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Root and shoot plasticity of the stoloniferous herb *Ajuga reptans* L. planted in a heterogeneous environment

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Summary

In a greenhouse experiment, single ramets of *Ajuga reptans*, a stoloniferous herb, were planted on the divider of two halves of trays. The two halves of a tray had the same or different nutrient supply. The aim was to study root and shoot plasticity and the placement of ramets and roots in response to the heterogeneous nutrient environment.

Number of primary stolons, number of secondary stolons, stolon internode length, number of leaf ramets, total root length (including fine and coarse roots) and root dry weight were greater, but biomass allocation to fine and coarse roots and specific coarse root length were lower under the homogeneous nutrient-rich (the HH-treatment) than under the homogeneous nutrient-poor (the LL-treatment) conditions. No significant response was observed in specific stolon length and specific fine root length.

In the heterogeneous nutrient environment (the HL-treatment), total root length, root dry weight, root biomass allocation and specific root length did not differ between the nutrient-rich and the nutrient-poor halves of the trays for both fine and coarse roots. The same response pattern was found for the number of primary and secondary stolons, the number of leaf ramets, spacer lengths between leaf-ramets (internode length) and specific stolon length. Only the number of shoot ramets was larger in the nutrient-rich than in the nutrient-poor patch.

Ajuga reptans responded strongly to the different homogeneous nutrient supplies (the HH-treatment vs. the LL-treatment) in terms of morphology and growth of roots and shoots. In the heterogeneous environment (the HL-treatment), the differences in response to local nutrient conditions seemed to be reduced due to intraclonal physiological integration. Predictions of an increase in root mass in the nutrient-rich patch as compared to root mass in the homogeneous HH-treatment or even in the nutrient-poor patch of the HL-treatment were not confirmed by the results. Apparently, behaviour of clonal plants in a heterogeneous environment cannot be simply predicted from their behaviour in different homogeneous environments.

Key words: clonal plant, heterogeneity, nutrients, plasticity, root, stolon

Introduction

In natural habitats, essential resources for plant maintenance, growth and reproduction, such as nutrients, often are patchily distributed in horizontal space (Bell et al. 1993; Caldwell & Pearcy 1994), even at scales relevant to plant individuals (Jackson & Caldwell 1993a, b; Stuefer 1996) and plant parts. In such a patchy habitat, a stoloniferous plant may have its interconnected ramets not only in different patches but also on the boundary between different patches. When a ramet grows on the boundary, it first grows out and produces roots (and leaves) and primary shoots (e.g. stolons) into the different patches, and then new daughter ramets with roots may be produced on the stolons in the different patches.

When growing in a patchy environment, a clonal plant may locally respond to the patchiness by altering its root and shoot traits in a way in which the exploitation of the environmental heterogeneity is improved (Lovell & Lovell 1985; Hutchings & de Kroon 1994). In an environment which is patchy in terms of nutrient supply, an increase of root proliferation in the nutrient-rich patch and a reduction of root thickness in

the nutrient-poor patch may improve the uptake of patchily distributed nutrients (Fitter & Hay 1981; Grime et al. 1991; Schortemeyer et al. 1993; Hutchings & de Kroon 1994; Robinson 1994; Fitter 1997; Robinson et al. 1999; Robinson & Rorison 1983). Based on this idea, we predict that when a clonal plant initiates its clonal growth on the boundary between a nutrient-rich and a nutrient-poor patch it would develop thicker roots and higher values of total root length and root weight in the resource-rich patch than in the nutrient-poor patch. Moreover, biomass allocation to roots in the nutrient-rich patch would be higher than that of plants growing in a homogeneously nutrient-rich environment (cf. Brouwer 1983).

A number of studies suggest that when a clonal plant grows in a patchy nutrient environment, selective placement of the ramets in the nutrient-rich patches as a result of a local response to nutrient availability may enhance the exploitation of nutrient patchiness by the whole genet (Hutchings & de Kroon 1994). This selective placement of ramets may be achieved by forming shorter spacers and by branching more intensively in the nutrient-rich than in the nutrient-poor patches (Slade & Hutchings 1987), and may also be due to directional outgrowth of primary branches towards the nutrient-rich patches (Kleijn & van Groenendael 1999). Accordingly, we predict that when a clonal plant initiates its clonal growth on the boundary between a nutrient-rich and a nutrient-poor patch it will direct more primary branches into the resource-rich than into the resource-poor patch and form shorter spacers in the resource-rich than in the resource-poor patch.

These predictions were tested in a greenhouse experiment initiated with individual ramets of *Ajuga reptans*, a stoloniferous herb, planted on the boundary between patches having the same or different nutrient supplies.

Material and methods

The species

Ajuga reptans L. (Lamiaceae) is a stoloniferous winter-green polycarpic herbaceous perennial. It is commonly found in pastures and woodlands in Europe (Grime et al. 1988). The seedlings usually form an orthotropic aboveground stem on which the consecutive pairs of decussate leaves are arranged in such a way, that finally leaves grow out in all directions. The apical buds of these orthotropic shoots develop into inflorescences later in the growing season. The internodes of the base of the stem are usually slightly thickened and very much shortened and compressed. From the base, lateral stolons grow out in different directions depending on the positions of axillary buds on the stem. Each stolon node bears two opposite leaves and usually has adventitious roots. This is called a leaf ramet (sensu Dong et al. 1996). After a certain period of

plagiotropic growth, the stolons turn upright and form orthotropic shoots usually having roots at their bases, i.e. shoot-ramets (sensu Dong et al. 1996). As a result, a genet of *Ajuga reptans* may comprise leaf-ramets and shoot-ramets interconnected by stolon segments. The stolon internodes connecting ramets (spacers) are able to persist rather long, usually for more than one growth season (Grime et al. 1988).

Plant material and experimental design

Plant material was obtained from a small population in the Uithof Botanical Garden at Utrecht University, The Netherlands. The experimental plants were cloned in the garden from three original plants; since it was unknown whether these plants represented different genotypes, we did not keep their clonal offspring separated. The material was kept outdoors for three months prior to the start of the experiment. The experiment was conducted in the greenhouse of the Uithof Botanical Garden at Utrecht University, The Netherlands, from June 29 to November 23, 1990. Initial experimental plants were single shoot-ramets similar in size in terms of plant height and number of leaves. Each experimental plant was grown on a plastic divider (0.5 cm thick and 8 cm high) separating the two halves of one tray (40 cm long, 40 cm wide and 10 cm high) fully filled with river sand. The plants were subjected to a uniformly high nutrient treatment (HH-treatment), a uniformly low nutrient treatment (LL-treatment) and a heterogeneous nutrient treatment (HL-treatment). In the HL-treatment, one of the two halves of the tray was randomly chosen to be a nutrient-poor half and the adjacent half a nutrient-rich half. The high-level nutrient solution contained 1.525 g NH_4NO_3, 0.896 g $NaH_2PO_4 \cdot 2H_2O$ and 1.013 g KCl per l deionized water; the concentration of the low-level nutrient solution was 5% of this. Once per two weeks, each half tray received 100 ml of the appropriate solution. Thus, the high nutrient level was equivalent to 150 kg N, 50 kg P and 150 kg K per hectare and per year. Care was taken to avoid enrichment of the nutrient-poor half tray of the HL treatment when applying the solution to the other half. There were 6 replicates for each treatment. During the experiment, the plants were watered as needed and the trays were regularly rearranged randomly. No breaking of stolons was observed throughout the experiment.

Harvesting and analyses

After 147 days of growth, the plants were harvested. We measured and calculated two groups of plant characters. The first group, consisting of whole-plant characters, included plant dry weight, biomass of inflorescences, stems, leaves, stolons, (fine and coarse) roots, and number of ramets (leaf-ramets and shoot-ramets). The second group referred to plant parts in each of the two halves of the tray, and included total fine root length and weight, biomass allocation to fine roots (g fine roots per g total plant mass), specific fine root length, total coarse root length and weight, biomass allocation to coarse roots, specific coarse root weight, number of primary stolons, number of secondary stolons, number of leaf-ramets and shoot-ramets,

spacer length between leaf-ramets (= internode length) and specific stolon length. The thinnest coarse roots were about 0.42 mm in diameter, while fine roots were always much thinner. Therefore, this size limit was used to distinguish between both root types. The root length was measured with the line-intersect method as modified by TENNANT (1975). The dry weights of different plant parts were determined after drying to constant weight at 75 °C.

The whole-plant characters were analyzed by means of a MANOVA, followed by two orthogonal planned comparisons to test for the effect of nutrient level (HH vs. LL) and of heterogeneity vs. homogeneity (HL vs. HH + LL; SAS 1994). In order to take into account, that both halves of the experimental plants were not independent of each other, the plant-part characters were analyzed by means of Repeated Measures ANOVA, with plant part (Side) as the repeated factor, followed by the same planned comparisons of high vs. low nutrients and heterogeneous vs. homogeneous treatment (SAS 1994).

Results

Whole-plant characters

The treatments clearly affected biomass of the plants and plant components, as well as the number of ramets (Table 1). The effects appeared to be due to differences in nutrient level (contrast H/L, $p < 0.01$) rather than the heterogeneity of the substrate (contrast heterogeneous/ homogeneous, $p > 0.05$). Plants in the HH-treatments accumulated more biomass in all their components than plants in the LL-treatments, with the HL-plants consistently showing intermediate values.

Plant-part characters

Length and dry weight of the fine roots were significantly higher in the HH-treatment than in the LL-treatment, but % biomass allocated to fine roots was lower in the former (Fig. 1, Table 2: contrast H/L). The heterogeneous/homogeneous contrast was significant for fine-root length and % biomass allocation, indicating that the HL-plants accumulated relatively more fine-root length, but allocated relatively less biomass to fine roots in comparison with the homogeneous treatments (Fig. 1, Table 2). For all three parameters, the overall effect of Side was not significant. Differences between the nutrient-poor and the nutrient-rich halves in the HL-treatment were not significant either, as indicated by the non-significant Side x heterogeneous/homogeneous interaction (Table 2). Specific fine-root length was apparently not affected by the treatments at all.

Length and dry weight of coarse roots and % biomass allocated to coarse roots showed much the same patterns

Table 1. Whole-plant characters of *Ajuga reptans* plants growing in the HH, HL and LL treatments, with standard errors in brackets, and summary of a MANOVA (procedure GLM, SAS 1994) with Wilks' Lambda for Treatment effect and the contrasts High/Low (HH vs. LL) and Heterogeneous/ Homogeneous (HL vs. HH + LL).

Characters	Treatments					
	HH		HL		LL	
Dry weight (g)						
Total plant DW	15.01	(1.85)	10.07	(1.34)	1.64	(0.27)
inflorescence	1.08	(0.49)	0.11	(0.05)	0.09	(0.03)
stem	1.26	(0.23)	0.55	(0.08)	0.11	(0.01)
leaves	7.30	(1.18)	5.49	(0.80)	0.56	(0.11)
stolon	1.39	(0.32)	0.50	(0.19)	0.01	(0.01)
fine roots	2.00	(0.32)	1.81	(0.29)	0.59	(0.11)
coarse roots	1.98	(0.25)	1.61	(0.18)	0.28	(0.05)
Number of ramets						
Leaf ramets	43.5	(4.9)	24.2	(4.2)	2.8	(1.2)
Shoot ramets	8.2	(3.8)	4.8	(2.9)	0	(0)

	df	F
Overall treatment effect	16	3.69**
contrast H/L	8	10.94**
contrast het/hom	8	1.68[ns]

** $P < 0.01$, [ns] non-significant

Table 2. Summary of Repeated Measures analyses of variance of high and low nutrient treatments on fine root (FR) characters of plants of *Ajuga reptans* growing on the divider between two tray halves, which received equal (homogeneous) or contrasting (heterogeneous) amounts of nutrients. Effects of fertilization and of heterogeneity versus homogeneity are indicated by the planned contrasts **H/L** and **h/h**, respectively. The interaction term Side x h/h indicates, whether differences between the nutrient-poor and nutrient-rich halves of the heterogeneous treatment were significant.

Effect	FR length		FR mass		alloc. to FR		specific FR length	
	df	F	df	F	df	F	df	F
between subjects								
Treatment	2	11.94***	2	7.41**	2	24.14***	2	3.01
contrast **H**igh/**L**ow	1	14.18**	1	12.56**	1	43.36***	1	1.93
contrast **h**eterog./**h**omog.	1	9.7**	1	2.25	1	4.93*	1	4.1
Error	15		15		15		15	
within subjects								
Side	1	0.17	1	0.82	1	0.01	1	0.23
S × T	2	0.09	2	0.33	2	1.07	2	0.8
S × H/L	1	0.17	1	0.54	1	1.15	1	0.05
S × h/h	1	0.01	1	0.12	1	0.99	1	1.55

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

as those of fine roots, but specific coarse-root length was significantly higher in the LL-treatment (Fig. 2, Table 3). Again, the S × h/h interaction was not significant, indicating that the two halves of the HL-treatment did not differ significantly in these parameters.

The numbers of primary and secondary stolons and the number of leaf ramets also responded strongly to nutrient level, but not to heterogeneity of the substrate (Figs. 3a–c, Table 4), with highest values for all three parameters in HH-plants. The number of shoot ramets was less clearly affected by nutrient level, as both the overall treatment effect and the H/L contrast were non-significant (Fig. 3d, Table 4). The HL-plants produced significantly more shoot ramets in the nutrient-rich halves than in the nutrient-poor halves, as indicated by the significant S × h/h contrast interaction (Table 4).

Stolon internode length was significantly lower in LL- than in HH-plants, with both sides of the HL-plants showing intermediate values which did not significantly differ from each other (Fig. 4a, Table 5). Specific stolon length did not respond significantly to the treatments; the significant S × T and S × H/L contrast interactions most likely represent spurious correlations, since the latter contrast only compares the homogeneous treatments HH and LL , while the S × T interaction will reflect the same pattern (Fig. 4b, Table 5).

Discussion

In the present experiment, most of the investigated plant traits responded significantly to the homogeneous high and the homogeneous low nutrient supplies in a similar way to that generally found for other clonal plant species (DE KROON et al. 1994; DE KROON & HUTCHINGS 1995; DONG et al. 1996). Most responses simply reflect a reduction in growth under nutrient-poor conditions, or well-known adaptations such as the increase in % biomass allocation to fine roots under such conditions. The increase in internode length under nutrient-rich conditions contrasts with the predictions of the foraging hypothesis of SLADE & HUTCHINGS (1987), but a similar response was found in several other species (DE KROON & HUTCHINGS 1995). The effect of nutrient level on internode length in *Ajuga reptans* may simply be an allometric effect of plant size.

Fig. 1. Effects of high (H) and low (L) nutrient treatments on fine-root characters of plants of *Ajuga reptans* growing on the divider between two tray halves, which received equal (homogeneous) or contrasting (heterogeneous) amounts of nutrients: a) total fine-root length, b) fine-root dry weight, c) biomass allocation to fine roots and d) specific fine-root length. In each panel, solid and open bars indicate mean ± SE in nutrient-rich and nutrient-poor tray halves, respectively. For the results of statistical tests see Table 2.

Fig. 2. Effects of high (H) and low (L) nutrient treatments on coarse-root characters of plants of *Ajuga reptans* growing on the divider between two tray halves, which received equal (homogeneous) or contrasting (heterogeneous) amounts of nutrients: a) total coarse-root length, b) coarse-root dry weight, c) biomass allocation to coarse roots and d) specific coarse-root length. In each panel, solid and open bars indicate mean ± SE in nutrient-rich and nutrient-poor tray halves, respectively. For the results of statistical tests see Table 3.

a

b

c

d

Fig. 1

a

b

C

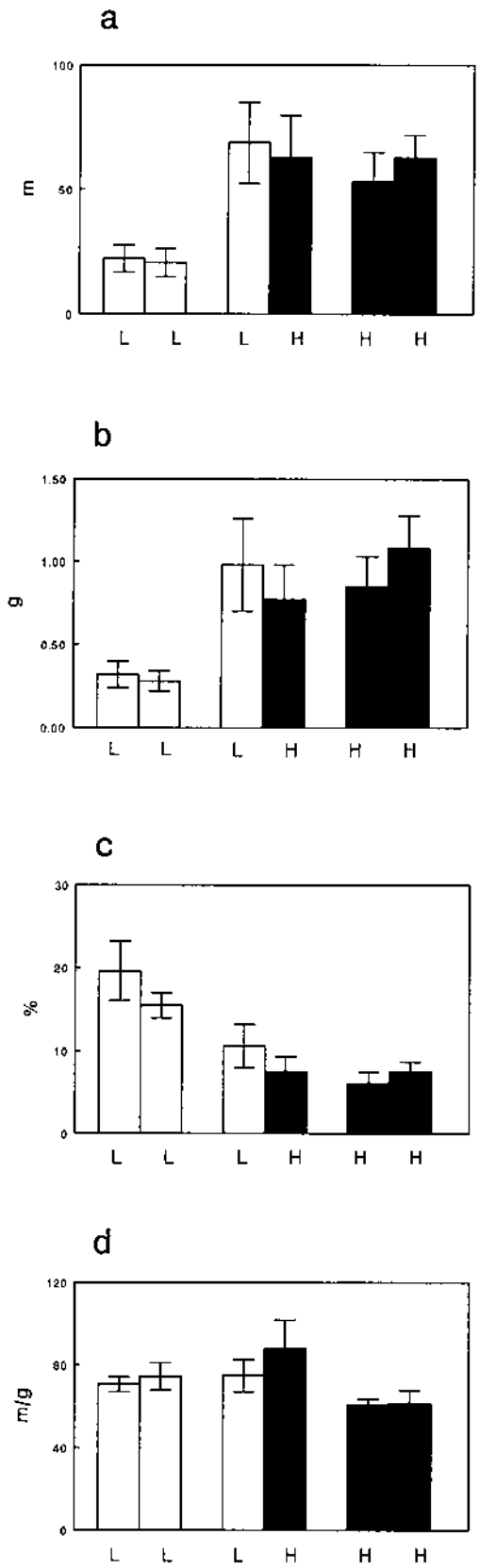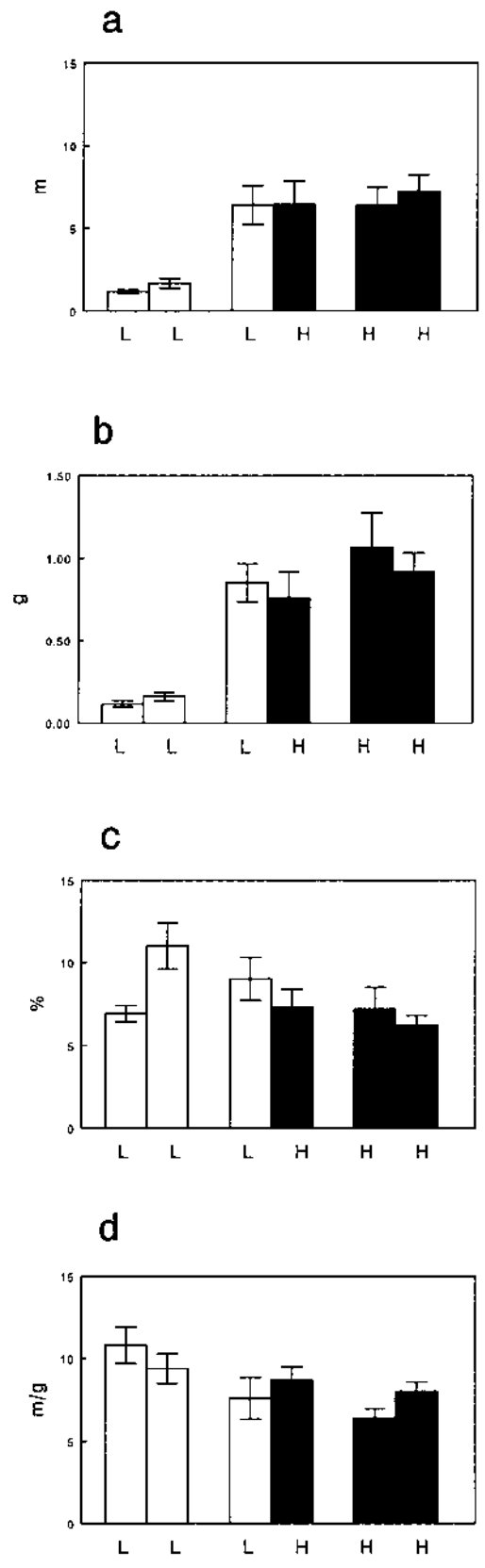## d

Fig. 2

Table 3. Summary of Repeated Measures analyses of variance of high and low nutrient treatments on coarse root (CR) characters of plants of *Ajuga reptans* growing on the divider between two tray halves, which received equal (homogeneous) or contrasting (heterogeneous) amounts of nutrients. Effects of fertilization and of heterogeneity versus homogeneity are indicated by the planned contrasts **H/L** and **h/h**, respectively. The interaction term Side × **h/h** indicates, whether differences between the nutrient-poor and nutrient-rich halves of the heterogeneous treatment were significant.

Effect	CR length		CR mass		alloc. to CR		specific CR length	
	df	F	df	F	df	F	df	F
between subjects								
Treatment	2	27.14***	2	24.44***	2	4.47*	2	4.04*
contrast **High/Low**	1	43.79***	1	44.19***	1	8.72**	1	7.83*
contrast **heterog./homog.**	1	10.49**	1	4.69*	1	0.23	1	0.26
Error	15		15		15		15	
within subjects								
Side	1	0.24	1	0.00	1	2.09	1	0.24
S × T	2	0.08	2	0.54	2	1.81	2	2.48
S × **H/L**	1	0.02	1	0.64	1	3.62	1	4.17
S × **h/h**	1	0.14	1	0.45	1	0.00	1	0.78

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4. Summary of Repeated Measures analyses of variance of high and low nutrient treatments on number of primary stolons (PS), secondary stolons (SS), Leaf ramets (LR) and Shoot ramets (SR) of plants of *Ajuga reptans* growing on the divider between two tray halves, which received equal (homogeneous) or contrasting (heterogeneous) amounts of nutrients. Effects of fertilization and of heterogeneity versus homogeneity are indicated by the planned contrasts **H/L** and **h/h**, respectively. The interaction term Side × **h/h** indicates, whether differences between the nutrient-poor and nutrient-rich halves of the heterogeneous treatment were significant.

Effect	PS		SS		LR		SR	
	df	F	df	F	df	F	df	F
between subjects								
Treatment	2	20.91***	2	5.26*	2	29.21***	2	2.17
contrast **High/Low**	1	41.11***	1	9.26**	1	58.4***	1	4.29
contrast **heterog./homog.**	1	0.72	1	1.25	1	0.02	1	0.05
Error	15		15		15		15	
within subjects								
Side	1	2.57	1	0.11	1	0.01	1	0.88
S × T	2	0.97	2	0.53	2	0.17	2	4.32*
S × **H/L**	1	0.96	1	0.09	1	0.14	1	0.74
S × **h/h**	1	0.98	1	0.97	1	0.19	1	7.91*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

In the heterogeneous treatment, however, most of the investigated plant traits did not differ significantly between the nutrient-rich and nutrient-poor patches. This result contrasts with data from a study on the effect of local heterogeneity in nutrient richness in *Glechoma hederacea*, a stoloniferous plant species which only makes leaf-ramets. In a comparison of the performance of *G. hederacea* in trays with a small, centrally placed high-nutrient patch with that in trays with the same amount of nutrients homogeneously distributed over the tray, BIRCH & HUTCHINGS (1994) found, that the plants in the heterogeneous treatment produced considerably more biomass and concentrated a large proportion of their roots in the nutrient-rich patch. The increase in biomass was wholly due to fast growth of the distal parts of branches with a ramet rooting in the rich patch, suggesting that basipetal transport of nutrients to other parts of the clonal system did not take place. Based on an additional experiment they showed, that the difference in rooting intensity between nutrient-poor and nutrient-rich parts of the tray was due to a difference in timing of root development: root growth started earlier on the ramets rooting in the rich patch, which together with the exponential growth of root length shown by all ramets
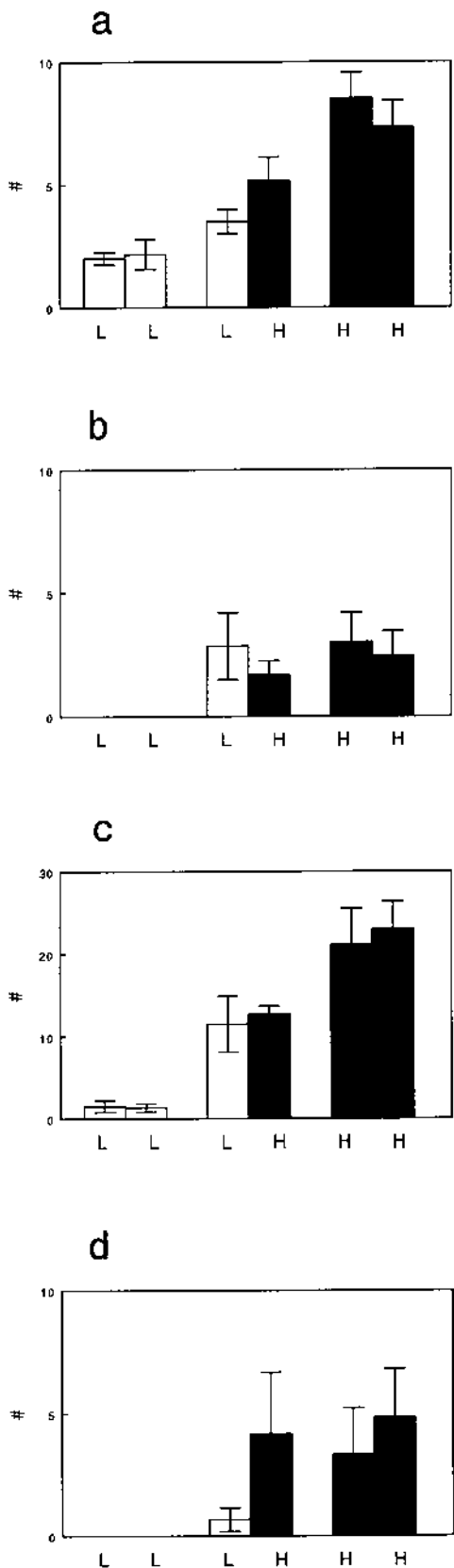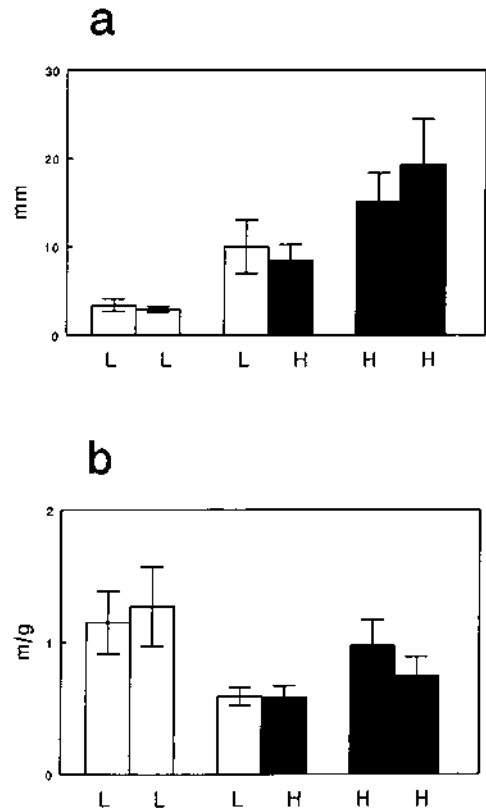
Fig. 3

Fig. 4. Effects of high (H) and low (L) nutrient treatments on internode characters of plants of *Ajuga reptans* growing on the divider between two tray halves, which received equal (homogeneous) or contrasting (heterogeneous) amounts of nutrients: a) spacer length between leaf ramets (= internode length), b) specific stolon length. In each panel, solid and open bars indicate mean ± SE in nutrient-rich and nutrient-poor tray halves, respectively. For the results of statistical tests see Table 5.

resulted in the observed large difference in root intensity. In our experiment almost all root mass was produced by the mother ramets; it is unlikely, that similar differences in timing of root initiation would occur within one and the same ramet, which may partly explain the absence of differences in root growth into both parts of the heterogeneous trays in *A. reptans*.

Fig. 3. Effects of high (H) and low (L) nutrient treatments on stolons and daughter ramets produced by plants of *Ajuga reptans* growing on the divider between two tray halves, which received equal (homogeneous) or contrasting (heterogeneous) amounts of nutrients: a) number of primary stolons, b)number of secondary stolons, c) number of leaf ramets and d) number of shoot ramets. In each panel, solid and open bars indicate mean ±SE in nutrient-rich and nutrient-poor tray halves, respectively. For the results of statistical tests see Table 4.

Table 5. Summary of Repeated Measures analyses of variance of high and low nutrient treatments on spacer length between leaf ramets (stolon internode length, SIL) and specific stolon length (SSL) of plants of *Ajuga reptans* growing on the divider between two tray halves, which received equal (homogeneous) or contrasting (heterogeneous) amounts of nutrients. Effects of fertilization and of heterogeneity versus homogeneity are indicated by the planned contrasts **H/L** and **h/h**, respectively. The interaction term Side × **h/h** indicates, whether differences between the nutrient-poor and nutrient-rich halves of the heterogeneous treatment were significant.

Effect	SIL		SSL	
	df	F	df	F
between subjects				
Treatment	2	4.6*	2	2.82
contrast **H**igh/**L**ow	1	8.94*	1	2.0
contrast **h**eterog./**h**omog.	1	0.02	1	4.66
Error	15		15	
within subjects				
Side	1	1.86	1	1.68
S × **T**	2	1.52	2	4.57*
S × **H/L**	1	2.75	1	6.99*
S × **h/h**	1	0.12	1	0.79

* $P < 0.05$

In a longer-lasting experiment with a similar set-up using five grass species, however, FRANSEN et al. (1998) found only limited increases in root proliferation into an initially nutrient-rich soil patch; they ascribed this to depletion of the patch. Only one species (*Anthoxanthum odoratum*) accumulated more nitrogen and produced more biomass in the heterogeneous than in the homogeneous treatment, but this species did not show an increase in root density in the high-nutrient patch.

Again working with *G. hederacea*, STUEFER & HUTCHINGS (1994) investigated the possibilities for reciprocal transport in a system starting with two connected ramets. In their heterogeneous treatment, one ramet was shaded but got ample nutrients, while the other ramet received more light but less nutrients. In this experiment, both parts of the clonal system responded only to the local environment, with faster growth of the clone part in the nutrient-rich environment but no evidence for nutrient transport to the connected ramet in the nutrient-poor environment. The authors suggested, that this absence of physiological integration was due to the lack of a mechanism for nutrient transport; nutrients are usually transported via the water flow in the xylem, and since both pots received ample water and the ramets in both environments were planted and developed a root system simultaneously, there was no gradient in water potential and thus, no water transport between the plant parts.

However, in experiments under more restrictive growing conditions with *Hydrocotyle bonariensis*, another stoloniferous species with only leaf-ramets, different patterns emerged (EVANS 1992). In a complex experiment in which some clone parts received less light and/or nutrients and/or water than the connected clone part in a high-resource patch, clear evidence of extensive physiological integration between both parts was obtained by studying the effects of severing the connection between both clone parts on their morphology and biomass production. While both parts responded clearly to the local conditions in terms of root development and plant size if the connection was severed, such differences were largely evened out if the connection was left intact. Thus, the difference in root weight per ramet between clone parts in nutrient-poor and in nutrient-rich patches, which was evident in the severed plants, was completely absent in the intact plants. Apparently, basipetal transport of nutrients was not restricted in this species. Only the number of branches and of new ramets produced was strongly affected by the nutrient availability, even if the connection was left intact.

The response of *A. reptans* resembled that of *H. bonariense* in many respects. As a consequence, most of our hypotheses had to be rejected. Plants growing on the boundary between a nutrient-rich and a nutrient-poor patch did not produce more roots (in terms of both dry weight and length) in the nutrient-rich patch than in the nutrient-poor patch or than in the two halves of the homogeneous high-nutrient treatment, did not make more primary or secondary branches into the rich patch, and did not show a difference in internode length between the two patch types. Only the number of new shoot ramets was significantly higher in the rich patch than in the poor patch, although less pronouncedly than in the case of *H. bonariense*. Together, these results strongly suggest that in our heterogeneous nutrient supply treatments the responses of most investigated plant traits to the local nutrient availability were evened out due to physiological integration. Only the structures produced farthest away from the mother ramet, the shoot ramets, showed a significant response to local nutrient conditions. It is possible, that this response is influenced by the conditions experienced by the (few) adventitious roots on the leaf ramets between mother and daughter shoot ramets.

Plant sectoriality, referring to physiological subdivision of a physically coherent plant structure (VUORISALO & HUTCHINGS 1996), may constrain the clonal plants' intraclonal translocation patterns of carbon assimilates, nutrient translocation, water or hormones. Such a sectorial translocation of carbon assimilates between the interconnected ramets and between the interconnected branches was revealed for the stoloniferous herb *Glechoma hederacea* in which sectoriality is determined

by its decussate phyllotaxy (Price et al. 1992, 1996). *Ajuga reptans* and *Glechoma hederacea* both are Lamiaceae and have the same decussate phyllotaxy. Therefore one would expect to find the same phenomenon for *Ajuga* as found for *Glechoma*. However, we found hardly any evidence for sectorial transport of nutrients among the plant parts and our data suggest that there was extensive physiological integration among the plant parts of *Ajuga reptans*. The difference between the two species may be partly due to their different growth form; while *Glechoma* ramets always consist of only two leaves with associated roots and axillary buds, the mother ramet and shoot ramets of *Ajuga* had a much larger number of leaves and a much more extensive root system. Moreover, in the experiment with *Glechoma* ramets were always located in one of the two nutrient environments, the plant parts in these different environments only being connected by internodes. In contrast, in our experiment the mother ramet itself grew on the boundary of the two environments, and therefore roots in the high-nutrient patch and stolons growing into the low-nutrient patch may have been connected directly. Apparently, a sectorial nutrient transport among interconnected plant parts cannot simply be predicted from anatomic features such as phyllotaxy.

Acknowledgements

References

Bell, G.; Lechowicz, M. J.; Appenzeller, A.; Chandler, M.; DeBlois, E.; Jackson, L.; Mackenzie, B.; Preziosi, R.; Schallenberg, M. & Tinker, N. (1993): The spatial structure of the physical environment. – Oecologia **96**: 114–121.

Birch, C. P. D. & Hutchings, M. J. (1994): Exploitation of patchily distributed soil resources by the clonal herb *Glechoma hederacea*. – J. Ecol. **82**: 653–664.

Brouwer, R. (1983): Functional equilibrium: sense or nonsense? – Neth. J. Agric. Sc. **31**: 335–348.

Caldwell, M. M. & Pearcy, R. W. (eds., 1994): Exploitation of environmental heterogeneity by plants: ecological processes above- and belowground. Academic Press, San Diego, USA.

de Kroon, H. & Hutchings, M. J. (1995): Morphological plasticity in clonal plants: the foraging concept reconsidered. – J. Ecol. **83**: 143–152.

de Kroon, H.; Stuefer, J. F.; Dong, M. & During, H. J. (1994): On plastic and non-plastic variation in clonal plant morphology and its ecological significance. – Folia Geobot. Phytotax. **29**: 123–138.

Dong, M.; During, H. J. & Werger, M. J. A. (1996): Morphological responses to nutrient availability in four clonal plants. – Vegetatio **123**: 183–192.

Evans, J. P. (1992): The effect of local resource availability and clonal integration on ramet functional morphology in *Hydrocotyle bonariensis*. – Oecologia **89**: 265–276.

Fitter, A. H. (1997): Nutrient acquisition. In: Crawley, M. J. (ed): Plant ecology (second edition). Blackwell Science, Oxford, 51–72.

Fitter, A. H. & Hay, R. K. (1981): Environmental physiology of plants. Academic Press, London.

Fransen, B.; de Kroon, H. & Berendse, F. (1998): Root morphology plasticity and nutrient acquisition of perennial grass species from habitats of different nutrient availability. – Oecologia 115: 351–358.

Grime, J. P.; Campbell, B. D.; Mackey, J. M. L. & Crick, J. C. (1991): Root plasticity, nitrogen capture and competitive ability. In: Atkinson, D. (ed): Plant root growth: an ecological perspective. Blackwell Scientific Publications, Oxford, 381–397.

Grime, J. P.; Hodgson, J. G. & Hunt, R. (1988): Comparative plant ecology: a functional approach to common British species. Unwin Hyman, London.

Hutchings, M. J. & de Kroon, H. (1994): Foraging in plants: the role of morphological plasticity in resource acquisition. – Adv. Ecol. Res. **25**: 159–238.

Jackson, R. B. & Caldwell, M. M. (1993a): The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. – Ecology **74**: 612–614.

Jackson, R. B. & Caldwell, M. M. (1993b): Geostatistical patterns of soil heterogeneity around individual perennial plants. – J. Ecol. **81**: 683–692.

Kleijn, D. & van Groenendael, J. M. (1999): The exploitation of heterogeneity by a clonal plant in habitats with contrasting productivity levels. – J. Ecol. **87**: 873–884.

Lovell, P. H. & Lovell, P. J. (1985): The importance of plant form as a determining factor in competition and habitat exploitation. In: White, J. (ed.): Studies on plant demography: a Festschrift for John L. Harper. Academic Press, London, 209–221.

Price, E. A. C.; Marshall, C. & Hutchings, M. J. (1992): Studies of growth in the clonal herb *Glechoma hederacea* L. I. Patterns of physiological integration. – J. Ecol. **80**: 25–38.

Price, E. A. C.; Marshall, C. & Hutchings, M. J. (1996): Causes and consequences of sectoriality in the clonal herb *Glechoma hederacea*. – Vegetatio **127**: 42–54.

Robinson, D. (1994): The responses of plants to non-uniform supplies of nutrients. – New Phytol. **127**: 635–674.

Robinson, D.; Hodge, A.; Griffiths, B. S. & Fitter, A. H. (1999): Plant root proliferation in nitrogen-rich patches confer competitive advantage. – Proc. R. Sci. Lond. **266**: 431–435.

Robinson, D. & Rorison, I. H. (1983): A comparison of the responses of *Lolium perenne* L., *Holcus lanatus* L. and *Deschampsia flexuosa* (L.) Trin. to a localized supply of nitrogen. – New Phytol. **94**: 263–273.

Sas (1994): SAS/STAT user's guide, version 6, 4th ed. SAS Institute, Cary.

Schortemeyer, M.; Feil, B. & Stamp, B. (1993): Root morphology and nitrogen uptake of maize simultaneously supplied with ammonium and nitrate in a split root system. – Ann. Bot. **72**: 107–115.

Slade, A. J. & Hutchings, M. J. (1987): The effect of nutrient availability on foraging in the clonal herb *Glechoma hederacea*. – J. Ecol. **75**: 95–112.

Stuefer, J. F. (1996): Potential and limitations of current concepts regarding the response of clonal plants to environmental heterogeneity. – Vegetatio **127**: 55–70.

Stuefer, J. F. & Hutchings, M. J. (1994): Environmental heterogeneity and clonal growth: a study of the capacity for reciprocal translocation in *Glechoma hederacea* L. – Oecologia **100**: 302–308.

Tennant, D. (1975): A test of a modified line intersect method of estimating root length. – J. Ecol. **63**: 995–1001.

Vuorisalo, T. & Hutchings, M. J. (1996): On plant sectoriality, or how to combine the benefits of autonomy and integration. – Vegetatio **127**: 3–8.