Advantages of Clonal Growth in Heterogeneous Habitats: An Experiment with Potentilla Simplex

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Advantages of clonal growth in heterogeneous habitats: an experiment with *Potentilla simplex*

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Summary

1 The ability to share resources between modules (ramets) is considered to be a benefit of the clonal growth habit. This type of physiological integration may buffer the entire clone against locally adverse conditions resulting from the patchy distribution of resources. The hypothesis that physiological integration is most advantageous in a heterogeneous habitat was tested using the clonal, perennial species *Potentilla simplex* (Rosaceae).

2 Five artificial habitat types differing in nutrient status were constructed in the glasshouse and the performance of intact and disconnected clones (clones in which all ramets were severed from each other following the establishment of roots) growing in them was compared. The habitat types ranged from homogeneously poor via three levels of spatial heterogeneity in nutrient supply to homogeneously rich.

3 Intact clones growing in the heterogeneous habitats weighed significantly more than their disconnected counterparts, supporting the hypothesis. The benefits of resource sharing were enhanced with increasing patchiness of the habitat. No differences in biomass between intact and disconnected clones appeared in the homogeneous settings.

4 Parent ramets supported their offspring at a large cost in biomass to themselves, but the offspring ramets benefited from clonal integration irrespective of the quality of the patches they occupied.

5 Across all habitats, intact stolons elongated more than the severed ones. This increased mobility of intact clones implies that clonal integration may allow this species to escape from unfavourable patches. The enhanced performance of connected ramets rooted in rich patches shows that clonal integration also enables clones to exploit resource-rich microhabitats, thereby maximising foraging ability and resource acquisition, particularly when resources are distributed in patches.

6 The cumulative effects of parent and offspring biomass and offspring ramet number appear to explain the trend in performance of intact and disconnected clones observed in the homogeneous and heterogeneous habitats.

Keywords: clonal integration, clones, patchy habitats

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Introduction

One of the advantages of clonal growth is the ability it confers on the organism to colonise and exploit a habitat rapidly (Silander 1985). Grime (1977) recognized the ability to maximise resource capture as an important characteristic of highly competitive plants. In modular, clonal organisms this ability may be enhanced by the physiological integration of modules (ramets) making up the clone. Physiological integration, or the sharing of resources between ramets, is considered to be of particular benefit when resources are distributed in discrete patches within the habitat (Cook 1983; Harper 1985; Pitelka & Ashmun 1985; Hutchings & Bradbury 1986). A number of studies (e.g. Noble & Marshall 1983; Salzman & Parker 1985; Slade & Hutchings 1987a; Abrahamson *et al.* 1991; Chapman *et al.* 1992) have shown that in

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clonal plants nutrients and photosynthates can be redistributed from ramets growing in favourable patches to those growing in poor patches. This may be true of clonal animals as well (Crowell 1957; Rees *et al.* 1970; Best & Thorpe 1985). This type of physiological integration is thought in some cases to buffer the entire clone against adverse effects resulting from spatial and temporal changes in the quality of a habitat (Hartnett & Bazzaz 1983; Pitelka & Ashmun 1985; Hutchings & Bradbury 1986).

Patchiness or heterogeneity of the habitat arises due to the uneven distribution of environmental features impinging on the organism (e.g. soil quality, topography, temperature, light, food, enemies, etc.). Levin & Paine (1974) and Wiens (1976) defined a patch as a discontinuity in a particular environmental character state within a homogeneous reference background. The extent of heterogeneity may vary depending on two factors; patch size and the relative quality differences between patches (Gillespie 1974). When a habitat consists of patches of very different sizes the organism may perceive it as less heterogeneous than when the patches are more equal in size. Similarly, when the discrepancy in the quality of adjacent patches is large, the habitat may be seen as more heterogeneous. The habitat will approach homogeneity when patches become less and less equal in size and more and more similar in quality (Gillespie 1974).

The present study attempted to extend the understanding of the ecological importance of clonal integration in heterogeneous habitats. The hypothesis that clonal integration is most advantageous in a heterogeneous habitat was tested by comparing the performance of intact and disconnected clones of the perennial herb *Potentilla simplex* growing in artificially constructed heterogeneous and homogeneous habitats. In this experiment, heterogeneity arose as a result of differences in patch size rather than discrepancy in patch quality. All heterogeneous habitats consisted of only two types of patches, nutritionally poor or rich.

The hypothesis tested predicts that for the entire clone:

1 if clonal integration improves performance in all habitats, then internode severing should reduce biomass in the disconnected clones in all experimental habitats;

2 if clonal integration is more advantageous in heterogeneous habitats than in homogeneous habitats, then clone biomass should be reduced more by severing as heterogeneity increases, with the magnitude of the reduction the highest in the most heterogeneous habitat.

Materials and methods

Potentilla simplex Michx. (Rosaceae) is a perennial herb native to eastern North America and is commonly found in pastures and old fields. Over-wintering rosettes of leaves of *P. simplex* begin growth in early spring by producing above-ground stolons. The internode connections between ramets remain intact throughout the growing season and shrivel during winter, as do unrooted ramets. Rooted ramets, both parents and offspring, are long-lived, persisting for more than four seasons (Wijesinghe 1993). *P. simplex* ramets rooted in nutrient-rich environments share resources with connected ramets growing in nutrient-poor environments, resulting in an increase in size and a greater production of secondary stolons and ramets by the recipient ramet (Wijesinghe 1993). Nutrient movement is mainly acropetal, from older to younger ramets within a single stolon, with some basipetal movement also occurring. By the sixth week of growth ramets can be completely independent, showing no adverse effects on growth when separated from their parent ramets (Wijesinghe 1994). In this species, clonal integration seems to be particularly important at the establishment stage of individual ramets (cf. Hartnett & Bazzaz 1983; Noble & Marshall 1983).

In June 1991, five habitat types were constructed in the glasshouse, ranging from homogeneously poor to highly heterogeneous to homogeneously rich. Each habitat type, replicated 20 times, consisted of 48 sand-filled 5.7 cm square plastic pots arranged in the shape of a cross (Fig. 1). Spatial heterogeneity was achieved by giving a nutrient solution to randomly-selected individual pots within these arrays, so that the resulting habitat contained nutrient-enriched and nutrient-poor patches in different proportions and sizes. Three of the habitats were heterogeneous, with 25, 50 and 75% of the pots given nutrients. The other two habitats were homogeneously rich (all pots given nutrients) or homogeneously poor (none given nutrients). The central pot containing the parent ramet was given 10 mL of a nutrient solution (Peters General Purpose Fertilizer 20:20:20, 20% N, P and K) in all five habitat types. The nutrient-enriched smaller pots received 2.5 mL of the solution once a week. All the pots in both fertility levels were watered every day. The patches in the most heterogeneous habitat were smaller, consisting of four contiguous pots or less, whereas patches in the two intermediate habitats contained as many as seven contiguous pots with the same fertility level (Table 1). In the 50%-enriched habitat 59% of the patches were of the smallest size, consisting of only one pot, whereas in the 25%- and 75%-enriched habitats not more than 38% of the patches were of this size. Therefore, the contrast in patch size was greater in the intermediate habitats, and this was reflected in the higher coefficients of variation for patch size for these two habitats (Table 1). Therefore, according to the definition of Gillespie (1974) the two intermediate habitats should be more homogeneous than the habitat in which 50% of the pots were nutrient-enriched. A clone growing throughout the most heterogeneous habitat encountered more changes in

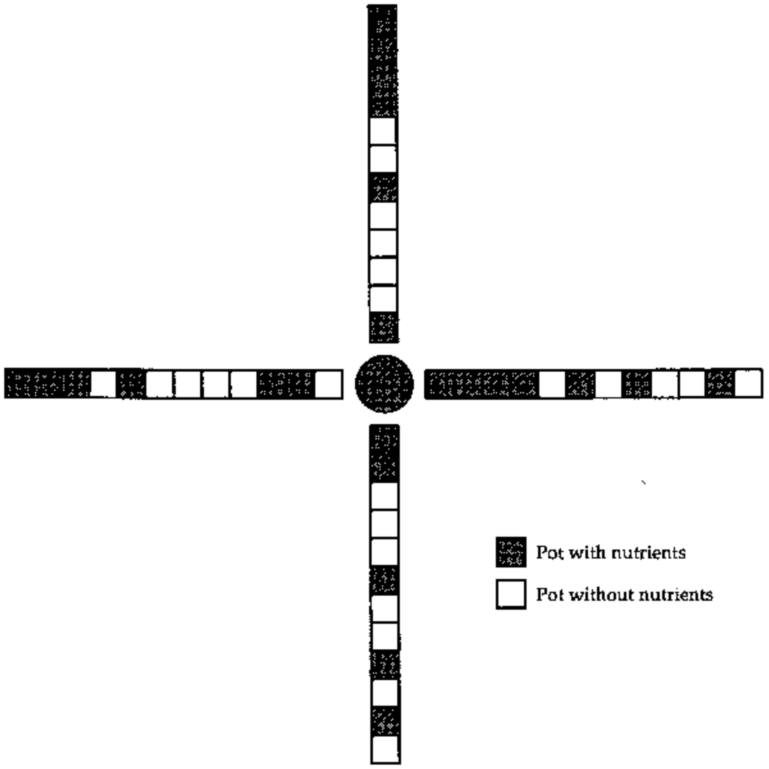

Fig. 1 Arrangement of pots in the most heterogeneous of the five habitats constructed in the glasshouse. In this habitat 50% of the pots were given a nutrient solution. The central circle represents the nutrient-enriched pot containing the parent ramet. Each square represents a pot, with (hatched) or without (open) nutrients, where an offspring ramet may root. Other habitats differed in the proportion of pots given nutrients and, consequently, the sizes of nutrient-rich and nutrient-poor patches.

patch type than clones growing in either of the two intermediately heterogeneous habitats. The frequency of patch changes was higher in the 50%-enriched habitat (Table 1).

Five genotypes of *P. simplex* were used and, each was replicated four times within each habitat type. They were collected from natural populations occurring in old fields at the Hutcheson Memorial Forest in East Millstone, Somerset County, New Jersey, USA, and propagated in the glasshouse. Each replicate was started as a two-leafed single-ramet plant in the central pot. Each of the first four stolons produced by the parent ramet was anchored to a different arm of the cross by pinning down ramets as they reached the first pot and then each successive pot in an arm. Any further primary stolons produced were removed immediately after initiation. In half the replicates of each habitat type, each ramet was disconnected from its neighbours 10 days after it had been anchored. Ramets were therefore disconnected at a time when they were still largely dependent on their neighbours for resources but had initiated at least some roots. Secondary stolons produced by the anchored ramets were not allowed to root and were left trailing from the pots. Five months later, at the cessation of new growth, both above- and belowground parts of all 100 clones were harvested and each individual ramet (with its roots and associated internode and secondary stolons) was dried separately in an oven to a constant weight. The number of arms

Table 1 Number and size of patches and the frequency of patch changes within each experimental habitat. For the homogeneous habitats patch number corresponds to the number of arms (each habitat consisted of four arms radiating from the pot containing the parent ramet, Fig. 1). Patch size is defined as the number of contiguous pots receiving the same nutrient treatment. Frequency of patch changes was calculated as the number of times patch type changed as a stolon grew along an arm over the total number of pots visited, beginning at the first pot. The number reported is the mean value for all four arms

Habitat	Patch no.	Patch size mean	SD	range	CV	Frequency of patch changes
Homogeneously poor	4	12.00	0	12	0	0
25% nutrient-enriched	21	2.28	1.62	1–6	71	0.39
50% nutrient-enriched	27	1.78	1.12	1–4	63	0.52
75% nutrient-enriched	19	2.53	1.81	1–7	72	0.34
Homogeneously rich	4	12.00	0	12	0	0

and pots occupied by each clone was recorded prior to harvest.

STATISTICAL ANALYSES

To test the hypothesis that clonal integration is most advantageous in a heterogeneous habitat the total biomass (dry weight of both above- and below-ground parts) of each clone was compared between habitat types and between intact and severed replicates. A fixed-model two-way ANOVA was performed on clone weights with habitat type and presence or absence of ramet connections as the main effects.

In addition, a two-factor ANOVA was performed to detect whether the weights of parent and offspring ramets of intact and disconnected clones differed in the various habitats. The weight of the parent ramet (i.e. the initial ramet from which the whole clone grew) and the mean weight of all other (offspring) ramets, were used as the two variates in each replicate in the analysis. A discriminant function analysis was performed to identify whether it was the parent or offspring ramets that contributed the most to the differences between treatments.

The influence of clonal integration on the growth of individual offspring ramets in different quality patches was tested by separating the ramets growing in nutrient-enriched and nutrient-poor pots into two groups and analysing each group separately. A fixed-model two-way ANOVA was performed on mean ramet weight of each replicate across all habitats.

A two-way ANOVA was performed on the proportion of arms within a habitat occupied by each clone across all habitats. An additional two-way ANOVA was performed to detect differences between treatments in the proportion of pots occupied by a stolon within each arm. In both cases data were angular-transformed prior to the analysis. These analyses should reveal the extent of primary stolon growth and ramet production, and the extent of lateral growth of clones in each treatment.

Results

THE PERFORMANCE OF CLONES

The two-way ANOVA testing the hypothesis that clonal integration is most advantageous in a heterogeneous habitat indicated that both main effects (habitat type, $F_{4,90} = 115.65$, $P = 0.0001$; presence or absence of ramet connections, $F_{1,90} = 12.39$, $P = 0.0007$) and the interaction effect (habitat type times presence or absence of ramet connections, $F_{4,90} = 4.17$, $P = 0.0038$) were highly significant. Disconnected clones weighed significantly less than intact clones. However, this depression in mean weight was seen only in the heterogeneous environments and was most marked in the patchiest habitat (Fig. 2). In this habitat, the disconnected clones weighed 35% less than the intact clones, whereas the depression in weight was less in the intermediately heterogeneous habitats (6 and 16% for the 25 and 75% enriched habitats, respectively). In contrast, in the spatially homogeneous habitats (0 or 100% of the pots with nutrients) the mean weights of intact and disconnected clones were almost identical (Fig. 2).

THE PERFORMANCE OF INDIVIDUAL RAMETS

The discriminant function analysis of parent and offspring ramet weights revealed that the significant differences in ramet performance in the five habitat types were largely due to the offspring (detected by the MANOVA, Wilks' Lambda: $F_{8,176} = 40.43$, $P = 0.0001$; Table 2; Fig. 3a,b). This indicates that the parent ramets' growth was independent of the type of habitat in which their offspring were rooted. Both the parents

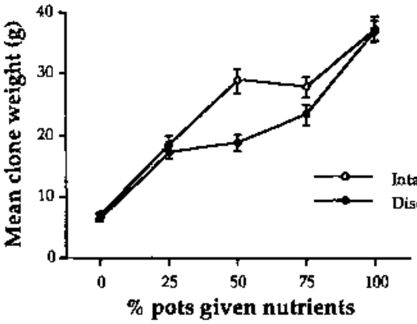

Fig. 2 Mean weights of clones (with standard errors) of *Potentilla simplex*, when ramets were connected to their neighbours and when ramets were disconnected from one another, across all habitats. The habitats are identified on the horizontal axis by the percentage of nutrient-enriched pots they contained. The two homogeneous habitats (0 and 100% of the pots given nutrients) flank the three heterogeneous habitat types (50% of the pots with nutrients being the most heterogeneous).

Table 2 Discriminant function analysis for the differences in performance of connected and disconnected parent and offspring ramets growing in the five habitat types. Discriminant function coefficients and the correlations between discriminant function scores and ramet weight (weight of parent and mean weight of offspring) are given. Variables contributing most to differences between treatments can be identified by this analysis. A higher correlation signifies a relatively larger contribution

Contrast / Ramet type	Coefficient	Correlation
Habitat		
Parent	−0.01674	−0.36
Offspring	1.07357	0.99
Connections		
Parent	0.16874	0.87
Offspring	−0.50299	−0.73
Habitat × connections		
Parent	0.04722	−0.12
Offspring	1.03094	0.98

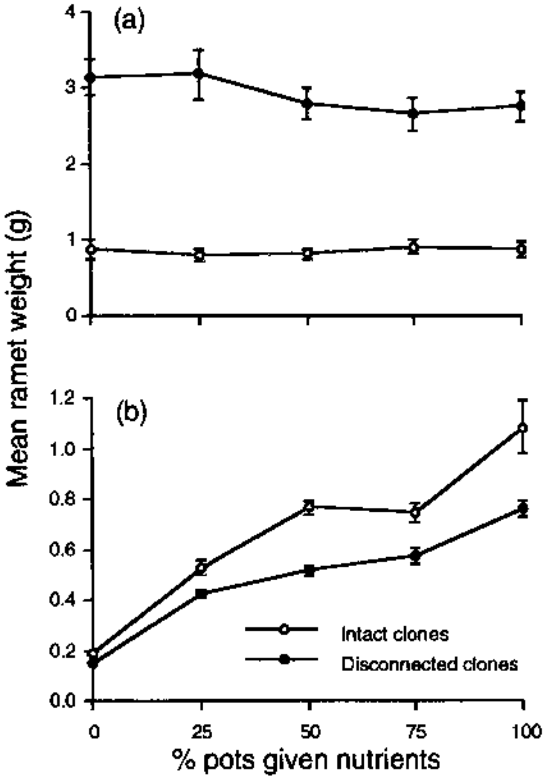

Fig. 3 Mean weights of parent (a) and offspring ramets (b) with standard errors, in intact and disconnected clones across all habitat types. Parent ramets in all habitats were rooted in nutrient-enriched pots. The habitats are identified on the horizontal axis as in Fig. 2.

and the offspring contributed to the differences in performance of intact and disconnected clones (Wilks' Lambda: $F_{2,88} = 209.67$, $P = 0.0001$; Table 2; Fig. 3a,b). The parental response was completely the opposite of that of the offspring. Parents severed from their offspring weighed more than three times as much as the connected parents (2.90 g vs. 0.84 g [mean weights pooled across habitats]), implying that the parents supported their offspring at a cost to themselves. On the other hand, the offspring ramets weighed more when connected to the parent ramets (Table 2, Fig. 3b). Only the offspring contributed to the significance detected for the interaction term (Wilks' Lambda: $F_{8,176} = 3.49$, $P = 0.0009$; Table 2).

Table 3 Analyses of variance of the performance of offspring ramets, growing in poor and rich patches, of intact and disconnected clones. Mean ramet weight of each replicate was used. Only four habitat types were used in each analysis since the homogeneously rich habitat did not have poor patches and the homogeneously poor habitat did not have rich patches

Source	d.f.	Sum of squares	F	P
Ramets in poor patches				
Habitat	3	0.026	6.34	0.0007
Connections	1	0.336	241.07	0.0001
Habitat × connections	3	0.088	21.01	0.0001
Error	72	0.100		
Ramets in rich patches				
Habitat	3	1.570	20.74	0.0001
Connections	1	1.033	40.93	0.0001
Habitat × connections	3	0.080	1.06	0.3705
Error	72	1.817		

Offspring ramets connected to their neighbours weighed significantly more than disconnected ramets across all habitat types irrespective of the quality of the patches they occupied (Table 3). The two-way ANOVA revealed a significant habitat times presence or absence of ramet connections interaction ($F_{3,72} = 21.01$, $P = 0.0001$; Table 3) for the ramets growing in poor patches but no significant effect was seen for the ramets growing in rich patches. The relative weights of disconnected and connected ramets (computed as the ratio between the weights of these two types of ramets) growing in poor patches indicated a sharp increase in the discrepancy in weight between these ramets when the percentage of nutrient-enriched pots increased from 0 to 25, and a subsequent levelling-off (Fig. 4). Such a response across habitat types was not observed for ramets growing in rich patches; in this case the relative weights were similar in all habitats (Fig. 4).

STOLON GROWTH

In all habitats, disconnected clones occupied significantly more arms than intact clones. Thus disconnected parent ramets produced more primary stolons than the parent ramets still attached to their offspring (ANOVA for the proportion of arms occupied: habitat type, $F_{4,90} = 1.25$, $P = 0.2961$; presence or absence of ramet connections, $F_{1,90} = 44.94$, $P = 0.0001$; habitat by presence or absence of connections, $F_{4,90} = 0.50$, $P = 0.7354$; Fig. 5a). In almost all intact clones, primary stolons occupied all the pots on a single arm. In contrast, for disconnected clones, the primary stolons occupied only a fraction of the pots forming an arm (ANOVA for the proportion of

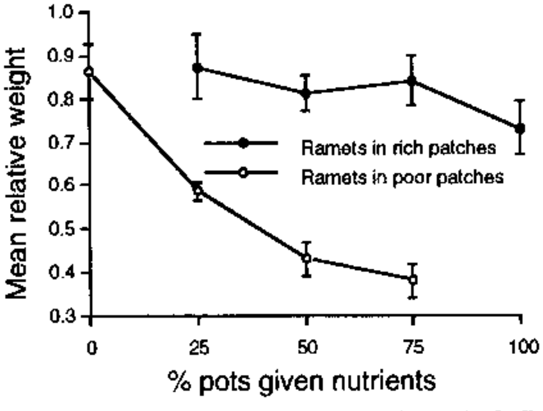

Fig. 4 Mean relative weights (with standard errors) of offspring ramets in rich and poor patches across all habitats. Relative weight was calculated as the ratio between disconnected and connected ramets in each habitat.

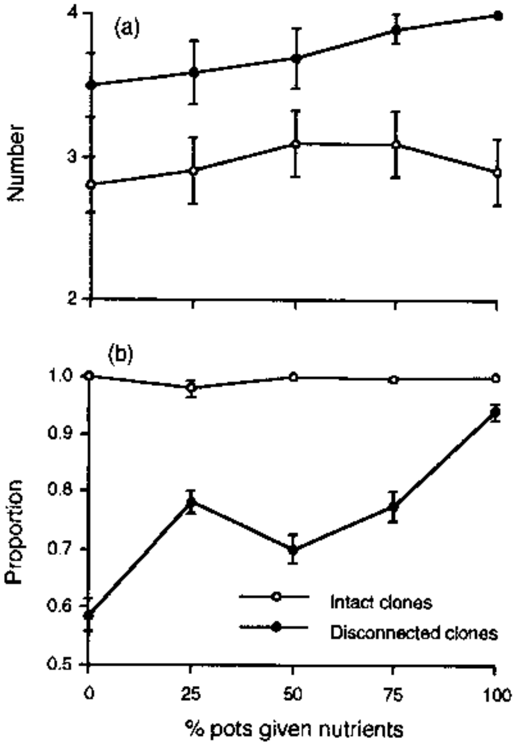

Fig. 5 Spread of intact and disconnected clones through the five habitats. (a) Mean number of arms within a habitat occupied by clones (each habitat consisted of four arms, Fig. 1). This number corresponds to the number of primary stolons rooted in each habitat. (b) Mean proportion of pots comprising an arm occupied by stolons (each arm consisted of 12 pots, Fig. 1).

pots on an arm occupied by a stolon: habitat type, $F_{4,90} = 20.54$, $P = 0.0001$; presence or absence of ramet connections, $F_{1,90} = 728.85$, $P = 0.0001$; habitat by presence or absence of connections, $F_{4,90} = 21.01$, $P = 0.0001$; Fig. 5b). These results indicate that each of the intact primary stolons produced more ramets than the disconnected stolons, in all habitat types. However, the disconnected primary stolons tended to produce increasingly more ramets as the quality of their habitat improved (Fig. 5b).

Discussion

The results of this study show that clonal integration is a benefit to the entire clone only when it occupies a heterogeneous habitat, and is most advantageous in the patchiest habitat. Severing of internode connections did not reduce the total biomass of disconnected clones in all habitats, contrary to the first prediction. Only those clones growing in heterogeneous habitats showed a depression in total weight. The reduction was highest in the most heterogeneous habitat, in accordance with the second prediction. The benefits of resource sharing increased with increasing patchiness of the habitat, demonstrating that clones of *P. simplex* clearly responded to the degree of heterogeneity of their environments.

For individual offspring ramets, clonal integration is a benefit in all habitat types, implying that for the initial establishment of ramets support from the parent and neighbouring ramets may always be necessary (Fig. 3). The discrepancy in weight between disconnected and connected offspring rooted in poor patches showed a sharp increase from homogeneous to heterogeneous habitats, indicating that connected ramets derived increasingly more benefits with an increase in the percentage of their siblings which were rooted in rich patches (Fig. 4). Conversely, there did not seem to be costs associated with the transfer of resources from ramets rooted in rich patches to those rooted in poor patches, as there was no difference in relative weight of the former when the percentage of the latter increased (Fig. 4). However, costs may not be incurred by ramets when they are rooted in patches that are as well enriched as in this experiment. Additional treatments, where rich patches are less favourable might disclose a threshold where transfer of resources is detrimental to the source ramet. This would represent a test of a different type of heterogeneity, in which patches are more uniform in quality. Such effects are predicted by Eriksson & Jerling (1990) and Caraco & Kelly (1991).

In contrast, clonal integration is a disadvantage for the parent ramets in all habitat types. These ramets subsidised their offspring at a large cost to themselves. These costs did not seem to diminish when the habitat the offspring occupied became more favourable. A mechanistic explanation for the pattern shown by the parent ramets is that the growing tips of the stolons act as strong sinks drawing resources from these ramets (Chapman *et al.* 1992). An alternative explanation is that the parents invest in a strategy of bet-hedging to reduce the potential losses to the entire clone. *P. simplex* shows a guerrilla-type growth pattern as defined by Lovett Doust (1981). Ramets are widely spaced on stolons, and, in natural populations offspring ramets root away (more than 50 cm) from the immediate local environment of the parent ramet (Wijesinghe 1993). Therefore, the first two contiguous rooted ramets (the parent and the first rooted ramet) can potentially encounter two very different microhabitats. The strategy of the parents may be to support their offspring until they become independent, whether or not the offspring are located in favourable patches. However, this strategy may be modified according to the quality of the microhabitat which the parent occupies. In this study all parent ramets were rooted in nutrient-enriched pots. However, Caraco & Kelly (1991) predict that detrimental temporal changes within the parental environment could force the parent to abandon dependent offspring before they become fully self-sufficient. The results from the analyses on lateral growth further confirm that parents support their offspring at a cost to themselves. Parents disconnected from their offspring not only weighed more than attached parents, but also produced more primary stolons, implying that resource-sharing by these ramets occurs at the additional cost of depressed clonal growth (Fig. 5a). The increased production of primary stolons could also have been caused by the release of axillary buds from apical dominance.

In all habitats intact stolons grew longer and produced more ramets than disconnected stolons. Although more primary stolons were produced by the disconnected clones, they were shorter, and consisted of fewer ramets than their intact counterparts. Therefore, intact stolons have the potential to explore a wider area. This is particularly important in unfavourable habitats (e.g. the homogeneously poor and heterogeneous habitats of the present experiment), where physiologically integrated ramets may enable clones to escape from poor patches.

Whole-clone responses to habitat heterogeneity can be explained by the cumulative effect of parent ramet performance, offspring ramet (primary ramet) performance and offspring ramet number. Both intact and disconnected clones occupied similar numbers of pots within each habitat. However, individual offspring ramets weighed more in intact clones than in disconnected clones, implying that connected offspring ramets may have been larger and/or produced more secondary stolons.

Branching and lateral spread of clonal plants can be thought of as a way of sampling the heterogeneous habitat (Bell 1984). When ramets of many species take root in favourable patches they begin producing branches and proliferating in these areas (Noble & Marshall 1983; Salzman 1985; Slade & Hutchings 1987a,b,c; Evans 1988; Chapman *et al.* 1992). Under low resource supply branches tend to move away from the unfavourable site into potentially more positive microsites. Hutchings (1988) referred to these specific responses to resource availability as a form of foraging, whereby the plant forages intensively in sites of ample resources and extensively in sites of scarce resources. Because of shorter primary stolons, the disconnected *P. simplex* clones growing in heterogeneous habitats were less able to move out of unfavourable patches and proliferate in favourable patches.

The data presented here show an advantage for clonal integration in an experimental setting where the scale of habitat heterogeneity is measured in centimetres. Such small scale patterns are known from natural communities where clonal plants are common. Lechowicz & Bell (1991) have shown that variations in nutrient availability to understorey herbs in deciduous forests can be detected at a scale of 10 cm. Heterogeneity in leaf cover on a scale of 1-cm^2 units was responsible for the differential establishment of seedlings in a chalk grassland (Silvertown 1981). Neighbour interactions can vary at extremely small scales in pastures (Turkington & Harper 1979; Turkington *et al.* 1991). The integrated response of ramets can buffer clones against all these sources of habitat heterogeneity (availability of nitrogen – Evans 1991; shade – Slade & Hutchings 1987b; neighbour density – Eriksson 1986; neighbour identity – Turkington *et al.* 1991).

All habitats are heterogeneous at some scale. As we better understand the behaviour of different clonal species in response to the level of heterogeneity they experience, we will be able to distinguish the ecological forces which have moulded their morphological and demographic responses to environmental patchiness. Under what habitat conditions should a clone behave as an integrated entity? When should ramets behave independently? The particular pattern of clonal integration shown by *P. simplex* may reinforce the ability of this species to exploit a heterogeneous habitat more efficiently. The acropetal movement of resources supplies the actively growing stolon tip at the critical time of ramet establishment (Wijesinghe, 1994). Pitelka & Ashmun (1985) suggested that this integration pattern would be typical of clonal species with an exploratory growth habit and allow a clone better to exploit a spatially and temporally patchy environment. However, complete integration may increase the residence time of ramets in unfavourable patches (de Kroon & Schieving 1990; Hutchings & Mogie 1990) and decrease the speed at which clone segments ramify within favourable microhabitats (Hutchings & Mogie 1990) Consequently, such a high level of integration may compromise the performance of the entire clone.

The results of this study show that resource movement between ramets enables clones to thrive in highly heterogeneous habitats. The integrated response of ramets not only enables an escape from adverse conditions but also exploitation of favourable conditions. This highly plastic behaviour of clonal plants may allow them to maximise resource acquisition in a heterogeneous habitat. In this way the movement and development of integrated clones become translated into a method for garnering space and critical resources.

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References

Abrahamson, W.G., Anderson, S.S. & McCrea, K.D. (1991) Clonal integration: nutrient sharing between sister ramets of *Solidago altissima* (Compositae). *American Journal of Botany*, **78**, 1508–1514.

Bell, A.D. (1984) Dynamic morphology: a contribution to plant population ecology. *Perspectives on Plant Population Ecology* (eds R. Dirzo & J. Sarukhán), pp. 48–65. Sinauer Associates Inc., Sunderland, MA.

Best, M.A., & Thorpe, J.P. (1985) Autoradiographic study of feeding and the colonial transport of metabolites in the marine bryozoan *Membranipora membranacea*. *Marine Biology*, **84**, 295–300.

Caraco, T. & Kelly, C.K. (1991) On the adaptive value of physiological integration in clonal plants. *Ecology*, **72**, 81–93.

Chapman, D.F., Robson, M.J. & Snaydon, R.W. (1992) Physiological integration in the clonal perennial herb *Trifolium repens* L. *Oecologia*, **89**, 338–347.

Cook, R.E. (1983) Clonal plant populations. *American Scientist*, **71**, 244–253.

Crowell, S. (1957) Differential responses of growth zones to nutritive level, age, and temperature in the colonial hydroid *Campanularia*. *Journal of Experimental Zoology*, **134**, 63–90.

Eriksson, O. (1986) Mobility and space capture in the stoloniferous plant *Potentilla anserina*. *Oikos*, **46**, 82–87.

Eriksson, O. & Jerling, L. (1990) Hierarchical selection and risk spreading in clonal plants. *Clonal Growth in Plants: Regulation and Function* (eds J. van Groenendael & H. de Kroon), pp. 79–94. SPB Academic Publishing, The Hague.

Evans, J.P. (1988) Nitrogen translocation in a clonal dune perennial, *Hydrocotyle bonariensis*. *Oecologia*, **77**, 64–68.

Evans, J.P. (1991) The effect of resource integration on fitness related traits in a clonal dune perennial, *Hydrocotyle bonariensis*. *Oecologia*, **86**, 268–275.

Gillespie, J. (1974) Polymorphism in patchy environments. *American Naturalist*, **108**, 145–151.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.

Harper, J.L. (1985) Modules, branches, and the capture of resources. *Population Biology and Evolution of Clonal Organisms* (eds J. B. C. Jackson, L. W. Buss, & R. E. Cook), pp. 1–33. Yale University Press, New Haven, Connecticut.

Hartnett, D.C. & Bazzaz, F.A. (1983) Physiological integration among intraclonal ramets in *Solidago canadensis*. *Ecology*, **64**, 779–788.

Hutchings, M.J. (1988) Differential foraging for resources and structural plasticity in plants. *Trends in Ecology and Evolution*, **3**, 200–204.

Hutchings, M.J. & Bradbury, I.K. (1986) Ecological perspectives on clonal perennial herbs. *BioScience*, **36**, 178–182.

Hutchings, M.J. & Mogie, M. (1990) The spatial structure of clonal plants: control and consequences. *Clonal Growth in Plants: Regulation and Function* (eds J. van Groenendael & H. de Kroon), pp. 57–76. SPB Academic Publishing, The Hague.

de Kroon, H. & Schieving, F. (1990) Resource partition in relation to clonal growth strategy. *Clonal Growth in Plants: Regulation and Function* (eds J. van Groenendael & H. de Kroon), pp. 113–130. SPB Academic Publishing, The Hague.

Lechowicz, M.J. & Bell, G. (1991) The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. *Journal of Ecology*, **79**, 687–696.

Levin, S.A. & Paine, R.T. (1974) Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences of the USA*, **71**, 2744-2747.

Lovett Doust, L. (1981) Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. *Journal of Ecology*, **69**, 743–755.

Noble, J.C. & Marshall, C. (1983) The population biology of plants with clonal growth. II. The nutrient strategy and modular physiology of *Carex arenaria*. *Journal of Ecology*, **71**, 865–877.

Pitelka, L.F. & Ashmun, J.W. (1985) Physiology and integration of ramets in clonal plants. *Population Biology and Evolution of Clonal Organisms* (eds J.B. C. Jackson, L.W. Buss & R.E. Cook), pp. 399–435. Yale University Press, New Haven, Connecticut.

Rees, J., Davis, L.V. & Lenhoff, H.M. (1970) Paths and rates of food distribution in the colonial hydroid *Pennaria*. *Comparative Biochemistry and Physiology*, **34**, 309–316.

Salzman, A.G. (1985) Habitat selection in a clonal plant. *Science*, **228**, 603–604.

Salzman, A.G. & Parker, M.A. (1985) Neighbors ameliorate local salinity stress for a rhizomatous plant in a heterogeneous environment. *Oecologia*, **65**, 273- 277.

Silander, J.A., Jr. (1985) Microevolution in clonal plants. *Population Biology and Evolution of Clonal Organisms* (eds J. B. C. Jackson, L. W. Buss & R. E. Cook), pp. 107–152. Yale University Press, New Haven, Connecticut.

Silvertown, J.W. (1981) Micro-spatial heterogeneity and seedling demography in species-rich grassland. *New Phytologist*, **88**, 117–128.

Slade, A.J. & Hutchings, M.J. (1987a) Clonal integration and plasticity in foraging behaviour in *Glechoma hederacea*. *Journal of Ecology*, **75**, 1023–1036.

Slade, A.J. & Hutchings, M.J. (1987b) The effects of light intensity on foraging in the clonal herb *Glechoma hederacea*. *Journal of Ecology*, **75**, 639–650.

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

Turkington, R. & Harper, J.L. (1979) The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. *Journal of Ecology*, **67**, 201–218.

Turkington, R., Sackville Hamilton, R. & Gliddon, C. (1991) Within-population variation in localized and integrated responses of *Trifolium repens* to biotically patchy environments. *Oecologia*, **86**, 183–192.

Wiens, J.A. (1976) Population responses to patchy environments. *Annual Review of Ecology and Systematics*, **7**, 81–120.

Wijesinghe, D.K. (1993) *The population ecology of clonal growth in the herb*, Potentilla simplex. PhD dissertation, Rutgers, the State University of New Jersey.

Wijesinghe, D.K. (1994) Temporal and structural components of ramet independence in the clonal perennial herb, *Potentilla simplex*. *Journal of Ecology*, **82**, 13–20.

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