

Root sprouting in *Rumex acetosella* under different nutrient levels

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Abstract

Growth of *Rumex acetosella*, a root sprouting plant, was studied in a pot experiment. Each plant of *R. acetosella* consisted of two ramets which were interconnected by a root about 9 cm long. One of the ramets was placed in a compartment with nutrient-rich soil, the other with nutrient-poor soil. The root connection between the ramets either remained intact or was severed at the nutrient interface after planting. Growth of new roots was prevented at the nutrient interface.

The presence of a connection between the ramets did not affect biomass or shoot production in either soil compartment, indicating a poor integration of the interconnected plant systems. In the nutrient-rich environment, two to four times more shoots and biomass were produced than in the low nutrient regime. A large proportion of buds initiated on roots remained dormant, forming a bud bank. When the number of shoots or buds was expressed per g of root dry weight or per m of root length, the nutrient response was no longer evident or, in a few cases, a significant effect in the opposite direction was obtained. These results show that the greater production of buds and shoots in the nutrient-rich environment reflected an allometric relationship between root biomass and the number of buds and shoots initiated on the roots.

Introduction

Plants producing buds on their roots possess several characteristics which make them potentially very efficient in the utilization of local resource-rich patches (Peterson 1975). Plasticity in branching frequency and growth rates is remarkably high in roots (Drew et al. 1973; Burns 1991), when compared with stemoriginated organs of clonal growth (Caldwell et al. 1991a, b; Jackson & Caldwell 1993). If the relationship between root length and the number of buds initiated in different environments is constant, then the producton of shoots by root-sprouting plants may be much higher in nutrient-rich patches than that of rhizomatous or stoloniferous species. This is due to the difference in the efficiency of foraging by roots and stem-originated structures. Roots 'sense' nutrient concentrations whereas the response of rhizomes and stolons to nutrients is indirect, mediated by the roots developed on them (Passioura 1988). In addition, in root sprouting plants, roots of different age may

produce numerous tightly-located buds (Rauh 1937; Peterson 1975). Therefore, the ratio between root length and the number of root buds may even increase in resource-rich environments.

In plants with stolons and rhizomes, the number of shoots which appear on a stem is determined by the number of nodes. This value, multiplied by two in plants with opposite leaves, may not be exceeded by the number of branches originating on a plant module (but see Huber et al., this volume). Plants with serial and colateral buds represent an exception, but this does not change the general pattern because in most plants these types of buds are restricted to the first seedling node (Sandt 1925). In contrast, buds on roots may appear simultaneously in high numbers, independently of root length. Moreover, the distance between individual buds on a stolon or rhizome is fixed soon after the buds have originated, whereas in plants with root buds new buds may establish between buds already present on a root. Therefore, plants with root buds concentrate their ramets in resource-rich patches due

to two processes: firstly, as more roots are produced there, proportionally more shoots appear in the 'good' patches – this corresponds to the increased branching frequency of stoloniferous and rhizomatous clonal plants; secondly, root sprouters may produce a potentially unlimited number of buds on their roots without producing any new root – this partly corresponds to the shortening of internodes.

The number of plant species sprouting from roots is relatively low: about 4% of species in central Europe regularly produce shoots from root buds even if their roots are not injured or otherwise artificially fragmented (Klimeš et al. 1997). Such species rarely attain a high abundance/dominance in plant communities. However, the range of habitats in which individual root-sprouting species occur is wider than that of rhizomatous and stoloniferous species (Klimeš & Klimešová 1999). Some of the most invasive weeds belong to root sprouters (Rauh 1937).

Rumex acetosella L. is one of the common European species regularly sprouting from lateral roots. It belongs to a taxonomically difficult species aggregate which includes several taxa of uncertain status (Löve 1983; den Nijs 1984). They partly differ in ploidy level, leaf and fruit morphology, habitat requirements and geographical distribution (den Nijs 1983). Plants with higher ploidy levels are usually common weeds, sprouting frequently from their roots and colonizing dry habitats disturbed by grazing and human activities. All microspecies belonging to the R. acetosella aggregate are dioecious, with males showing more extensive clonal behaviour than female plants which allocate more biomass to generative reproduction (Putwain & Harper 1972; Vézina et al. 1986; Escarré & Houssard 1991).

The clonal behaviour of R. acetosella in heterogeneous environments is little known. Similarly, the foraging response of other plants sprouting from roots have also rarely been studied. Efficient spreading from saline soils to less-stressed environments by root sprouters has been described by Salzman (1985) in Ambrosia psilostachya. In Sonchus arvensis, a rootsprouting plant of arable land, no ¹⁴C translocation between its ramets interconnected by horizontal roots was observed (Fykse 1974). This indicates that integration of ramets in root sprouters may be much weaker than in plants with stolons and rhizomes in which extensive ¹⁴C translocation has been found in many cases (reviewed by Pitelka & Ashmun 1985 and Jónsdóttir & Watson 1997). In this paper, we focus on clonal growth in a heterogeneous environment, using *R. acetosella*. We pay special attention to bud and shoot formation on the lateral roots of the plant. In particular, we consider on the following questions:

(1) Do the ramets located in a nutrient-rich environment support ramets growing in a poor environment via roots interconnecting the ramets? (2) Is shoot production promoted in nutrient-rich environments? If the answer is yes, then (3) is the number of shoots and buds initiated on roots proportional to root biomass or root length, or does the species form more buds and shoots on roots located in a nutrient-rich as opposed to a nutrient-poor environment?

Methods

Plant material was collected on 10th April, 1996, from an abandoned sand-pit near Suchdol nad Lužnicí, South Bohemia, ca. 400 m a.s.l. The collection site was very nutrient-poor and *R. acetosella* was the dominant species. Natural populations in this area are hexaploids (2n = 42) (Kubát 1990). We collected about 100 female plants which consisted of two ramets and an interconnecting root growing horizontally at a depth of 3–5 cm. Of these, 30 plants of similar ramet size and distance between ramets were selected for the experiment.

The ramets consisted of 3-4 leaves, each about 2 cm long. The length of the horizontal root between the two ramets was 6 to 12 cm. The plants were placed across an interface between nutrient-rich and nutrientpoor soils in pots $46 \times 12.5 \times 10$ cm, as shown in Figure 1. Two soil mixtures corresponding to the two nutrient levels were prepared from standard garden soil (N 350 mg/l, P₂O₅ 300 mg/l, K₂O 400 mg/l, pH 6.0) and pure washed quartz sand. The substrates were mixed in a ratio of 1 volume of sand to 1 volume of garden soil for the low nutrient availability, and one to two volumes for the nutrient-rich soil. The pots were divided into two equal parts at the nutrient interface by a plastic sheet to separate the root systems of the two ramets. The root interconnecting the ramets was placed through an incision in the centre of the plastic sheet. The root was then severed in one half of randomly selected pots at the nutrient interface to prevent resource translocation between the two soil compartments via the root. The plants were grown outside over the summer and autumn, and watered when necessary. No additional nutrients were applied. The number of shoots was counted on 23 April, 6 July and 5 October and plants were harvested between 5 and 10 October,



Figure 1. Arrangement of the experiment. Two interconnected ramets of *Rumex acetosella* were planted across an interface of nutrient availability (Time 1). In one half of the pots the horizontal root connecting the ramets was cut at the interface after planting (black arrow). The plants were harvested after 180 days (Time 2).

1996. Four plants died soon after planting, and so only 26 pots were evaluated. Plants in the nutrient-poor and the nutrient-rich compartments of the pots were harvested separately and the number of flowering and non-flowering shoots were counted. The root system of each compartment was washed in the laboratory and separated into four size classes, determined by root diameter: D1 (<0.2 mm), D2 (0.2-0.49 mm), D3 (0.5-1 mm) and D4 (>1 mm). The length of roots of size classes D2, D3 and D4 were measured. For each class, the number of buds, below-ground shoots (i.e., not reaching soil surface), and emerged shoots with leaves, were counted. The separated components were dried at 90 °C to constant weight and weighed.

Differences between the number of shoots of interconnected and severed plants were evaluated by Repeated Measures of ANOVA, using the General Linear Model procedure in SPSS for Windows, release 7.5.2, with horizontal root length connecting original ramets as the covariable. Differences between mean values of variables estimated in the nutrient-poor and nutrient-rich parts of the pots were evaluated using the paired *t*-test. The numbers of leafy shoots, belowground shoots and buds initiated on the roots, and the sum of these three variables, were also expressed per g of root and per m of root length.



Figure 2. The effect of nutrient availability and connection between ramets on the number of shoots (mean + S.E.) of *Rumex acetosella* with time.

Results

The number of shoots in the nutrient-poor and nutrient-rich environments increased rapidly up to the second harvest and then declined in rate or did not change further (Figure 2). The differences between interconnected and severed plants were negligible both in the nutrient-poor (F = 1.1, P = 0.3) and nutrient-rich environments (F = 0.5, P = 0.5; GLM –



Figure 3. The effect of nutrient availability on roots of *Rumex acetosella* on the number of shoots and buds initiated on roots of different diameter (mean + S. E.). Root diameter classes: thin – (D2): 0.2–0.49 mm, medium (D3): 0.5–1 mm, thick (D4): >1 mm. * – number of shoots/buds is different between poor and rich environments at *P* < 0.05.

Repeated Measures), indicating little nutrient transport between the interconnected ramets. The effect of the distance between the two planted ramets, which was used as a covariable in the Repeated Measures of ANOVA when comparing the number of shoots in the two environments, was also non-significant (nutrient-poor environment: F = 1.639, P = 0.3; nutrient-rich environment F = 0.06, P = 0.8; GLM – Repeated Measures). Data within nutrient treatments were therefore pooled for statistical analysis.

Plants growing in the nutrient-rich environment produced significantly more non-flowering and flowering shoots than plants in the nutrient-poor environment (Table 1). Similarly, the above- and below-ground biomass of shoots and the length and dry weight of roots of different diameter class were also greatly increased under high nutrients (Table 2). Most values for the above-ground parts of the plants were higher in the nutrient-rich environment compared to the poor by a factor of 3 to 4, and for below-ground parts by a factor of 2 to 3. Significant differences were also found for the number of buds and shoots initiated on roots. Shoots were not initiated on very thin roots with diameter less than 0.2 mm (size class D1 in Tables 2 and 3). For individual plants, the number of leafy shoots, and the number of buds on roots, were 2 to 4 times higher in the rich environment than in the poor one (Figure 3).

The numbers of emerged and below-ground shoots and buds, and the totals of these three variables expressed per m of root length and g of root dry weight (Table 3) were very similar in both nutrient regimes. However, overall the number of root-derived structures per unit of root length and mass tended to be greater in the nutrient-poor environment. Only for thick roots (size class D4) was the trend inconsistent. Statistically significant results were obtained only for the greater number of buds and the number of buds + shoots per g of dry weight of all pooled root size classes in nutrient-poor conditions.

Discussion

There was a far greater production of roots of *R. ace-tosella* in the nutrient-rich environment. The length and dry weight of root size classes differing in root diameter was also markedly higher in the nutrient-rich environment than in the poor one. Many other plants respond to variation in soil resource level in a similar way (Hutchings & de Kroon 1994). Roots are very plastic, especially in fast-growing species, however, in unproductive habitats where *R. acetosella* mostly occurs, extensive root production has also been found in some species (Hutchings & de Kroon 1994).

The number of shoots and buds formed on roots in the nutrient-rich soil was also higher. The same effect has been observed in some other root sprouters, such as *Bryophyllum proliferum* (Ossenbeck 1927), *Euphorbia esula* (McIntyre & Raju 1967) and *Hieracium florentinum* (Peterson 1975). The negative correlation between outgrowth from buds on shoots, and from buds on roots, resulting in a prolonged dormancy of buds on roots in fertilized plants of *Euphorbia esula* (McIntyre 1972), was not a problem in *R. acetosella* because most of its shoots were initiated from buds on roots. In *Chondrilla juncea*, no effect of a high nutrient input was observed, but the growth of already-established buds was promoted (Kefford & Caso 1972).

Enhanced root production in the nutrient-rich environment, and the proportionally higher number of buds and shoots on them, corresponds to the effect of stolon or rhizome branching in clonal plants with stem-derived organs of clonal growth. The increase in branching intensity is a 'passive' way of foraging (Cain 1994); the plants have more resources at their disposal and, therefore, they produce more ramets. The difference between the number of shoots, or buds,

Table 1. The effect of nutrient availability on shoot number and dry mass in *Rumex acetosella*.

	Substr		
	Poor	Rich	Signif.
Number of non-flowering shoots	7.57	23.79	* * *
Number of flowering shoots	5.86	16.82	* * *
Dry mass of emerged leafy shoots [g]	0.12	0.42	* * *
Dry mass of below-ground shoots [g]	0.11	0.43	*

* - P < 0.05, * * * - P < 0.001; paired *t*-test.

Table 2. The effect of nutrient availability on root length and dry mass in *Rumex* acetosella.

	Root diameter class (mm)	Substrate		
		Poor	Rich	Signif.
Root length [cm]	D2 (0.2–0.49)	153.64	326.54	* * *
	D3 (0.5–1)	57.5	131.46	* * *
	D4 (>1)	28.96	59.18	*
	All	240.11	517.18	* * *
Dry mass [g]	D1 (<0.2)	0.19	0.48	* * *
	D2 (0.2–0.49)	0.13	0.21	*
	D3 (0.5–1)	0.17	0.42	**
	D4 (>1)	0.26	0.74	*
	All	0.74	1.85	* * *

* P < 0.05, ** P < 0.01, *** P < 0.001; paired *t*-test.

on roots, calculated per g of root dry weight or m of root length in the two environments was either not significant or the opposite to that expected (for buds and buds + shoots per g of root in total). Moreover, there was a weak, but consistent tendency for the production of more buds or shoots per m or g of root in the nutrient-poor as opposed to the nutrient-rich environment, in contrast to general expectation (Sutherland & Stillman 1988). The allometric relationship between dry weight of roots or root length, and the number of shoots or buds on roots may explain this unexpected result. The relationship between the number of buds (n) and dry weight of roots (w) was non-linear (D2) roots may serve as an example: $n = 126.95w^{0.482}$, $R^2 = 0.33$, DF= 50; P < 0.01; data for nutrient levels were pooled). Plants growing in the nutrient-poor environment were on average smaller than plants in the nutrient-rich environment. The non-linear allometric relationship therefore resulted in a higher number of buds produced per g of root biomass in the nutrientpoor environment. Similar results were obtained for the number of buds per m of root length and for the number of leafy shoots and below-ground shoots (not

shown). Examples of apparent differences between plants of the same age, but differing in their ontogenetic development, have been recently reported from various environments (Coleman et al. 1994; Huber & Stuefer 1997; Reekie 1998).

The proportion of buds on roots which produced shoots increased with root thickness at both nutrient levels in a similar way: on the thick roots about 45% of buds on average developed leafy shoots; on medium size roots it was about 20% and on thin roots less then 8%. Therefore, in a similar way as in shoots and rhizomes most buds on roots of R. acetosella remained dormant, waiting for a particular condition that overcomes their dormancy, for example, by disturbance of the root (cutting into fragments) or by an increase in nutrient supply (Petersen 1975). This response corresponds to a 'sit-and-wait' strategy as described for other plants (Hutchings & de Kroon 1994). Dormancy of the buds can be broken by soil resource pulses (McIntyre 1979; Hsiao & McIntyre 1984). In this case the plant would be capable of producing numerous daughter ramets within a short time (McIntyre & Hunter 1975).

	Root diameter class	Per m of root length Substrate		Per g of root length Substrate			
		Poor	Rich	Signif.	Poor	Rich	Signif.
Number of leafy shoots	D2 (0.2–0.49)	3.5	4.5	ns	67.9	84.3	ns
	D3 (0.5–1)	13.6	12.3	ns	44.5	52.0	ns
	D4 (>1)	41.8	31.9	ns	53.0	34.5	ns
	D2+D3+D4	5.7	7.2	ns	62.5	53.1	ns
	D1+D2+D3+D4	_	_	-	31.3	29.1	ns
Number of below-ground shoots	D2 (0.2–0.49)	3.2	2.6	ns	56.3	46.6	ns
	D3 (0.5–1)	8.0	6.9	ns	30.5	28.9	ns
	D4 (>1)	5.1	1.8	ns	6.8	1.5	ns
	D2+D3+D4	3.9	3.5	ns	45.6	33.5	ns
	D1+D2+D3+D4	-	-	-	22.0	15.4	ns
Number of buds	D2 (0.2–0.49)	31.3	27.5	ns	563.5	503.1	ns
	D3 (0.5–1)	65.2	41.9	ns	316.2	155.1	ns
	D4 (>1)	60.7	41.3	ns	87.4	51.1	ns
	D2+D3+D4	38.9	33.2	ns	451.1	284.8	ns
	D1+D2+D3+D4	_	_	-	241.1	135.4	*
Number of shoots and buds	D2 (0.2–0.49)	38.0	34.5	ns	687.6	633.9	ns
	D3 (0.5–1)	85.4	62.5	ns	391.2	236.0	ns
	D4 (>1)	107.5	75.0	ns	147.2	87.0	ns
	D2+D3+D4	48.4	43.9	ns	559.2	371.4	ns
	D1+D2+D3+D4	_	_	-	294.4	180.0	*

Table 3. The effect of nutrient availability on roots and root-originated structures of *Rumex acetosella*. The results are expressed per m of root length or g of dry mass of roots.

ns P > 0.05, * P < 0.05, ** P < 0.01; paired *t*-test.

Generative reproduction may be an alternative to sprouting from roots, however, the small amount of resources stored in the seeds make germination and seedling establishment very uncertain. In contrast, the mother plant of a root-sprouting plant supports the newly-growing plant and its successful establishment is more probable. However, the size of daughter plants sprouting from root buds is relatively small during the early stages of daughter plant development, relative to the mother plant, and nutrient import from the mother plant is relatively weak (Fykse 1974; this study). Therefore, daughter plants of root-sprouting species are intermediate between daughter plants of rhizomatous clonal plants and non-clonal plants with seedlings established from seeds, when support from the mother plant and the size of the daughter plant are considered. This position can be beneficial in small nutrient-rich patches which are unpredictable and which persist over a short time. Root-sprouting plants with their extensive root systems have a relatively high probability of having their roots in a position where a new patch may form, and the support of the young daughter plant by the mother plant makes establishment faster and safer than in generatively reproducing plants. Therefore, we predict that root-sprouting herbs may be particularly successful in regions with a strongly seasonal climate where they may dominate open vegetation with newly-emerged, small, resource-rich patches.

Conclusions

- There is no evidence for the hypothesis that ramets of *R. acetosella* growing in a poor environment are supported by ramets located in a nutrient-rich environment via roots interconnecting the ramets.
- Shoots and buds on roots of *R. acetosella* accumulate in the nutrient-rich environment. However, their number is proportional to the root biomass and root length. This indicates an allometric relationship between the number of shoots and root biomass.

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