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Causes and consequences of sectoriality in the clonal herb *Glechoma hederacea*

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Abstract

The causes of sectoriality and consequences for clone behaviour are examined using data from the stoloniferous herb *Glechoma hederacea*. The proximal causes of physiological integration patterns are investigated using anatomical studies, acid fuchsin dye to reveal patterns of xylem continuity between ramets, and ^{14}C as a label to reveal quantitative photoassimilate translocation patterns in the phloem. Dye movement in the xylem was acropetal and sectorial, and the sectoriality was determined by phyllotaxy. Patterns of ^{14}C-labelled photoassimilate allocation were qualitatively similar to those of xylem based resources, although there was some basipetal movement of photoassimilate. The patterns of physiological integration and independence between ramets are shown to be governed by rules which depend on vascular continuity and discontinuity between ramets. Physiological support to stolon apices results in acquisition of relative branch autonomy (branches become semi-autonomous integrated physiological units, IPUs).

This paper evaluates whether observed physiological integration patterns may be modified by altering normal source-sink relationships or by modifying environmental conditions. An experiment using different defoliation intensities, and different defoliation patterns at the same overall intensity, demonstrated that the precise positions of leaves removed from a clone had unique consequences for its subsequent development. Individual ramets of a given clone may be located in microhabitats of differing quality. An experiment in which competition was either present or absent throughout the space occupied by the clone, or patchy in distribution, showed that *G. hederacea* did not respond to competition at the whole clone level. Instead, connected stolons (IPUs) responded independently to local competition. Sectoriality may promote the restriction of lethal, localised enviromental factors within the affected IPU. A study investigating the uptake and translocation of zinc by clones revealed that quantified patterns of zinc distribution resembled patterns of ^{14}C movement in the phloem, and that there was no significant transport of zinc from one stolon to another.

Although sectorial patterns of resource movement in *G. hederacea* can be modified in the short term, in the long-term, physiological integration may not allow this species to integrate the effects of environmental heterogeneity. A mobile clonal species with a high growth rate and relatively short-lived ramets, such as *G. hederacea*, is likely to benefit from a semi-autonomous response to patch quality at the level of the stolon, since the alternative of widespread intra-clonal support may increase the residence time of the clone in unfavourable patches.

Introduction

By proliferating modules or ramets in the horizontal plane, clonal species may produce structures which occupy considerable areas. As abiotic and biotic conditions in most environments are highly variable (Gibson 1988; Svensson & Callaghan 1988; Lechowicz & Bell 1991; Jackson & Caldwell 1993), individual

ramets of a given clone may be located in microhabitats of differing quality. Negative correlations between the spatial distribution of different essential resources, such as light and nutrients, produce heterogeneous habitats in which most patches are unlikely to be wholly favourable or unfavourable for plant growth (Stuefer & Hutchings 1994). In many clonal species, ramets are physically linked by stolons or rhizomes, and may be physiologically integrated (Pitelka & Ashmun 1985; Marshall 1990). The scale of such integration determines whether the ramets respond to the environment as independent individuals or as functionally integrated parts of a clone. A knowledge of the extent and consequences of ramet integration is therefore fundamental to an understanding of the ecology of clonal plants (Callaghan 1988; Bullock et al. 1994; Herben et al. 1994).

The development of new ramets in clonal plants may be supported by the transport of resources from mature ramets (Pitelka & Ashmun, 1985; Marshall 1990), and this increases the probability of young ramets becoming established and surviving to maturity (Callaghan et al. 1992). Physiological integration may confer other benefits on clonal species (Pitelka & Ashmun 1985). For example, it may enable the clone to function in a coordinated fashion (Slade & Hutchings 1987a–c; Sutherland & Stillman 1988, Friedman & Alpert 1991), and may allow the alleviation of adverse conditions experienced by one part of a clone by subsidy from another part (Ong & Marshall 1979; Hartnett & Bazzaz 1983; Wijesinghe & Handel 1994). In heterogeneous conditions, resource sharing between physiologically integrated ramets through reciprocal translocation of different essential resources may produce a net benefit to the clone in terms of biomass accumulation (Stuefer et al. 1994). It has been proposed that such subsidies between parts of clones should only evolve when the benefit to the whole clone exceeds the cost to the part of the clone providing the subsidy (Salzman & Parker 1985; Slade & Hutchings 1987d).

Despite these benefits, physiological integration may not be advantageous in all circumstances (Pitelka & Ashmun 1985). Breakdown of physiological integration might function as a risk-spreading mechanism; the genet will have a lower risk of mortality if the death of some ramets has little impact on the survival of other connected ramets (Cook 1979; Eriksson 1988). Physiological independence would also prevent those parts of the clone exploring favourable patches of a heterogeneous habitat from having their growth compromised by supporting other parts of the clone in unfavourable patches (Slade & Hutchings 1987a). Fragmentation may therefore be favoured in environments where favourable sites are patchy both in time and space (Pitelka & Ashmun 1985).

The costs and benefits of physiological integration may be influenced by scales of temporal and spatial environmental heterogeneity. For example, risk spreading mechanisms would become relevant when events causing mortality operate at smaller spatial scales than the size of the whole clone, and the cost to a donor part of a clone of providing physiological support could become growth-limiting if the need for subsidy persists for a long time.

Breakdown of physiological integration, despite persistent physical connections between ramets, may occur at a variety of structural levels (Hoshino 1974; Ryle et al. 1981; Pitelka & Ashmun 1985; Watson 1986). For example, clones may become assemblages of semi-autonomous integrated physiological units (IPUs), where the IPU has been defined as 'that level of morphological organization within which the assimilation, distribution and utilization of carbon is regulated' (Watson & Casper 1984). The sizes and boundaries of IPUs are not static, but depend on the plant's vascular organization and developmental maturity (Watson & Casper 1984). In a number of species, semi-autonomous IPUs appear as sectorial structures within which the movement of tracers, mineral and carbon resources is clearly confined (Watson & Casper 1984; Watson 1986; Thomas & Watson 1988; Shea & Watson 1989). For example, carbon movement may be confined within orthostichies of leaves and flowers within branches or stems (e.g. Barlow 1979; Pate & Farrington 1981; Shea & Watson 1989). The sectorial patterns of distribution are due to particular vascular connections between leaves and are highly predictable for a given type of phyllotaxy (Barlow 1979). Thus, phyllotaxy controls sectorial patterns of assimilate movement (Larson 1977; Kirchoff 1984; Oparka & Davies 1985; Watson 1986) and therefore influences which plant parts will be physiologically integrated, i.e. which will be part of the same IPU. Conditions which alter the normal source-sink relationships for assimilate within the plant, such as defoliation (e.g. Joy 1964; Gifford & Marshall 1973) may however modify the boundaries of IPUs, i.e. sinks may become supported by source leaves from another orthostichy.

Glechoma hederacea (Lamiaceae) L. is a stoloniferous clonal herb that typically grows in patchily-shaded, fertile habitats with moist soils (Grime et al. 1988). It is also widespread on spoil heaps, includ-

ing areas of metalliferous waste (Grime et al. 1988). *G. hederacea* is a food plant for many invertebrates, including some folivores (Price 1991). This paper will describe the vascular anatomy and sectorial patterns of resource allocation in *Glechoma hederacea*, and determine whether these patterns can be modified by altering normal source-sink relationships or by modifying environmental conditions by imposing experimental defoliation, competition or heavy metal treatments. The consequences of these sectorial patterns for a clonal plant that spreads in the horizontal plane will then be evaluated.

Causes of sectoriality in *Glechoma hederacea*

Anatomical studies

Glechoma hederacea has opposite decussate phyllotaxy (Bell 1991). Leaves are thus arranged in four files or orthostichies. Each node bears two leaves which emerge from the opposite faces of a quadrangular stolon. Adjacent pairs of leaves are set perpendicular to one another. All nodes can develop roots under suitable environmental conditions, although in the field, rapidly developing clones of *G. hederacea* are commonly observed to have restricted nodal rooting. The leaf axils each contain a lateral meristem which may develop into a higher order (i.e. secondary, tertiary) stolon, thus giving the clone a branched structure (Slade & Hutchings 1987a; Price et al. 1992). Each nodal complex can be regarded as a ramet, i.e. an actually or potentially independent part of a genet (Jackson et al. 1985; Mogie & Hutchings 1990). Experimental material may be derived from single ramets (parent ramets) which develop daughter ramets along primary and higher order stolons (Slade & Hutchings 1987a; Price et al. 1992).

The organization of the vascular system of a species will influence its sectorial characteristics (Gifford & Foster 1989; Fahn 1990). Anatomical studies of *G. hederacea* have shown that the vascular tissue of the stolon is concentrated into four major vascular bundles, and that leaf traces connect each leaf of a ramet to the proximal pair of vascular bundles (Price et al. 1992) (Figure 1). These two vascular bundles also provide vascularization for the secondary stolon developing from the axil of that leaf. Each of the two proximal vascular bundles of the primary stolon divides into two to form the four vascular bundles of the secondary stolon, i.e. there is a direct vascular connection between a leaf and its axillary stolon (Figure 1). A leaf has one vascular bundle in common with each of the two leaves at each of the adjacent nodes (Figure 1).

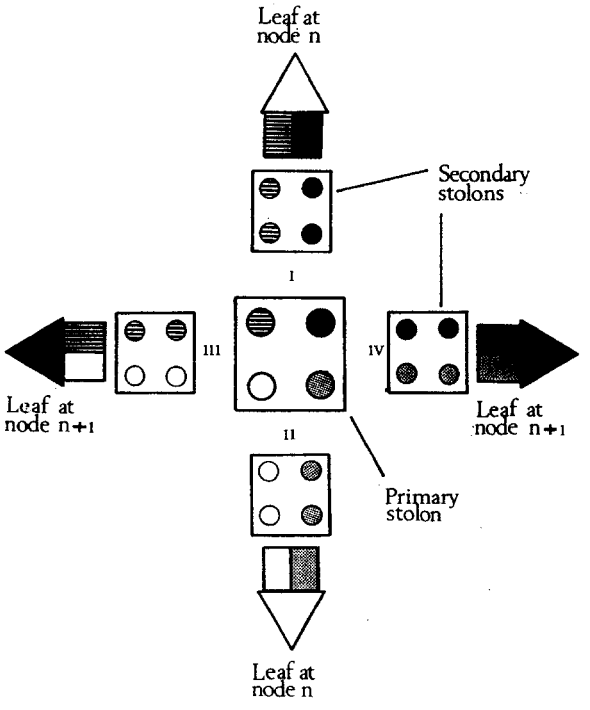

Figure 1. Diagrammatic representation of the relationship between the four vascular bundles (shaded circles in the large central square) in the primary stolon of *Glechoma hederacea* and (i) the vascular bundles in the secondary stolons (small squares at the top & bottom of the diagram) and the petioles of their subtending leaves (arrows with white heads) at primary stolon node *n*, and (ii) the vascular bundles in the secondary stolons (small squares to the left and right of the diagram) and the petioles of their subtending leaves (arrows with black heads) at primary stolon node $n + 1$. Each leaf is served by a leaf trace derived from the proximal pair of vascular bundles in the primary stolon. A leaf has one vascular bundle in common with each of the leaves at adjacent nodes. There is a direct vascular connection between a leaf and its axillary stolon. Each of the two proximal vascular bundles of the primary stolon divides into two to form the four vascular bundles of the secondary stolon.

Xylem transport – acid fuchsin dye

Acid fuchsin dye was applied ('injected', Roach 1939) to the cut petiole of a selected ramet on a clone, in which all daughter ramets were unrooted (Price et al. 1992). All movement of dye in the xylem, which is readily detected by eye, was acropetal (Figure 2). Patterns of dye distribution demonstrated the xylem continuity between ramets. Leaves and secondary stolons distal to, and in the same orthostichy as the leaf injected with dye, became fully infused with dye. They

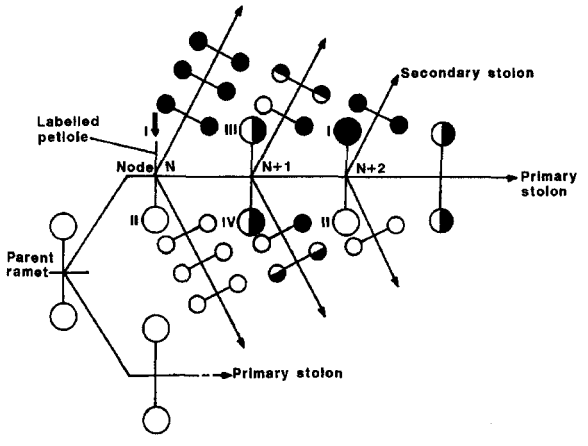

Figure 2. Schematic diagram of part of a clone of *Glechoma hederacea* permeated with acid fuchsin dye, showing the characteristic staining of leaves of primary and secondary stolons distal to the point of application of the dye. The vertical arrow shows the point at which dye was applied.

were thus entirely integrated for transport of xylem-based resources. Leaves and secondary stolons in the opposite orthostichy did not receive dye and therefore appeared to be independent. Leaves and secondary stolons distal to, and in the adjacent orthostichies to the injected leaf, were half infused with dye, and were therefore partially integrated with the injected leaf (Figure 2).

The cause of the pattern was determined by examining sections of stolon nodes (Figure 3). At node n (dye applied), only the two xylem bundles nearest the injected petiole contained dye. At node $n + 1$ each leaf was seen to be served by one xylem bundle which contained dye, and one which did not.

Dye movement in the xylem of *G. hederacea* is therefore highly sectorial and the sectoriality is determined by phyllotaxy. The functional association between leaves and ramets of secondary stolons can therefore be described using simple rules (Figure 3). Firstly, there is no significant xylem continuity between leaves and secondary stolons in opposite orthostichies. Secondly, leaves and secondary stolons in adjacent orthostichies are potentially partially integrated. Thirdly, leaves and secondary stolons in the same orthostichy are capable of full integration.

Phloem transport – ^{14}C assimilate

The patterns of movement of ^{14}C-labelled photoassimilate in the phloem have also been investigated and quantified (Price et al. 1992). Movement in the phloem did not exhibit such clear sectoriality as movement in the xylem, although the degree of support to different parts of the clone was also clearly regulated by orthostichy and vascular connections. For example, the pattern of assimilate translocation after 24 hours from the leaf of a parent ramet of a young clone indicated there was significantly more export of assimilate ($P < 0.01$) to the stolon in its axil (53% of all ^{14}C exported from the labelled leaf) than to the stolon in the axil of its opposite counterpart (15% of the ^{14}C exported) (Price et al., 1992). The pattern of assimilate translocation from an established ramet of a large unrooted primary stolon (Figure 4a), indicated that similar proportions (approximately one-third) of the exported assimilate were exported acropetally and basipetally along the primary stolon (Figure 4b). Most of the remainder (21%) was detected in the secondary stolon arising in the axil of the ^{14}C-labelled leaf; only a trace of assimilate (1%) was detected in the secondary stolon arising from the leaf in the opposite orthostichy. The difference both in specific activity and in the percentage of exported ^{14}C received by stolons in opposite orthostichies, was highly significant ($P < 0.01$). This pattern of differential accumulation of ^{14}C, influenced by phyllotaxy, was repeated in the secondary stolons arising two nodes nearer the apex of the stolon ($P < 0.05$) (Figure 4b). In contrast, neither the proportion of exported assimilate received nor specific activity, differed significantly between the secondary stolons emerging from the node adjacent and acropetal to the labelled leaf. The secondary stolons at this node were inserted in adjacent orthostichies to that of the treated leaf, and both received a small proportion of the exported ^{14}C. These results show that although vascular connections clearly influenced the pattern of differential accumulation of ^{14}C in opposite stolons, this phenomenon was less marked in young primary stolons growing from a parent ramet than in secondary stolons of structurally more complex clones. This difference suggests that, in addition to vascular connections, relative sink strength and proximity of parts are also factors that regulate the distribution of photoassimilate between connected ramets.

Further experiments (Price et al. 1992) have shown that movement of ^{14}C between primary and developing secondary stolons is predominantly acropetal, suggesting that when a new stolon can support its own maintenance and growth it becomes relatively autonomous, acquiring the status of a new IPU. Thus, clones commence growth as highly integrated structures, but as they grow larger and increase in structural complex-

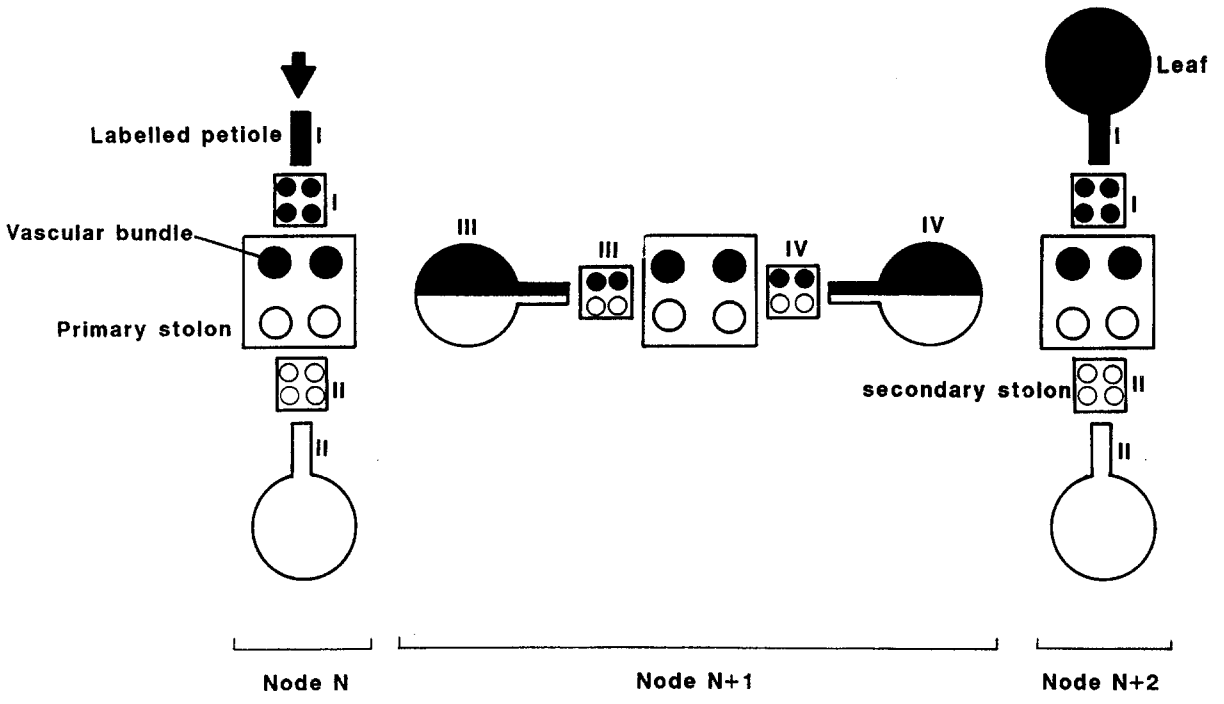

Figure 3. Schematic diagrams of cross sections through a primary stolon of *Glechoma hederacea* which has been permeated with acid fuchsin dye. Cross sections are shown at nodes N, $N + 1$ and $N + 2$. Dye was applied to the petiole of a leaf in orthostichy I at node N (shown by an arrow). The distribution of dye (shown by shaded areas) in the xylem and leaves is shown at node N and at the next two nodes, $N + 1$, $N + 2$, towards the stolon apex. The orientation of the primary stolon is the same in all three diagrams. The diagrams also show the relationship between the four vascular bundles in the primary stolon (circles within the large squares), the vascular bundles in the secondary stolons (circles within the small squares), and the leaves and petioles subtending the secondary stolons. The orthostichies (I–IV) in which leaves and their axillary stolons arise, are also shown.

ity they develop into a number of semi- autonomous structures.

These studies reveal the short-term patterns of resource distribution within clones, and suggest that the most significant consequence of sectoriality in this horizontally spreading species is likely to be the establishment of stolon semi-autonomy. Although vascular connections clearly influence patterns of resource movement within clones, other factors such as relative sink strength seem to be important. Complementary experiments, described below, have investigated the long-term effects on the clone of physiological connections between ramets. These studies aimed to reveal whether physiological integration patterns are modified following the imposition of local defoliation or local competition treatments or whether these sectorial patterns significantly influence growth in the long-term.

Consequences of sectoriality for *G. hederacea*

Responses to defoliation

Defoliation of ramets in a clonal species will affect the subsequent growth of newly developing parts by a major reduction in the provision of translocated materials. The loss of any part will only affect that part of the clone with which it is physiologically integrated (i.e. the IPU in which it occurs). For example, loss of leaves in one orthostichy of a primary stolon should only affect further growth of leaves and secondary stolons in the same and adjacent orthostichies. Thus, different patterns of ramet or leaf removal are likely to have unique effects on the future growth of the clone if new source-sink links are not established in response to the loss of source leaves. An experiment was carried out to document the long-term effects on clone development of removing leaves or ramets from *G. hederacea* plants in a number of precise patterns (Price & Hutchings 1992a,b). The proportion of leaves removed was

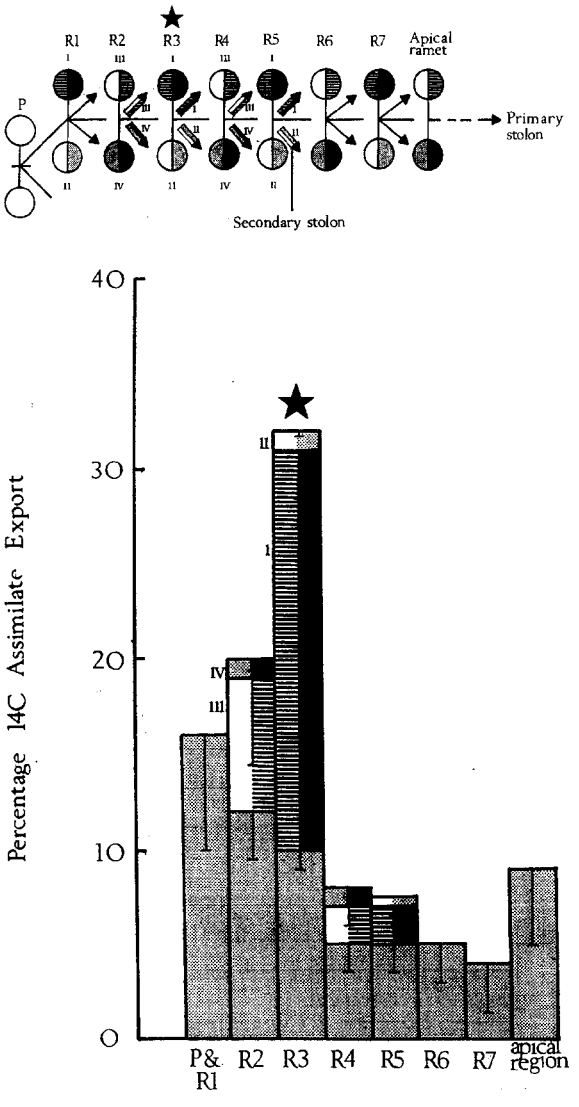

Figure 4. (a) Schematic diagram of *Glechoma hederacea* plants used in investigations of ^{14}C-translocation patterns. The different parts of the plants which were used for analysis of ^{14}C content are drawn as separate, although all ramets were connected at the time of labelling. The treated leaf and the remainder of the treated ramet were sampled separately. A leaf of ramet R3, indicated by an asterisk, was labelled. Different shadings show which vascular bundles enter each leaf and secondary stolon. Leaves with the same shading are in the same orthostichy. Only secondary stolons drawn with differential shading were samples separately. I–IV refer to leaves and secondary stolons in each of the four orthostiches. (b) Mean (±S.E., $n = 5$) percentage export of ^{14}C photoassimilate from a labelled leaf to different parts of *Glechoma hederacea* plants, including the rest of the labelled ramet. The asterisk indicates the ramet to which ^{14}C was applied. All parts of the plant are labelled as in Figure 4a. Primary ramets and their associated internodes are shaded (■). Secondary stolons arising in the four orthostiches I–IV are shaded as in Figure 4a. The labelled leaf was in orthostichy I, shaded (■).

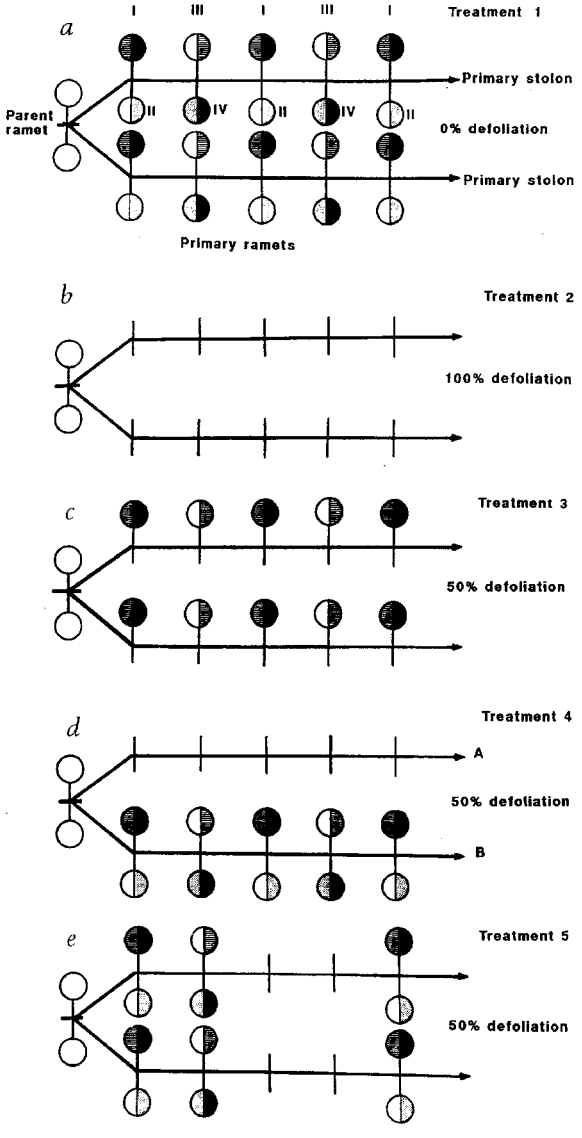

Figure 5. (a–e) Schematic diagram of the defoliation treatments 1–5 respectively. The leaves are labelled according to the orthostichy (I–IV) from which they have arisen, and their shading indicates which of the four vascular bundles in each stolon provides the two leaf traces for each of the leaves (see Figure 1). The labelling of orthostichies cannot be regarded as consistent between different stolons of the same clone.

varied between treatments, from 0% (treatment 1) to 50% (treatments 3, 4 & 5) to 100% (treatment 2), and the pattern of removal was also varied in three different treatments all receiving 50% defoliation (Figure 5).

Since phyllotaxy determines which leaves have common vascular connections, the defoliation regimes can be described in phyllotactic terms (Figure 5). In treatment 3 (50% defoliation), one leaf was removed

from every ramet. The removed leaves were consistently in the same two adjacent orthostichies, so that these were prevented from providing photoassimilate to younger parts of the plant (2 orthostichies defoliated on each stolon). In treatment 4 (50% defoliation), all ramets on one primary stolon were defoliated (4 orthostichies defoliated on one stolon), whereas all of the ramets on the other primary stolon were left intact. In treatment 5 (50% defoliation), pairs of adjacent ramets on both primary stolons were alternately left intact and defoliated, so that leaves in all orthostichies could contribute intermittently as sources of photoassimilate for stolon apices.

Plants were grown from isolated parent ramets which were left intact throughout the experiment. All parent ramets produced two primary stolons and leaves were removed from selected primary ramets when they had reached a diameter of 5mm. Ramets on secondary stolons arising from the axils of defoliated petioles were also defoliated. Five treatments were imposed, with six replicate plants per treatment (Figure 5).

After 12 weeks, the growth response was recorded for each of the two primary stolons and for whole plants in each treatment. At the whole plant level, in comparison with the control, all defoliation regimes caused a significant reduction in all measured aspects of growth except for the number and total mass of primary ramets and the mean length and mass of primary stolons in treatment 5 (Table 1). The most severe defoliation treatment (treatment 2) had the greatest effect on growth; the plants in this treatment had only achieved 7% of the total biomass of the control plants at the end of the experiment (Figure 6). The three 50% defoliation treatments caused different effects on plant development. Growth of plants in treatment 5 was less severely affected in many respects than that of plants in treatments 3 & 4 (Table 1). For example, treatment 5 plants produced 69% of the total biomass of control plants, whereas treatment 3, in which one leaf of every ramet was removed, and treatment 4, in which one primary stolon was defoliated while the other remained intact, produced only 29% and 32% of the control plant biomass respectively (Figure 6) (Price & Hutchings 1992b).

Patterns of physiological integration and independence between ramets seem to have influenced the response of plants to differential defoliation, at different structural levels. Firstly, the results of treatment 3 indicate that there is little integration between leaves across ramets, because the loss of two of the four orthostichies as producers of photoassimilates has dra-

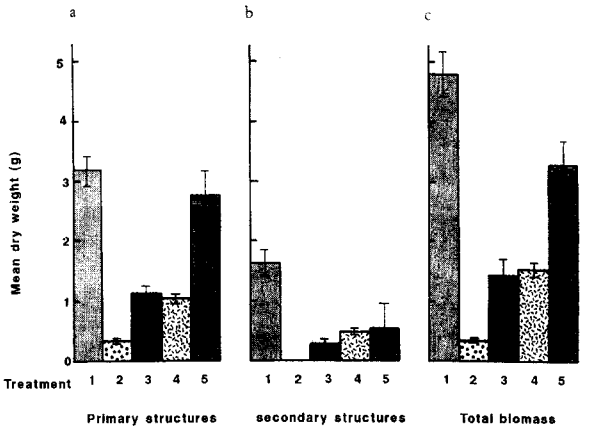

Figure 6. Mean (± S.E., $n = 6$) dry weight of (a) primary structures, (b) secondary structures, (c) whole plants of *Glechoma hederacea* subjected to five experimental defoliation regimes.

matic effects upon all aspects of plant growth (Table 1). These effects are clearly not alleviated by transfer of resources from the intact orthostichies due to the constraints that the vascular anatomy places on resource movement.

Secondly, the results of treatment 5 provide evidence of extensive physiological integration between ramets along individual stolons, since the intermittent loss of sources of photoassimilates has little effect on primary stolon expansion.

Thirdly, the two primary stolons of the plants in treatment 4 differed significantly in many aspects of their growth (Table 1). Although the defoliated stolons of plants in treatment 4 closely resembled those in treatment 2, their intact stolons grew less well in many respects than the intact stolons of the control plants (Table 1). This suggests that integration between the young stolons of treatment 4 plants may have been increased in magnitude and/or duration following defoliation, enabling greater movement of assimilate from the intact stolons to the defoliated stolons. There is some evidence that this may occur in *G. hederacea* (Price et al. 1992). Increased integration may have retarded the growth of the intact stolons before support was withdrawn, but it is clear from these results that, in the long term, physiological integration did not significantly ameliorate the effect of local defoliation on different parts of the plant. Sustained support of the defoliated stolon would have involved significant transport of resources from one stolon to another. This strengthens the view that, in established clones, the point at which stolons branch from the parent structure is the point of disjunction between IPUs in this species.

Table 1. Mean (± S.E., $n = 6$) values for development of different structural components of *Glechoma hederacea* plants grown under five different defoliation treatments. Within each horizontal line of the table, values which are not significantly different are followed by the same letter. All other values are significant at least at the $P < 0.05$ level. * Stolon A is the defoliated stolon in treatment 4, and stolon B is the intact stolon in treatment 4. One stolon was designated A & one B at random in plants in all other treatments, to provide comparisons with the growth of stolons in treatment 4.

	Treatment				
	1	2	3	4	5
Total number of primary ramets	26.50 ± 0.76 c	12.83 ± 0.98 a	17.33 ± 0.67 b	17.50 ± 1.63 b	27.00 ± 0.45 c
Number of primary ramets on stolon A*	13.33 ± 0.76 c	6.67 ± 0.76 ab	8.33 ± 0.80 b	6.00 ± 0.58 a	13.00 ± 0.73 c
Number of primary ramets on stolon B*	13.17 ± 0.48 d	6.17 ± 0.31 a	9.17 ± 0.87 b	11.33 ± 0.33 c	14.00 ± 0.68 d
Total dry mass (g) of primary ramets	2.60 ± 0.22 c	0.11 ± 0.04 a	0.90 ± 0.21 b	0.78 ± 0.11 b	2.25 ± 0.38 c
Number of secondary ramets	45.17 ± 0.83 d	0 a	11.67 ± 2.20 b	13.40 ± 0.88 b	26.17 ± 3.32 c
Number of secondary ramets on stolon A*	21.50 ± 2.17 d	0 a	6.00 ± 1.48 b	0 a	13.33 ± 1.87 c
Number of secondary ramets on stolon B*	23.67 ± 1.87 d	0 a	5.67 ± 0.96 b	13.40 ± 0.88 c	12.83 ± 2.33 c
Mean length (cm) of primary stolons	194.1 ± 14.0 c	78.1 ± 3.37 a	99.2 ± 18.7 ab	109.9 ± 7.8 b	182.7 ± 10.1 c
Dry mass (g) of primary stolons	0.59 ± 0.06 b	0.19 ± 0.01 a	0.24 ± 0.04 a	0.24 ± 0.08 a	0.51 ± 0.03 b

The rigid patterns of defoliation imposed in this experiment are unlikely to mimic closely those produced by herbivores under field conditions. Nevertheless, this experiment clearly demonstrates that the impact of defoliation on subsequent plant growth may be strongly determined by the particular pattern of ramets which are defoliated, rather than by the area of leaf removed, as a result of sectorial patterns of physiological integration between connected ramets.

Responses to competition

The morphology of *Glechoma hederacea* is highly responsive to resource availability (Slade & Hutchings 1987a–c). At different levels of resource supply the frequency of branching at stolon nodes, stolon internode length and stolon weight/length ratio and pattern of allocation of biomass to different structures is altered. In high resource conditions, plants produce short stolon internodes, many stolon branches and many, large ramets. In low resource conditions, few stolon branches with long internodes and few, widely-spaced ramets are produced (Slade & Hutchings 1987a, b). Such plastic morphological responses may promote escape from competitors which cause shortages of essential resources (Callaghan 1988; Hutchings & Mogie 1990). In view of its sectoriality, *G. hederacea* would not be expected to respond to resource availability or competition at a whole clone level. Instead, connected stolons arising from a node would be expected to respond independently to local competition in terms of growth and morphology, because studies of resource movement suggest that they are separate IPUs. This hypothesis was tested by growing connected stolons in different degrees of competition.

In this experiment, competition was either present or absent throughout the space occupied by the clone (pure treatments), or patchy in distribution (split treatments). Plants were grown from isolated parent ramets. All parent ramets produced two primary stolons. Five treatments were imposed, with six replicate plants per treatment. (Figure 7) Plants of *G. hederacea* were grown with either clipped (short) or unclipped (tall) *Lolium perenne* (Treatments TG and SG). In two of the treatments involving competition, one of the two primary stolons of each plant grew with competitors (tall or short grass) while the other stolon grew without competition (Treatments TGS and SGS). Control plants were also grown without competition (Treatment C, Figure 7) (Price & Hutchings, 1996).

Plants were harvested after 12 weeks. Data were collected on whole plants in each treatment and for each of their two primary stolons separately.

Total biomass, and the biomass of both primary and secondary structures, were significantly reduced when whole plants were grown with competition, but surprisingly, all of these components of yield were depressed equally by competition from tall and short grass (Figure 8). Whereas yields for both stolons were similar for plants in the pure treatments, the stolons grown without competition in the split treatments grew significantly more than those subjected to competition (Figure 8). Growth of the isolated stolons in the long grass split treatment was substantially greater than in the control treatment. The reasons for this difference are discussed elsewhere (Price & Hutchings 1996). The morphology

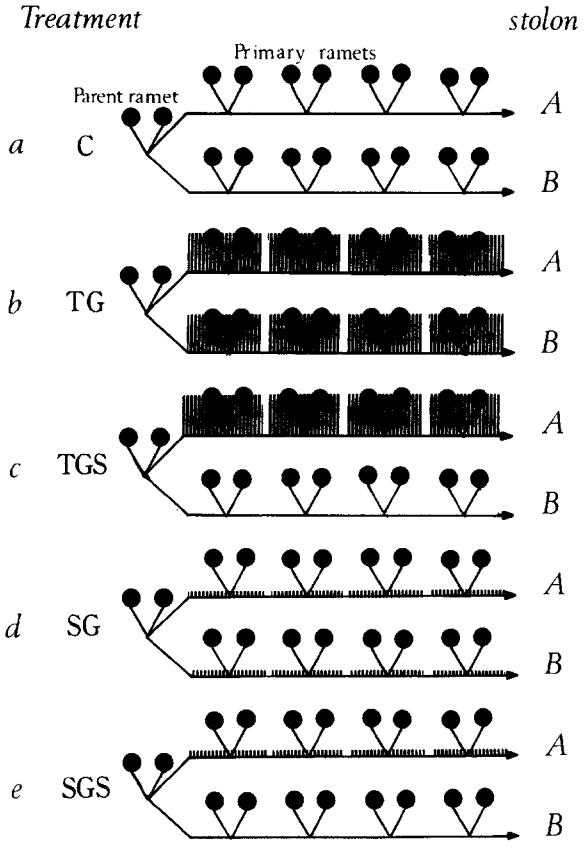

Figure 7. Schematic diagrams of the five experimental competition treatments. Shading indicates which of the stolons in Treatments TG, TGS, SG & SGS were grown in competition with long or short swards of *Lolium perenne*, but is not drawn to scale with respect to *G. hederacea* ramets. Long swards are represented by ■, short swards by ■. For clarity, no secondary structures are shown. In the split treatments, stolon A grew under competitive conditions and stolon B grew in isolation. One stolon was designated A & one B at random in plants in all other treatments, to provide comparisons with the growth of stolons in the split treatments.

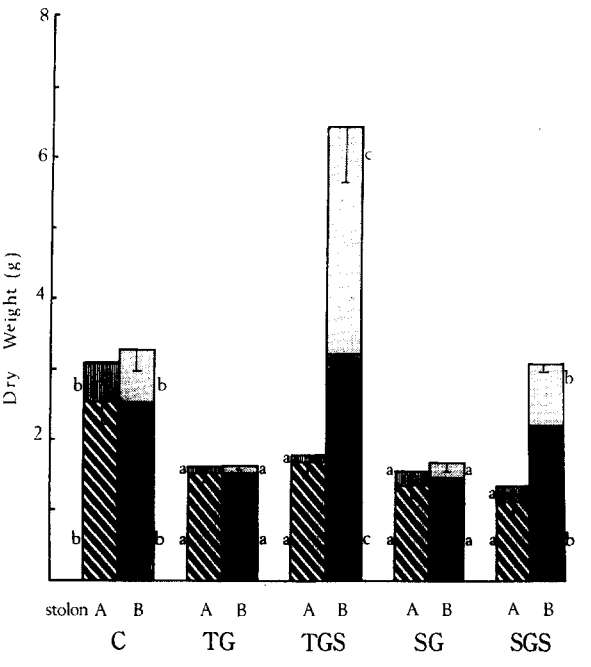

Figure 8. Mean (± S.E., $n = 6$) dry weight of primary and secondary structures on stolons A & B of *G. hederacea* plants in five experimental competition treatments. Statistically significant differences (at least $P < 0.05$) between mean values for each treatment are indicated by different letters beside the bars. Statistical comparisons are only made *between* treatments. (■) = primary structure on stolon A; (■) = primary structures on stolon B; (■) = secondary structures on stolon A; (■) = secondary structures on stolon B.

of *G. hederacea* was also highly responsive to competition (Table 2). Competition, both at the whole plant and individual stolon level, reduced both secondary stolon production and secondary ramet growth. Mean petiole length was significantly greater under tall grass competition than in the control plants, but short grass competition had no significant effect upon mean petiole length. Connected parts of *G. hederacea* plants grown with and without competition developed different morphologies; each primary stolon behaved as an integrated physiological unit, developing a morphology appropriate for the conditions in which it was growing (Price & Hutchings 1996).

Uptake and transport of phytotoxic ions

Metals are often patchily distributed in contaminated soils (e.g. Kuzel et al. 1994). Where this is the case, clonal species may benefit from a breakdown of physiological integration, while species which are highly integrated, or which recycle pollutants internally, may be disadvantaged (Callaghan et al. 1992). In a sectorial species, for example, sectoriality may promote the restriction of toxic concentrations of metals within parts of the clone growing through metal-rich microsites, so that the growth of connected parts growing through uncontaminated patches is not compromised. Thus two experiments were carried out to determine the effect of zinc-contaminated soil on the growth of *G. hederacea* clones to determine possible advantages and disadvantages of physiological integration under adverse environmental conditions.

Plants were grown from isolated ramets. In the first experiment, parent ramets were rooted in 7cm diameter pots containing 50% compost, 50% sand, and developed a single primary stolon bearing daugh-

Table 2. Mean (± S.E., $n = 6$) length (cm) of primary and secondary stolons, and mean petiole heights (cm) of *Glechoma hederacea* plants grown under five different competition treatments. Within each horizontal line of the table, values which are not significantly different are followed by the same letter. All other values are significant at least at the $P < 0.05$ level. * In the split treatments, stolon A grew under competitive conditions and stolon B grew in isolation. One stolon was designated A & one B at random in plants in all other treatments, to provide comparisons with the growth of stolons in the split treatments.

	Treatment				
	C	TG	TGS	SG	SGS
Total length of primary stolon A*	131.2 ± 10.1 a	118.8 ± 8.3 a	116.2 ± 6.6 a	117.8 ± 6.5 a	113.0 ± 5.7 a
Total length of primary stolon B*	132.2 ± 7.2 a	123.9 ± 8.1 a	133.5 ± 5.0 a	113.9 ± 7.7 a	127.0 ± 6.9 a
Total length of secondary stolons, stolon A*	175.7 ± 28.3 b	9.4 ± 6.1 a	24.1 ± 1.5 a	59.7 ± 17.9 a	44.1 ± 11.5 a
Total length of secondary stolons, stolon B*	181.0 ± 49.1 b	8.8 ± 5.6 a	558.2 ± 69.3 c	64.7 ± 33.3 a	189.3 ± 45.8 b
Mean length of petioles, stolon A*	3.9 ± 0.1 a	6.9 ± 0.3 b	7.3 ± 0.2 b	4.1 ± 0.1 a	4.2 ± 0.2 a
Mean length of petioles, stolon B*	4.1 ± 0.3 a	7.3 ± 0.2 b	4.9 ± 0.2 a	4.1 ± 0.1 a	4.0 ± 0.2 a

ter ramets. Daughter ramets were not rooted. Parent ramets were supplied every three days with either 25 ml of water or of 10 mM, 50 mM, 100 mM or 200 mM zinc sulphate solution. Treatments were replicated three times. After 13 days, new daughter ramets were counted, and plants were harvested and divided into parent ramet, parent ramet roots and daughter ramets. Plants were dried and weighed and the 10 mM treatment plants and control plants were analysed for zinc content by inductively coupled plasma spectrometry (I.C.P.) to determine the patterns of zinc distribution.

In this experiment, death of the entire plant occurred after five days in the 200 mM treatment, after 9 days in the 100 mM treatment and after 13 days in the 50 mM treatment. The 10 mM treated plants appeared chlorotic after 13 days. On harvesting, the root systems of all treated plants were very poorly developed compared with control plants. Control and 10 mM treated plants produced significantly more ramets than other treated plants ($P < 0.001$) (Figure 9). Comparison of control and 10 mM treatment plants revealed that the mean zinc content was significantly higher in the shoots (leaves, petioles and stolons) of the latter (0.61 ± 0.08 mg g^{-1}) than in the control plants (0.15 ± 0.1 mg g^{-1}) ($P < 0.01$), but that there was no significant difference in zinc content of roots (data not shown). Analysis of zinc content in the 10 mM treatment plants showed no significant difference between the zinc content of parent or daughter ramets (Figure 10), indicating that zinc was translocated from the parent ramet to daughter ramets, but in contrast to the higher zinc concentration treatments which resulted in rapid stolon death, the tissue level was sublethal.

In the second experiment, parent ramets were rooted as above, but developed two primary stolons bearing daughter ramets and secondary stolons.

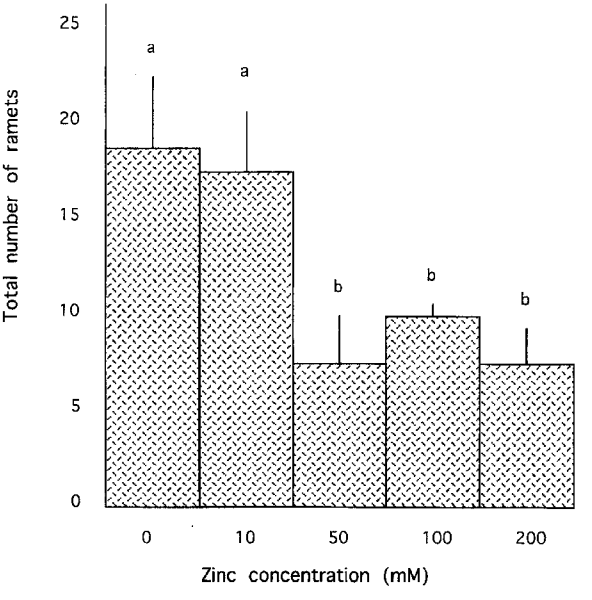

Figure 9. Mean (± S.D., $n = 3$) total number of ramets produced by plants in the different zinc treatments (0–200 mM Zn). Statistically significant differences between mean values for each treatment are indicated by different letters above the bars.

Ramets on both primary stolons were rooted. The third, fourth and fifth primary ramets on one primary stolon (Stolon A) of treated plants were supplied with 25 ml of 25 mM zinc sulphate solution every three days. Ramets on the other primary stolon (Stolon B) of treated plants, and both primary stolons of control plants were supplied with 25 ml water. Treatments were replicated three times. After 11 days, plants were harvested, divided into component parts (Figures 11 & 12) and analysed for zinc content.

On harvesting, the root systems of treated ramets appeared, as in the first experiment, to be restric-

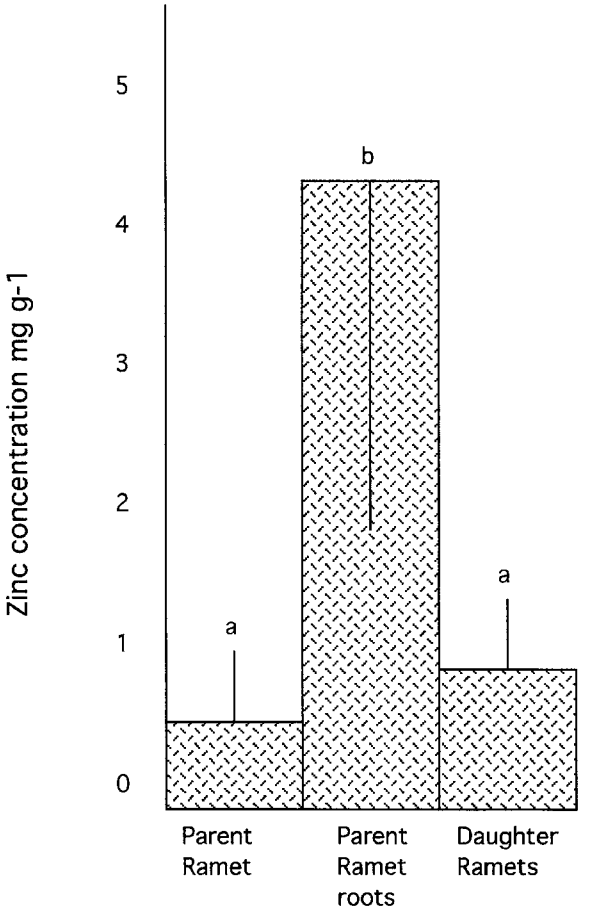

Figure 10. Mean (± S.D., $n = 3$) zinc content of component parts of 10 mM zinc treatment plants. Statistically significant differences (at least $P < 0.05$) between mean values for each treatment are indicated by different letters above the bars.

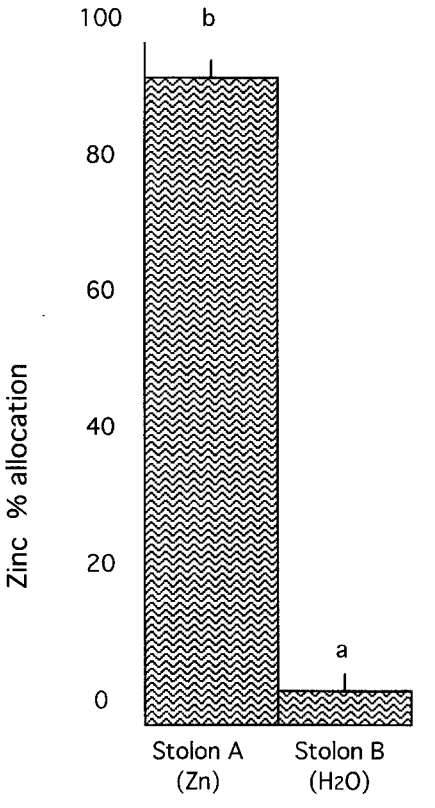

Figure 11. Mean (± S.D., $n = 3$) percent allocation of zinc to Stolon A (zinc applied) and Stolon B (zinc not applied) of *G. hederacea* plants. Statistically significant differences between mean values for each treatment are indicated by different letters above the bars.

ted in growth. Comparison of zinc content of connected stolons, showed that Stolon A (zinc applied) contained a significantly greater proportion of zinc than Stolon B (control) ($P < 0.001$) (Figure 11). Stolon B of the treated plants contained a greater amount of zinc (3.02 ± 1.8 mg g^{-1}) than control plants (0.04 ± 0.02 mg g^{-1}), but this difference was not significant. Figure 12 indicates that the greatest proportion of zinc remained within the zinc treated ramets and their associated secondary stolons (Stolon A, R3–R5). Relatively little zinc was translocated basipetally or to the unrooted ramets and primary stolon apex.

It has been shown for most clonal species investigated that young ramets are supported by a flow of carbohydrates, minerals and water from older ramets (Pitelka & Ashmun 1985; Marshall 1990). In the first experiment, zinc was transported acropetally from the treated ramet to the primary stolon apex, causing reduced growth and death of the stolon at higher zinc concentrations. In this instance, translocation from the parent ramet was clearly detrimental to younger ramets, although parental support may be of value in supporting daughter ramets *entering* a metal-rich microsite. Environmental heterogeneity may operate at a variety of spatial scales, e.g. at the level of the whole clone, the stolon or the ramet. The response of a clonal plant to environmental heterogeneity will therefore depend upon both the extent of habitat patchiness and the scale of physiological integration. Further studies are needed to investigate the influence of rooting position and metal patch size on translocation patterns and clonal growth.

The quantified patterns of zinc distribution (Figure 12) resemble patterns of ^{14}C movement in the phloem (e.g. Figure 4b, Price et al. 1992). Translocation of zinc was predominantly acropetal, although some basipetal movement did occur. A ramet is sup-

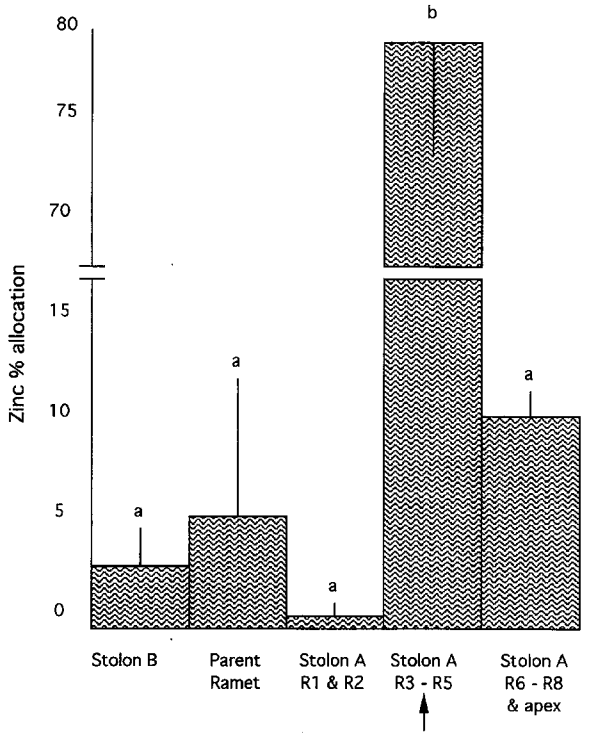

Figure 12. Mean (± S.D., $n = 3$) percent allocation of zinc to component parts of *G. hederacea* plants. Stolon B = stolon supplied with water; Parent ramet = ramet connecting Stolons A & B; Stolon A R1 & R2 = primary ramets 1 & 2 & associated secondary stolons, zinc not applied; Stolon A R3–R5 = primary ramets 3–5 and associated secondary stolons, zinc applied, indicated by arrow; Stolon A R6–R8 & apex = primary ramets 6 – apex, zinc not applied. Statistically significant differences (at least $P < 0.05$) between mean values for each treatment are indicated by different letters above the bars.

plied with inorganic solutes by both xylem and phloem (Marshall 1990). Whereas phloem transport follows source-sink principles, transport in the xylem is driven by the transpiration stream. In the acid fuchsin study, in which all dye movement was acropetal, daughter ramets were unrooted. In this study, xylem connections between rooted ramets will allow gradients of water potential to develop between ramets (Marshall 1990), so that inorganic solutes may be transported in both directions along a stolon axis.

These preliminary studies of zinc translocation show that young clones are widely integrated, but that as they increase in structural complexity they develop into a number of semi-autonomous branches. Such a pattern of development is consistent with earlier work on assimilate translocation patterns in the species (Price et al. 1992). The results of this study show that there was no significant transport of zinc from one stolon to another. A structure of semi-autonomous branches may thus be superior to a system of integrated stolons for exploiting a patchy habitat (Slade & Hutchings 1987a; Price & Hutchings 1996), particularly if localised environmental factors are lethal to ramets. Further experiments are needed to determine whether the small amount of zinc translocated from one stolon to a *semi*-autonomous stolon growing in an uncontaminated patch affects its growth in the long-term.

It is clear that environmental heterogeneity may affect the growth of clonal species, but horizontally spreading clonal species may also modify the local environment. For example, this experiment clearly reveals internal redistribution of zinc by a clonal species, which may have implications for the spreading of metals within a contaminated site. These results are supported by a study by Jaramillo & Detling (1992), which has shown that *Agropyron smithii*, a clonal grass species, spatially spread the effect of localised artificial urine pulses applied to semi-arid grassland.

Conclusion

At different structural levels, *Glechoma hederacea* shows both physiological integration and independence between its physically connected ramets, as revealed by acid fuchsin and ^{14}C studies. There would seem to be little doubt that well-established *G. hederacea* clones consist of a number of semi-autonomous IPUs, and that the boundaries of IPUs are caused by vascular architecture. The development of IPUs is also influenced by the predominantly acropetal translocation of resources. The very young, rapidly developing ramets are the strongest sinks for carbohydrates, water and nutrients.

There is evidence to suggest that patterns of resource movement in *G. hederacea* governed by vascular continuity can be modified, at least in the short term (Price et al. 1992). Clones may benefit from the ability of ramets that are situated in habitat patches of differing quality to share resources to a limited extent (Pitelka & Ashmun 1985). Physiological integration enables many clonal species to buffer spatial and temporal heterogeneity in the short-term (Callaghan et al. 1992). However, in the long-term, physiological integration may not allow *G. hederacea* to integrate the effects of environmental heterogeneity (Hutchings & Price 1993), as indicated by the results of the defoliation and competition experiments. Rather, this species is responsive to local environmental conditions at a

variety of structural scales, and there are clear architectural and physiological reasons for the localised, semi-autonomous nature of these responses. Further work is needed to determine the influence of these localised growth responses on flowering and seed production in this species.

Different growth strategies have been proposed for clonal species in relation to resource allocation patterns, growth rate and habitat type (de Kroon & Schieving 1990). For example, species living in habitats where the overall levels of resources are low are likely to be slow growing and have extensive physiological integration and long- lived ramets. The benefits to these species of widespread integration include resource resorption and the maintenance of extensive root systems and bud banks (Callaghan et al. 1992). However, such attributes may be of little benefit to a species such as *G. hederacea*. This is a mobile clonal species with a high growth rate and relatively short-lived ramets. It grows in heterogeneous environments where the overall level of resources is high, but the vigour of potential dominants is controlled by a combination of shade and disturbance (Grime et al. 1988). The predominantly acropetal movement of resources within a stolon facilitates rapid lateral spread of the clone. The degree of spreading in *G. hederacea* is plastic in a way that may facilitate the exploitation of new, resource-rich patches of habitat and the rapid vacation of sites that are, or become, unsuitable. This pattern of growth has been termed 'foraging' (Slade & Hutchings 1987a, b; Hutchings & de Kroon, 1994; de Kroon & Hutchings 1995).

The results of the studies presented here suggest that the physiological integration patterns seen in *G. hederacea*, although influenced by vascular *constraints*, do not seem to be a *handicap* to this mobile, foraging species. While physiological integration *within* IPUs has been shown to be advantageous for clonal plants growing in spatially patchy environments (Birch & Hutchings 1994; Stuefer et al. 1994), foraging species are likely to benefit from an autonomous response to patch quality at the level of the stolon, since the alternative of *widespread* intra-clonal support may increase the residence time of the clone in unfavourable patches (de Kroon & Schieving 1990). Further studies are now needed to relate the extent and consequences of ramet integration to realistic scales and patterns of environmental heterogeneity.

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