Harper 1977; Cook 1985). Efficient long-distance dispersal of seeds is viewed as an important prerequisite for high invasiveness. Clonal plants, which rely more or less on (short-distance)

vegetative propagation, might therefore be less invasive on average than non-clonal plants with higher generative reproduction and seed dispersal (Pyšek (1997) and references therein; plant species are termed 'invasive' in this paper if they increase in abundance in areas where they are not native, following the suggestion of Pyšek (1995)). Furthermore, most invasive plants are associated with disturbed habitats (Rejmánek 1989), conditions which favour short-lived species with rapid reproduction and efficient dispersal (Bazzaz 1983, 1986), whereas clonal plants are apparently more dominant and invasive in less disturbed habitats and in later stages of succession (Prach and Pyšek 1994). Correspondingly, clonal

plants were found to be less frequent than non-clonal plants in disturbed habitats (Klimeš et al. 1997).

Compared to clonal growth by stolons or rhizomes clonal growth by adventitious buds on roots has drawn less attention (Klimeš et al. 1997). This might be partly attributed to the relatively low percentage of clonal plants showing vegetative spread by root-derived organs of clonal growth. However, opposite to the general picture given above, clonal growth by lateral roots is regarded to be typical for opportunistic species growing in disturbed habitats due to the high number of buds which can be produced on lateral roots (Peterson 1975) and the higher foraging efficiency of roots as compared to rhizomes or stolons (Klimeš et al. (1997); Klimeš and Klimešová (1999a) and references therein). Clonal growth by lateral roots may, therefore, result in a higher invasion potential as compared to other clonal growth forms.

For example, shoot production by buds on laterally expanding roots is recognized as an important factor contributing to the high invasiveness of *Euphorbia esula* L. in North America (Selleck et al. 1962; Lym 1998). Additionally, a variety of invasive perennial forbs showing clonal growth by lateral roots can be found within the family of the Brassicaceae, among them *Lepidium latifolium* L. and *Cardaria draba* (L.) Desv. which are problematic mass weeds in several western states in the US (Young et al. 1997; R.D. Richard, *personal communication*) and *Rorippa austriaca* (Crantz) Besser which is locally invasive in the US (cf. Hultén and Fries (1986); Dietz, *personal observation*). The latter two species are also invasive in parts of western or northern Europe (Jalas and Suominen 1994) making them favourable species to study the role of root-derived clonal growth for invasion ability.

In the present study we focus on *Rorippa austriaca* which has mainly spread along river valleys in western Europe (Haeupler and Schönfelder 1988; Jalas and Suominen 1994). In the Middle Main valley in Germany between Lohr (49°59' N, 9°35' E) and Schweinfurt (50°03' N, 10°14' E), where *R. austriaca* was confined to the river banks and riverine meadows twenty years ago (Ullmann 1977), the species has recently spread into a great variety of disturbed habitats including roadsides, orchards, vineyards, meadows and ruderal sites in general (Dietz & Ullmann, *personal observation*). When present in vineyards it is of major concern for the vine-growers because it has deep-reaching rootstocks which seem to compete efficiently with the grape vines for water, a

limiting resource in the vineyards of sun-exposed slopes.

R. austriaca combines clonal growth by lateral roots with the ability to regenerate from root fragments produced and translocated by anthropogenic management. In contrast, sexual reproduction in the field seems to be very restricted because *R. austriaca* often fails to produce significant amounts of viable seeds and few seedlings have been observed in the field (Woitke 2001). Stands of *R. austriaca* can be found growing in sandy soils as well as in nutrient-rich loamy soils in habitats with greatly differing vegetation structure ranging from open, intensively or patchily disturbed sites to sites with dense, more successional herbaceous vegetation.

Based on these observations, the aim of our study was to obtain a better understanding of the role of lateral roots and related traits for high invasiveness of *R. austriaca* under different site conditions typical for unpredictably changing habitats. We hypothesized that (i) a high regeneration potential and (ii) rapid establishment of the semi-rosette species would be crucial for its success. We further assumed that *R. austriaca* shows (iii) plastic responses in its resource allocation pattern and (iv) high and early investment in both clonal and sexual reproduction to be able to efficiently exploit and propagate in unpredictable habitats. Nutrient availability and intensity of competition are highly variable at frequently disturbed sites. Therefore, we analysed the regeneration growth of *R. austriaca* in a fully-factorial (nutrient availability × intensity of competition) design in container experiments.

Material and methods

Species

Rorippa austriaca (nomenclature follows Tutin et al. (1964–1980)) is a polycarpic, perennial hemicryptophyte. It has the potential to reproduce sexually but was found to spread mainly by vegetative propagation via sprouting from lateral roots (Dietz, *personal observation*). Following plagiotropic growth the lateral roots bend downward and the vertical parts become stark and might eventually develop into taproots and produce new shoots and second order lateral roots (Gädeke 1998). In May and June, the species develops flowering stalks of 40 to 100 cm height. The species flowers copiously in June and July but seed

set varies greatly between different sites and years (Dietz, *unpublished*). *R. austriaca* seems to be a rather long-lived species, with fragments of clones attaining ages of at least 13 years (as determined by herbchronology, Dietz and Ullmann (1997)).

Experimental setup

The experiment was run from April to October 1997. Root fragments of *R. austriaca* were collected at a ruderal field site (in the vicinity of Würzburg, Germany, 49°47' N, 9°56' E) where all fragments could be obtained from one large clone. The roots were cut into fragments of similar size (length 12 – 15 cm, diameter 0.8 – 1.2 cm). Three abundant co-occurring herbs were chosen as competitors: the grass *Arrhenatherum elatius* (L.) P. B. ex J. et C. Presl and the forbs *Bunias orientalis* L. and *Urtica dioica* L. (hereafter, 'matrix vegetation'). Individuals of these species were dug up at ruderal sites in the vicinity of Würzburg. *A. elatius* bunches were trimmed to yield evenly-sized fragments of 7 – 9 cm diameter. Likewise, clones of *U. dioica* were cut to yield rhizome fragments of 0.5 – 1 cm diameter supporting 2 – 3 shoots. One-year old vegetative *B. orientalis* plants were used with a rosette diameter of 13 – 15 cm and main roots cut at 15 – 20 cm depth.

Large plastic tubs (volume 80 l, height 36 cm, diameter 62 cm) were used to reduce the effects of limited container space. The tubs were filled with a mixture of loamy soil and silica sand (1:1) above a 5 cm thick gravel layer with holes at the bottom of the tubs to allow for drainage. Two fertilization treatments were used, the addition of 30 g per tub of a commercial depot fertilizer (Multicote N-P-K [20% N, 10% P, 20% K w/w]) at the beginning of the experiment and a control treatment of no added fertilizer. The per area amount of nitrogen applied to the fertilized tubs is comparable to annual applications in agricultural fields (Bayerische Landesanstalt für Bodenkultur und Pflanzenbau 1997). Additionally, three competition intensity designs were set up. Each tub was subdivided in four quadrants (Figure 1). A quadrant was either left untreated or two individuals each of the three matrix species were randomly assigned to six planting positions. Missing (MC), patchy (PC) and full (FC) interspecific competition intensity, respectively, were simulated by planting no, the two diagonally opposite or all four quadrants (Figure 1). Aboveground plant parts of the matrix vegetation species growing into the bare quadrants of the PC treat-

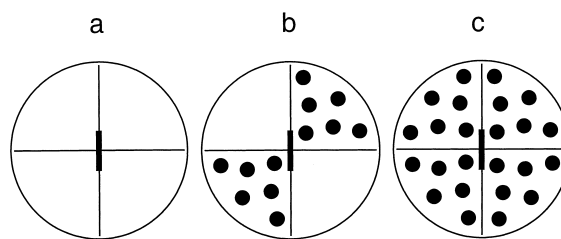


Figure 1. Schematic representation of the experimental setup within the tubs for the three interspecific competition treatments: a, no competition (MC); b, patchy competition with 6 matrix plants in each of two opposite quadrants (PC); c, full competition with 6 matrix plants in each of all four quadrants (FC). The position of the root fragment of *R. austriaca* is indicated by the bar in the centre in each case.

ments were trimmed regularly. The fertilization and the competition treatment factors were combined in a fully-factorial design. One root fragment of *R. austriaca* was planted into each tub (5 cm below the soil surface) with the long axis of the fragment oriented horizontally and the centre of the root fragment aligned with the centre of the pot (Figure 1). The tubs were installed in a flat and fully sun-exposed area of the Botanical Garden of the University of Würzburg. Ten replicates of each of the 6 treatment combinations were used (i.e. a total of 60 tubs). The tubs were arranged in ten blocks of six positions with one replica tub of a given treatment combination assigned to each block. Ten additional MC tubs (MC_h), five of them fertilized and five of them unfertilized, were set up to allow for monthly harvests of *R. austriaca* regenerates growing without interspecific competition. Replica tubs were rotated to allow even exposure to the sun. The tubs were watered on demand and herbivores (slugs) were removed during the whole experimental period. A few transplants of the matrix species, which did not survive, were replaced during the first four weeks of the experiment.

Data collection

Within each tub the total number of shoots and, as a non-destructive estimate of aboveground biomass, the cumulative shoot length (the sum of the lengths of the main axes and the first order basal branches of all shoots) of the regenerating *R. austriaca* clone were determined monthly in the period from May to August. Cumulative shoot length of *R. austriaca* showed a strong linear relationship with aboveground biomass ($R^2 = 0.97$, regression analysis using the monthly data from the MC_h tubs). The positions of

the shoots were mapped to the nearest cm. In June and July the number of flowers and the number of fruits produced per *R. austriaca* clone were determined.

In September, a random sample of 6 tubs of the 10 replicates of each treatment combination was harvested for the homogeneous MC and FC treatments. All 10 tubs were harvested for the PC treatments to increase sample size for the analysis of biomass differences between distinct sections within these heterogeneous tubs. Above- and belowground biomass of *R. austriaca* and of the matrix vegetation were collected separately for each of the four quadrants per tub. For collection of the belowground biomass the soil cores of the tubs were sectioned with a spade and the soil was gently washed off the roots to prevent excessive loss of finer roots. Shoots directly originating in the planted fragment were handled separately (hereafter, the respective tub area is termed 'fragment zone'). The original root fragment and centre root material were not included in determination of per quadrant belowground biomass.

Above- and belowground biomass of *R. austriaca* in each of the fertilized and unfertilized MC_h tubs were harvested at the beginning of each month in the period from June to October. Prior to harvest, total number of shoots and cumulative shoot length were determined. The root systems were analysed for length of first and second order lateral roots still connected to the originally planted root fragment. In all cases dry mass was measured after oven-drying (70°C, 48 h).

Data analysis

STATISTICA for Windows 5.5 (Statsoft Inc., 1999, 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.

Two-factor ANOVA was used for testing the effects of fertilization and competition intensity on final aboveground- and belowground biomass and on the number of flowers per clone. Two-factor ANOVA was also performed to test for biomass differences between the distinct quadrants within the PC tubs. Raw data were square-root transformed in all cases prior to analysis to reduce heteroscedasticity. Although a part of the transformed data sets still showed significant heteroscedasticity this should not seriously affect our results because the F-test is quite robust against violations of the homogeneity of variance as-

sumption (Lindman 1974; Milliken and Johnson 1984).

Log-linear analysis was used to test for significant differences in the number of shoots per tub quadrant or in the fragment zone, respectively, at the different fertilization and competition treatment levels and for different months. The number of shoots totalled over all replications of a given quadrant type was used for the analysis. In August, in the MC tubs the number of shoots was apparently reduced by density effects caused by an intense buildup of shoots at the border of the tubs. These tubs were omitted from analysis for August to avoid the inclusion of artefactual data. Two separate log-linear analyses were run, one including the PC and FC treatments for June to August and the second one including the MC and PC treatments for June and July only. An automatic model fitting procedure was used which first tests the fit of the model without any interactions between factors and, upon lack of fit, proceeds by inclusion of all two-way interactions. If this model does not fit either, higher-order interactions are included. The procedure then eliminates all non-significant interactions from the model. A P-level of >0.1 was chosen as the criterium for sufficient model fit (maximum likelihood χ^2).

Results

General regeneration success

All planted root fragments of *R. austriaca* regenerated rapidly and produced viable clones surviving up to the end of the experiment. New shoots emerged at first in the root fragment zone during May. In the course of the experiment, the developing clones expanded to the border of the tubs so that newly developed shoots could be found as far as possible from the centre of the tubs - irrespective of the treatment combination involved. For MC (missing competition) and fertilized PC (patchy competition) the first shoots emerging at the border of the tubs were observed in June, whereas for the other treatments (unfertilized PC and FC [full competition]) the first shoots at the border of the tubs were observed in July. All clones produced flowering shoots in June.

Table 1. Number of shoots of *R. austriaca* in (a) the different quadrants or (b) the 'fragment zones' within the tubs at three different levels of interspecific competition, at two levels of nutrient availability and at three different months. The values shown represent cumulative values over all replicates. S0, quadrants with reduced competition (bare quadrants); SC, quadrants with full competition (planted quadrants). S1 and S2 correspond to these notations for the tubs without designed differences between quadrants (no competition and full competition treatments). See text and Figure 1. for further information.

a

Month	No competition (MC)				Patchy competition (PC)				Full competition (FC)			
	Unfertilized		Fertilized		Unfertilized		Fertilized		Unfertilized		Fertilized	
	S1	S2	S1	S2	S0	SC	S0	SC	S1	S2	S1	S2
Jun	50	45	166	179	5	0	9	5	1	0	0	0
Jul	226	265	536	494	10	4	65	36	1	2	1	3
Aug	–	–	–	–	50	36	140	65	11	13	14	13

b

Month	No competition		Patchy competition		Full competition	
	Unfertilized	Fertilized	Unfertilized	Fertilized	Unfertilized	Fertilized
Jun	102	152	71	77	66	71
Jul	115	203	68	77	64	64
Aug	–	–	58	74	58	61

Development of *R. austriaca* clones

Shoot population

The shoot population development of *R. austriaca* in the tubs outside of the fragment zone was significantly affected by all four factors (quadrant, competition, fertilization and time) included in the experimental design. The shoot populations were generally denser if grown under reduced interspecific competition, higher nutrient availability and in later months (Table 1). The highest total numbers of shoots (the number of shoots summed over all 10 replica tubs per treatment) were obtained for the unfertilized and fertilized MC treatments in July (491 and 1030 shoots, respectively), compared to only 24 and 27 shoots in the corresponding FC treatments in August (Table 1). The total number of shoots in the PC treatments was intermediate between these extreme values.

Differences in shoot population density within and between the PC and FC tubs were accounted for by three significant interaction terms (quadrant \times competition, competition \times fertilization and fertilization \times month), providing a good model fit (df 14, $\chi^2 = 12.2$, $P = 0.59$). The significant quadrant \times competition term demonstrates an effect of the sectioned design of interspecific competition in PC in comparison to the FC and MC 'controls'; the shoot populations in

the bare quadrants of the PC treatments had about twice the density of those in the planted quadrants whereas there were no considerable and consistent differences between quadrants in the FC and MC treatments (Table 1). While the number of shoots per tub was much higher under fertilized conditions in the PC tubs, there was no such difference between the fertilized and the unfertilized tubs of the FC treatment (significant competition \times fertilization term).

If the MC and PC treatments were compared, there was a positive fertilization effect on the total number of shoots that was relatively stronger in the PC tubs. However, this difference became apparent only in July and may be explained by the limitation of space within the tubs reducing shoot population growth in the fertilized MC treatment. These differences were accounted for by the higher-order interaction competition \times fertilization \times month (implicating significant interactions among all possible pairs of the three factors; model fit: df 6, $\chi^2 = 8.0$, $P = 0.23$) and there was also a significant competition \times quadrant term (see above).

The shoot populations developing in the fragment zone of the tubs were less affected by the different treatments (Table 1). The total number of shoots ranged from 58 to 77 or 71, respectively, in the PC and FC treatments and did not change significantly

over time. The fertilization and competition effects were insignificantly weak with $P \geq 0.15$ (a high model fit was obtained by the sole inclusion of the competition effect: df 10, $\chi^2 = 5.3$, $P = 0.87$). However, if MC and PC were compared, all treatment factors had a significant effect on the total number of shoots produced in the fragment zone. This can be mainly attributed to the high shoot density which developed in the MC tubs (Table 1). In contrast to the PC (and the FC) treatments, fertilization led to a significant increase in the number of shoots in MC and the number of shoots also increased over time (model fit: df 3, $\chi^2 = 3.9$, $P = 0.27$, including significant time and competition \times fertilization effects).

Lateral roots

In the MC_h tubs first order lateral roots (originating in the planted root fragments) started to grow in May and reached their maximum mean length at the beginning of July (Figure 2). The mean length of first order lateral roots did not differ much between the clones obtained from the fertilized and the unfertilized tubs, both ranging from 41 to 47 cm in July and August. Thus, lateral root extension was sufficient for the growing clones to reach the border of the tubs in June given the tub radius of 31 cm which corresponds to the time the first shoots emerged at the border of the tubs. The development of secondary lateral roots occurred mainly in June. Secondary lateral roots were shorter than first order lateral roots with mean values ranging from 21 to 29 cm in July and August. Again, the lengths of the lateral roots were not clearly affected by the fertilization treatments. Even if only mean first- and second order lateral root lengths are summed (July values) this adds up to a minimal mean spread radius of approximately 70 cm which *R. austriaca* could attain by regeneration from one root fragment within just three months.

Biomass (cumulative shoot length)

Shoot growth of *R. austriaca* occurred mostly between May and July, levelling off afterwards (Figures 3 and 4). In the fertilized MC tubs cumulative shoot length increased steeply and reached 5700 cm in August. In comparison, *R. austriaca* reached only low cumulative shoot length in the unfertilized MC tubs (1400 cm in July and August). The strong effect of the fertilization treatment on cumulative shoot length (MC tubs) is reflected in strong biomass differences between *R. austriaca* clones growing under different levels of nutrient availability in the MC_h tubs (Fig-

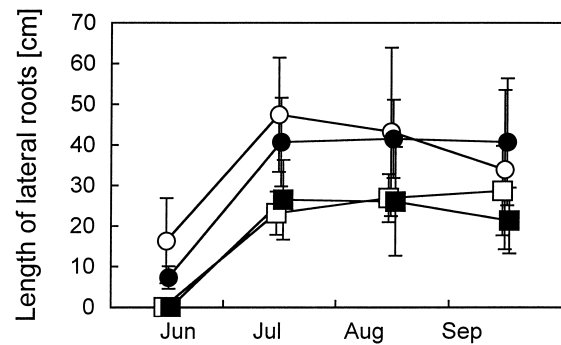


Figure 2. Elongation of first order (circles) and second order (squares) lateral roots within the MC_h tubs (no interspecific competition) between June and September. For individual lateral roots it was required that they could be traced back to their insertion points at either the original root fragment or first order lateral root to be included and classified as either first or second order lateral root, respectively. Filled symbols, fertilized tubs; open symbols, unfertilized tubs. Shown are means of one tub at harvest time \pm S.D.

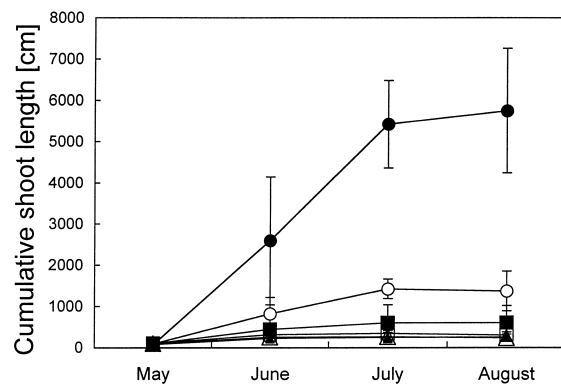


Figure 3. Shoot development (measured as cumulative shoot length) within the tubs between May and August. Filled symbols, fertilized treatments; open symbols, unfertilized treatments. Circles, no competition; squares, patchy competition; triangles, full competition. Error bars indicate \pm S.D.

ure 4). In the presence of interspecific competition the growth of the regenerating clones was particularly weak and, except for the fertilized PC tubs, above-ground growth in the PC and FC tubs levelled off as early as June at low cumulative shoot lengths of 220 to 350 cm (Figure 3).

Whereas aboveground growth of the *R. austriaca* clones decreased early in the MC_h tubs, belowground biomass increased steadily until October (Figure 4). Therefore, the ratio of above- to belowground biomass constantly declined from values of approximately 1 to 2 in June and July to less than 0.15 in October (Figure 4). Apart from variations in June and

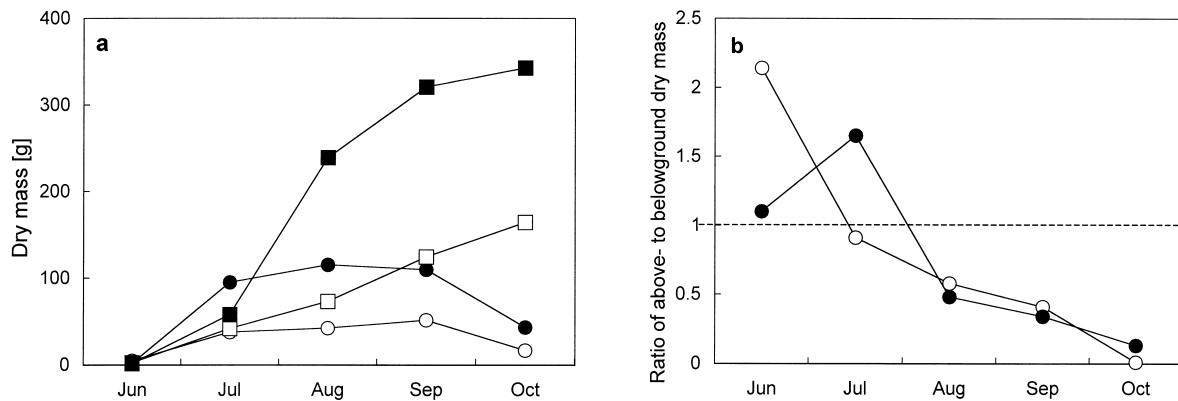


Figure 4. Biomass accumulation within the MC_h tubs (no interspecific competition) between June and October. Each data point represents the biomass value of one tub harvested at the given time. In (a) squares denote belowground bio-mass and circles indicate aboveground biomass. Filled symbols, fertilized tubs; open symbols, unfertilized tubs.

July, this decline was very similar for the fertilized and the unfertilized clones.

By the end of the experiment, fertilization, as well as competition had a significant effect on both aboveground and belowground biomass of *R. austriaca* (Figure 5). Aboveground and belowground biomass were considerably lower under unfertilized conditions ($df\ 1$, $F \geq 24$, $P < 0.001$) and under (increased) interspecific competition intensity ($df\ 2$, $F \geq 393$, $P < 0.001$). However, there were only weak biomass differences between *R. austriaca* clones growing under different levels of nutrient availability in FC although biomass of the matrix vegetation roughly doubled in fertilized as compared to unfertilized tubs. On the other hand, *R. austriaca* could clearly profit from higher nutrient availability under reduced competition in MC and PC (Figure 5; significant interaction term between the fertilization and the competition treatments with $df\ 1$, $F \geq 11$, $P < 0.001$).

Aboveground and belowground biomass of *R. austriaca* were consistently, but not significantly, lower in the planted quadrants of the PC treatments (Figure 5; $df\ 1$, $F \leq 1.25$, $P \geq 0.27$) while aboveground and belowground biomass of the matrix vegetation was absent or strongly reduced in the bare quadrants, respectively. Biomass of *R. austriaca* was markedly and significantly reduced under unfertilized conditions for both, the bare and the planted quadrants in the PC treatment (Figure 5; $df\ 1$, $F \geq 13$, $P \leq 0.001$). However, there was a significant interaction between the fertilization and the quadrant effect for biomass of *R. austriaca* in the PC tubs (multivariate test with $df\ 2$, Wilk's $\lambda = 0.74$, $F = 5.2$, $P = 0.012$) with biomass of *R. austriaca* being more strongly re-

duced in the planted quadrants under unfertilized than fertilized conditions (Figure 5).

Aboveground biomass of *R. austriaca* in MC was less than half of that of the matrix vegetation in FC whereas belowground biomass of *R. austriaca* in the MC treatments was similar to that of the matrix vegetation in the corresponding FC tubs (Figure 5). Thus, in the tubs, the root biomass regenerating from one root fragment of *R. austriaca* could fully compensate for the root biomass developed by 24 planted forbs. However, *R. austriaca* could neither build up nor at least maintain an amount of standing crop comparable to that of the matrix vegetation.

Reproductive effort and reproductive output

All regenerating clones of *R. austriaca* began flowering in June but there were significant differences with respect to the number of flowers produced per clone depending on the fertilization and the competition treatments. Clones growing under fertilized conditions or under less intense competition produced more flowers (Figure 6; $df\ 1$, $F = 8.0$, $P = 0.007$ and $df\ 2$, $F = 10.2$, $P < 0.001$, respectively). These differences can be mainly attributed to the large amount of flowers (1400 per clone) produced by the plants growing in the fertilized MC tubs. The plants in all other treatments produced less than 400 flowers per clone and no clear differences between plants growing in the PC and the FC tubs could be found (Figure 6; $P \geq 0.61$, Duncan post-hoc test).

Despite the considerable reproductive effort of *R. austriaca* there was no reproductive output because seeds produced were inviable.

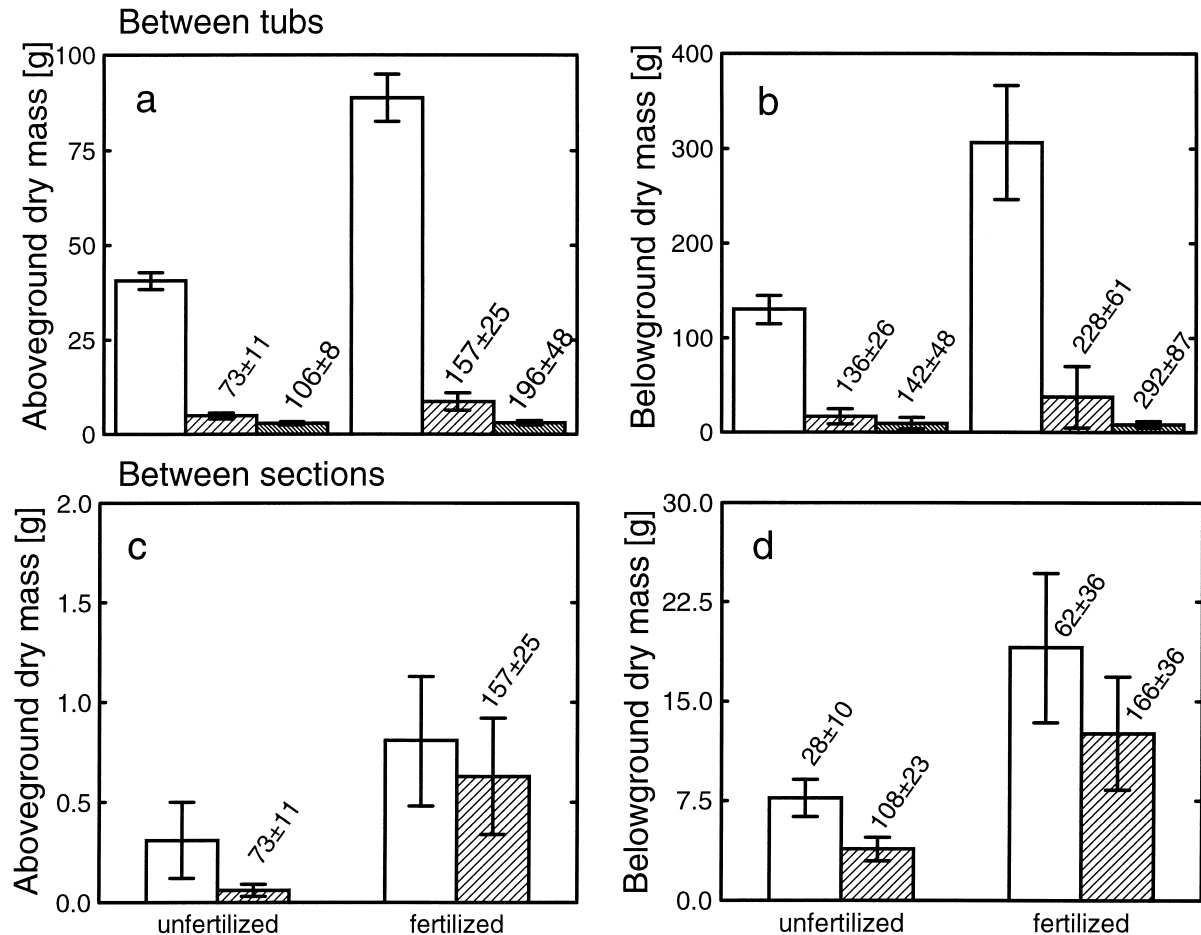


Figure 5. Aboveground and belowground biomass of *R. austriaca* at two different levels of fertilization and three different levels of inter-specific competition intensity at harvest time (September). The numbers above the columns indicate the corresponding biomass values for the matrix vegetation. Biomass values shown are means of tub totals (a and b) or totals of the two different quadrant types in the PC treatment (c and d), respectively. Open columns, no competition (MC, a and b) or bare quadrants (c and d); gray columns, patchy competition (PC, a and b) or planted quadrants (c and d); dark columns, full competition (FC, a and b). Error bars/values denote \pm S.E. Note the different scales on the y-axes.

Discussion

Our results indicate a high potential of *R. austriaca* to invade new sites by regeneration from translocated root fragments. Regeneration success was 100% and clonal spread by lateral roots was rapid in a variety of simulated conditions from high nutrient supply without interspecific competition to low nutrient supply and intense interspecific competition.

Unlike species that only regenerate from the crown region of the roots, e.g. *Heracleum mantegazzianum* Somm. and Lev. (Tiley and Philip 1997), *Silene cucubalus* Wibel (Lubke and Cavers 1970), *Rumex obtusifolius* L. and *Arctium tomentosum* Mill. (Dietz and Steinlein 1998), *R. austriaca* can regenerate from any

position on the roots similar to a variety of other invasive forbs e.g. *Euphorbia esula* (Raju et al. 1964), *Taraxacum officinale* Web. (Maun and Cavers 1979) and *Bunias orientalis* (Steinlein et al. 1996). Furthermore, in contrast to the latter two species, *R. austriaca* develops an extensive, horizontally distributed root system due to lateral root growth providing a massive amount of root material for regeneration. The regeneration capacity of *R. austriaca* appears to be constantly high over the year (Dietz, *unpublished*) whereas in other species it may vary seasonally (e.g. Maun and Cavers (1979) and references therein).

The development of lateral roots in our experiment suggests that *R. austriaca* is able to spread over distances of approximately 1 m within one growth pe-

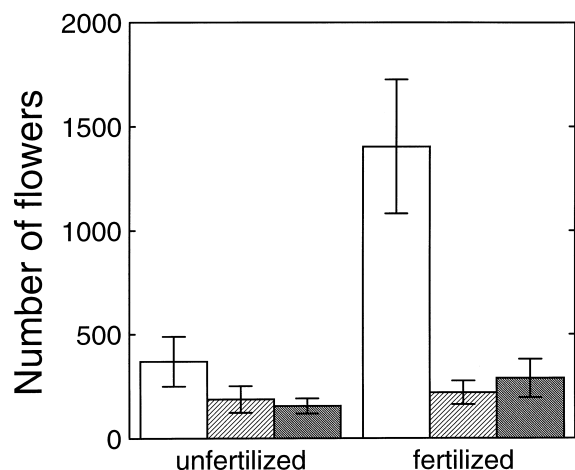


Figure 6. Mean (\pm S.E.) number of flowers of *R. austriaca* per clone (tub) at two different levels of fertilization and three different levels of interspecific competition intensity. Treatment level indication as in Figure 5.

riod in a wide variety of habitat conditions. This figure is within the range of spread by lateral roots observed for other invasive forbs. Depending on habitat conditions, patches of *Euphorbia esula* increased between 9.1 and 1.2 m in radius per year in the US (Selleck et al. 1962). *Lepidium latifolium* was found to expand 1 to 3 m from the main colony by creeping rootstocks in western US (Young et al. 1997).

Clone performance of *R. austriaca* (biomass, number of shoots and number of flowers) was strongly reduced if nutrient availability was low and, particularly, in the presence of interspecific competition even if 'bare' quadrants were present in the matrix vegetation. The species clearly reacts highly positively to elevated resource levels but appears to have low competitive ability. The weak competitive ability of *R. austriaca* is particularly indicated by its failure to profit from fertilization (both in terms of biomass and number of shoots) in the tubs with dense matrix vegetation (FC) while the matrix vegetation in the tubs developed twice as much biomass than in unfertilized tubs. Compared to vegetative performance, reproductive effort of *R. austriaca* was less affected under increasing competition, especially in the unfertilized tubs. This is an unexpected result because a species with weak sexual propagation should allocate more resources to vegetative growth or storage organs rather than sexual functions under resource deprivation. On the other hand, among the ramets that appeared in mid-May or later, developing flowering stalks were restricted to the fertilized MC tubs. This

indicates the elevated resource demand for the development of flowering structures.

In *R. austriaca* biomass ratios were not considerably affected by different levels of nutrient supply or differences in competition intensity, while an increased ratio of above- to belowground biomass under higher nutrient supplies was found for the rhizomatous forb *Urtica dioica* (Šrůtek 1995) and opposite results were obtained for the rhizomatous species *Aster lanceolatus* Willd., *Solidago gigantea* Ait. and *Solidago canadensis* L. (Schmid and Bazzaz 1992). However, the ratio of above- to belowground biomass constantly decreased over time in *R. austriaca* and belowground biomass reached high values towards the end of the experiment. These results correspond well to field observations where larger clones were found to have extensive systems of thick and solid roots. Clonal growth forms with high survival due to extensive long-lived rhizomes or root systems seem to be typical for clonal plants with broad ecological niches (Klimeš and Klimešová 1999b). The high investment in belowground biomass of *R. austriaca* may therefore be viewed as an adaptation to the unpredictability of its wide variety of habitats (Chapin et al. 1990; Suzuki and Stuefer 1999).

The differences in biomass or number of shoots of *R. austriaca* between the different quadrants in the PC tubs were relatively weak given that aboveground biomass of the matrix species was absent and belowground biomass strongly reduced in the bare quadrants of PC. Although *R. austriaca* deployed more shoots in the bare quadrants, as expected, it did invade the dense quadrants of the matrix vegetation to a considerable extent. In contrast to rhizomatous species whose vegetative spread may be mechanically impeded by a dense root horizon (Schmid and Bazzaz 1992; Cheplick 1997), vegetative spread by lateral roots may be less restricted in dense vegetation as creeping roots often run deeper in the soil than do rhizomes (Gädeke 1998). Similarly, in *Euphorbia esula*, competing herbaceous vegetation did not prevent horizontal extension of lateral roots (Selleck et al. 1962).

The observed pattern of shoot growth within and outside of the fragment zone demonstrates that *R. austriaca* clones can grow by first developing a dense centre (phalanx) and then spread by producing more scattered and distant shoots (guerilla strategy). This pattern of growth is also suggested by field observations of scattered *R. austriaca* clones showing a dense centre of large shoots surrounded by a corona of scat-

tered smaller shoots intermingling with the matrix vegetation (Gädeke 1998). A compact genet architecture can be related to the ability to tolerate competition, whereas a spreading genet architecture is viewed as a strategy to escape competition, i.e. to place new ramets in more resource-rich microsites (de Kroon and Schieving 1990; Schmid 1990; Schmid and Bazzaz 1992). In later stages of succession, the proportion of clonal plants with guerilla growth has been found to be higher than that of clonal plants with phalanx growth indicating that the guerilla growth strategy might be favoured when there is the necessity to penetrate dense vegetation (Prach and Pyšek 1994). On the other hand, Cheplick (1997) suggested that more phalanx-like genotypes can be selectively favoured under intense competition as genets of the rhizomatous perennial grass *Amphibromus scabrialvis* Trin. Swallen, with shorter inter-ramet distances, were less affected by competition. Therefore, given their relatively weak competitive ability, *R. austriaca* clones appear to have a mixed strategy to persist by maintaining a compact centre part of the clone which seems to be able to resist interspecific competition. In addition, it uses the potential for rapid clonal growth (guerilla strategy) which can be important for early colonization of gaps in the vegetation after disturbances (Fahrig et al. 1994; Brewer and Bertness 1996). Our results indicate that a period of high resource availability after disturbance is important for the development of large phalanx clone centres with consequent gain of higher competitive ability. The expansion of the clone by guerilla strategy does not seem to be as dependent on habitat conditions.

Although *R. austriaca* showed a strongly varying reproductive output at different field sites with strikingly fluctuating proportions of viable seeds (Dietz, unpublished), *R. austriaca* did not produce seeds at all in the container experiment, not even under the most favourable conditions of the fertilized MC tubs where the species flowered copiously. This is consistent with a field experiment, where the species also did not produce seeds in the first year following establishment (Woitke 2001). It seems that the species cannot adaptively reduce its allocation towards flower production in response to decreased resource levels which, in turn, may prevent resource demanding seed set in young clones.

Like the related non-clonal invasive forb *Bunias orientalis* (Dietz and Steinlein 1998; Dietz et al. 1999) *R. austriaca* shows an opportunistic growth and

regeneration strategy that is advantageous in disturbed habitats. However, unlike the former, opportunistic traits of *R. austriaca* are probably not partly based on sexual reproduction but are favoured through clonal growth by lateral roots. High regeneration ability and vigorous growth under increased resource availability are particularly efficient traits given the rapid area occupation by lateral growth of regenerates and the mixed strategy of phalanx and guerilla growth of the species. Although *R. austriaca* suffers strongly from interspecific competition its mode of clonal spread indicates an efficient escaping strategy by rapid and, in dense vegetation, mechanically less impeded lateral clonal growth, conferring a high potential to reach and exploit vegetation gaps. Additionally, high allocation towards the extensive fleshy root system appears to promote persistence of established clones during periods of high competition intensity. The combination of these traits certainly contributes to the high invasiveness of the species in unpredictable environments.

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