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NUTRIENT FORAGING IN WOODLAND HERBS: A COMPARISON OF THREE SPECIES OF *UVULARIA* (LILIACEAE) WITH CONTRASTING BELOWGROUND MORPHOLOGIES[1]

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We compared the ability of three closely related species, *Uvularia perfoliata, U. sessilifolia,* and *U. puberula,* to forage and explore patches in nutritionally homogeneous and heterogeneous environments. The species differed in type and function of plagiotropic stems and the extent of clonality and physiological integration. Our aim was to determine (1) whether selective placement of roots in high-nutrient patches, i.e., foraging, was accompanied by facilitatory morphological changes such as internode elongation or increased branching, (2) whether foraging ability of species depended on the extent of physiological integration, and (3) how variability in environmental quality influenced the performance of each species. We studied the growth of each species over two seasons in experimental environments. *Uvularia perfoliata* and *U. puberula* foraged in high-nutrient patches in heterogeneous environments. *Uvularia sessilifolia* did not show selective placement of roots. The two clonal species, *U. perfoliata* and *U. sessilifolia,* did not show any changes in architectural traits predicted to facilitate foraging. The nonclonal species, *U. puberula,* was the strongest forager and the most physiologically integrated species, *U. sessilifolia,* was the weakest forager, in line with the view that physiological integration limits foraging efficiency. Variability in environmental quality had little effect on the performance of the three species. Yield and estimators of fitness were not greater in treatments where more high-quality patches were encountered consecutively than in treatments where fewer high-quality patches were encountered consecutively during growth.

Key words: clonal plants; environmental heterogeneity; foraging; patch selection; *Uvularia perfoliata*; *Uvularia puberula*; *Uvularia sessilifolia.*

Morphological plasticity enables plants to exploit favorable patches and escape from unfavorable patches in heterogeneous habitats. The former is accomplished by the selective placement of resource-acquiring organs, i.e., leaves and roots, in resource-rich sites (foraging sensu de Kroon and Hutchings, 1995). Simulation models of clonal plants predict that foraging can be aided by other morphological changes in plagiotropic stems such as stolons and rhizomes in response to patch quality (Sutherland and Stillman, 1988; Cain, 1994; Oborny, 1994). Increased branching frequency and shortening of internodes in favorable patches can position ramets, which contain resource-acquiring organs, more effectively for maximizing resource uptake. Conversely, suppression of branching and the lengthening of internodes in unfavorable patches may promote escape from such patches. However, these morphological changes may contribute largely to the fine-tuning of the foraging response rather than being obligatory for its expression. For example, although there is a consistent increase in branching of plagiotropic stems in response to resource-rich patches, internode length is relatively unresponsive to patch quality even when there is selective placement of organs (Hutchings and de Kroon, 1994). The unresponsive nature of internodes may allow clones to explore their environments continuously. When high-quality patches are located, they are exploited by means of localized morphological adjustments in leaves and roots (de Kroon and Hutchings, 1995).

Plagiotropic stems perform multiple functions. In addition to supporting ramets, these stems are reservoirs of meristems and storage products (Jónsdóttir and Watson, 1997). When storage is their primary function, plagiotropic stems do not show architectural plasticity in the way predicted by simulation models (de Kroon and Knops, 1990; Dong and de Kroon, 1994). Instead, the pattern of branching, internode elongation, and biomass allocation in these stems appears to be an outcome of resource acquisition rather than a means of selecting favorable patches (''passive'' growth vs. ''active'' foraging; Cain, 1994). Therefore, in order to understand the ability of these species to exploit heterogeneous habitats, a careful distinction has to be made between growth and foraging responses. De Kroon and Hutchings (1995) have suggested that a suitable null model for foraging is that resource availability affects biomass accumulation (growth) without accompanying selective distribution of resource-acquiring organs in high-quality patches (foraging). However, while there is evidence that some fast-growing species may forage for resources by selective placement of leaves or roots in high-quality patches (e.g., Wijesinghe and Hutchings, 1996; Einsmann et al., 1999), other species may acquire patchy resources by physiological adjustments in uptake rather than by morphological adjustments in resource-acquiring organs (e.g., Jackson and Caldwell, 1996; Fransen, de Kroon, and Berendse, 1998).

An important attribute of clonal plants that modulates the foraging response is physiological integration of ramets. Numerous studies have shown that neighboring ramets in integrated clones share resources (see review by Jónsdóttir and Watson, 1997). Thus, physiological integration can mitigate

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local shortfalls in resources experienced by individual ramets, resulting ultimately in an ''averaging'' of the habitat patchiness experienced by the entire clone (Pitelka and Ashmun, 1985; Jónsdóttir and Watson, 1997; Marshall and Price, 1997). There is great variation among clonal plants in the duration of physical connections or physiological integration between ramets. Jónsdóttir and Watson (1997) recognized several categories of integration patterns, ranging from ''disintegrators'' (or ''genet splitters'' sensu Eriksson and Jerling, 1990) with ramets that become independent soon after birth to ''integrators'' with large, fully integrated ramet systems maintained for many seasons. There are two contradictory views of the influence of physiological integration on foraging. Some authors have suggested that integration enhances foraging efficiency (e.g., Hutchings and Slade, 1988; Evans and Cain, 1995). However, de Kroon and Schieving (1990) have suggested that clones with physiologically autonomous ramets should be more effective at searching for high-quality patches than highly integrated clones, which tend to linger in unfavorable patches as a result of subsistence from ramets in favorable patches. Thus, this view implies that disintegrators or clones with restrictive patterns of integration (sensu Jónsdóttir and Watson, 1997) should show a stronger foraging response in heterogeneous environments than fully integrated clones.

In this paper, we present a study that compared the ability of three closely related woodland species to forage and explore patches in nutritionally heterogeneous environments by means of morphological plasticity. Our first objective was to determine whether or not the foraging response in clonal species, i.e., selective placement of roots in favorable patches, was accompanied by other morphological changes conducive for foraging. The second was to determine whether or not the species differed in foraging ability depending on the extent of physiological integration. Our third objective was to determine how variability in environmental quality influenced the performance of the three species irrespective of their foraging abilities. The order in which high- and low-quality patches are encountered by a plant (patch configuration) can have a significant effect on its overall performance (Wijesinghe and Hutchings, 1996). In this study, biomass was greater when plants grew in environments with contiguous high-quality patches or when plants grew from high- to low-quality patches than when they grew from low- to high-quality patches.

We selected three species belonging to the genus *Uvularia* (*U. perfoliata, U. puberula,* and *U. sessilifolia*), which differ in type and function of plagiotropic stems and the extent of physiological integration. Harvey and Pagel (1991) have suggested that comparisons of congeners should be highly informative because all variables in common to the species under consideration are automatically held constant. An additional feature of this study is that all three species occur in woodland habitats where resource availability is both temporally and spatially variable (Hicks and Chabot, 1985; Chazdon, 1988; Lechowicz and Bell, 1991; Zak and Grigal, 1991).

We tested the following hypotheses. Hypothesis 1: All three species should show preferential location of roots in high-nutrient soil patches, i.e., all three species should forage actively. Hypothesis 2: Clonal species of *Uvularia* should show architectural changes in response to nutrient availability that are theoretically predicted to facilitate foraging. Stolons or stolon internodes should be shorter, and rhizome branching and ramet density should be greater in high- than in low-nutrient patches, whereas rhizome internode length should not respond to patch quality. Hypothesis 3: The ability to locate and exploit nutrient-rich patches should increase with increasing degree of physiological integration. Conversely, if physiological integration limits foraging efficiency, the ability to locate and exploit nutrient-rich patches should decrease with increasing degree of physiological integration. Hypothesis 4: For all three species, the order in which high- and low-quality patches are encountered would affect performance. Yield and estimators of fitness should be greater in treatments where more high-quality patches are encountered consecutively than in treatments where fewer high-quality patches are encountered consecutively during growth.

MATERIALS AND METHODS

The species—The genus *Uvularia* consists of five herbaceous species endemic to eastern North America (Wilbur, 1963; Hayashi et al., 1998). They are deciduous, spring-flowering forest understory perennials and most show some form of clonal growth. All species typically produce only one flower per shoot. Seeds are shed in late summer and dispersed by ants (Whigham, 1974). The aerial shoots die back in autumn, leaving only the belowground structures to overwinter. The nomenclature of the species used in this study follows that of Wilbur (1963).

U. perfoliata L.—Each plant (parent ramet) bears a single aerial shoot and a cluster of fleshy storage roots arising from a short caudex (<1 cm long). These roots are replaced annually. Individuals in patches propagate clonally by producing one or two offspring ramets per season (Wijesinghe and Whigham, 1997). Each offspring ramet consists of a shoot bud and a cluster of storage roots borne at the tip of a slender, unbranched, subterranean stolon (<2 mm in diameter). The stolon grows centrifugally from the caudex of the parent and is, on average, 20 cm in length. The offspring ramet separates from its parent and becomes fully independent sometime during autumn or early winter of the year of its birth when the connecting stolon decays. Thus, the stolon is not important for long-term storage, but acts more as a conduit between parent and offspring for transfer of carbon and mineral nutrients. The offspring is fully dependent on the parent for photosynthates during the year of its birth, since its bud develops into an aerial shoot only in the following year. In addition to the aerial shoot, the offspring may also produce up to two third-generation ramets in its first year of independent life (Wijesinghe and Whigham, 1997). The third-generation ramets develop from lateral buds initiated in the previous growing season. Although the production of offspring ramets lessens the likelihood of survival of the parent, some parent ramets can persist for at least 3 yr and continue to produce offspring (Wijesinghe and Whigham, 1997). This species can be categorized as a disintegrator because the longevity of its physiological ramet connections is similar to its ramet generation time (see Jónsdóttir and Watson, 1997).

U. sessilifolia L.—Each plant consists of several aerial shoots arising from a sympodially branched, fleshy, subterranean rhizome system that stores resources over the long term. During the growing season, up to two new rhizome branches (on average ~10 cm long), each of which bears an upright bud, are produced from the base of each shoot. These buds develop into aerial shoots the following spring. Each new branch also bears between 2 and 10 fleshy roots, usually at the distal half of the branch. In contrast to the aerial shoots, the rhizome system is perennial and will remain intact for several seasons. New aerial shoots are formed at the distal, growing edge of the rhizome system, which has a roughly fan-shaped ''zone of occupation'' (sensu Angevine and Handel, 1986; see also Geber, de Kroon, and Watson, 1997). In contrast, roots are formed on both young and old segments of the rhizome. This species is an integrator because the longevity of its physiological ramet connections is greater than ramet generation time (see Jónsdóttir and Watson, 1997).

U. puberula Michx.—This species is not clonal. Each plant produces several aerial stems that arise in a clump from a caudex that is ~1 cm long (Wilbur,

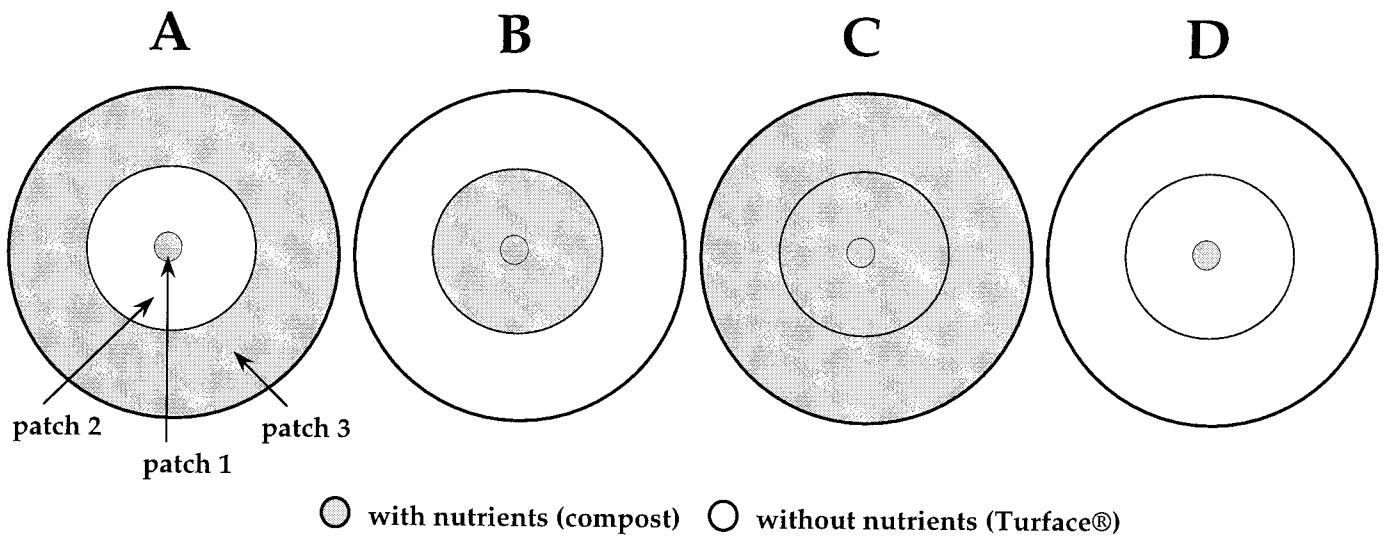

Fig. 1. The experimental treatments. Each replicate consisted of a 60 cm diameter arena with patches of high- or low-nutrient status depending on treatment. A ramet or rhizome segment of *Uvularia perfoliata, U. sessilifolia,* or *U. puberula* was planted in the center of patch 1 in each arena and allowed to grow for 2 yr.

1963) and bears a cluster of fleshy, sparsely branched roots. The roots, which can persist for more than one season, function as nutrient-acquiring, exploratory, and storage organs. At the end of each growing season, new buds are formed on the caudex, some of which may develop into shoots the following spring.

The experiment—The experiment was conducted in a shadehouse at the Smithsonian Environmental Research Center in Edgewater, Maryland, USA. The three species were collected in September 1993 from natural populations in Maryland and Virginia and planted in experimental arenas. A single plant was placed in each arena which was a circular area 60 cm in diameter with its perimeter delimited with plastic lawn edging (Fig. 1). It was filled to a depth of 10 cm with two substrates in different patterns depending on treatment. The nutrient-rich substrate was peat-based potting compost enriched with a slow-release granular fertilizer, Osmocote 13-13-13 (with a 1:1:1 ratio of N, P, K released over 8–9 mo; Scotts-Sierra Horticultural Products Company, Marysville, Ohio, USA), mixed in a ratio of 2 g per 1 L of compost. The nutrient-poor substrate was Turface® (AIMCOR, Deerfield, Illinois, USA), a granular clay material that can be used as an inert potting medium for plants. It has good water-holding capacity but does not provide any mineral nutrients for plant growth. The arenas were assembled on three 1.5 × 15 m raised beds, the surfaces of which were first covered in plastic sheeting with holes cut out for drainage. The gaps between the arenas were filled with chipped bark. Each species was allocated its own bed. All beds were similar in the amounts of light and water received.

Each arena was assigned to one of four treatments providing plants with nutrients in different spatial configurations and different overall levels of supply (Fig. 1). In treatment A, there was a small circular compost patch 5 cm in diameter in the center of the arena surrounded by two concentric rings, the inner of which was 12.5 cm wide and consisted of Turface, while the outer ring was 15 cm wide and consisted of compost (Fig. 1). In treatment B, there was a large circular compost patch 30 cm in diameter in the center surrounded by an outer 15 cm wide ring consisting of Turface. The substrate in treatment C consisted entirely of compost. Treatment D contained a circular 5-cm compost patch in the center of the arena surrounded completely by Turface (Fig. 1). Each treatment was replicated ten times (N = 40) for each species. The replicates were distributed randomly within each bed. The concentration of nutrients per unit volume in the favorable substrate, compost, was the same in the four treatments. However, the overall availability of nutrients to the plant in each treatment depended on patch size, with environments with larger favorable patches having more nutrients than those with smaller favorable patches, i.e., nutrient availability fell between treatments in the order C > A > B > D.

In each replicate containing *U. perfoliata,* a single ramet, newly produced in the summer of establishing the experiment, was planted in the center of the arena. In replicates with *U. sessilifolia,* rhizome segments ~10 cm long, with a single bud at the tip, were used. These rhizomes were also newly produced in the summer. In this case, one rhizome segment was planted in each arena with the bud positioned directly in the center. For each replicate of *U. puberula,* a cluster of roots with one or more shoot buds was planted with the buds positioned in the center of the arena. For all three species, the fresh mass of the material used was determined before planting.

Plants in all treatments were provided, throughout the growing season, with 20% of ambient full daylight. This corresponded to average light levels observed in canopy gaps in woodlands where *Uvularia* species occur. The plants were watered regularly with tap water. The experiment was continued for two growing seasons. At the end of the 1994 growing season, the substrate was removed from the surface of each arena in order to expose belowground structures of the plants while taking care not to disturb them. These structures were mapped, and the number and distribution of roots in each patch were recorded. The presence of new shoot buds or offspring ramets was also noted. The substrate was then replaced and plants were allowed to continue growth for another season. In April of 1995, the compost patches in each treatment were enriched for a second time with Osmocote granules applied in the same concentration as the year before. The granules were gently worked into the top layer of compost in each patch taking care not to disturb the plants. At the end of the 1995 growing season, data were recorded as in the previous year before shoots and belowground structures were harvested separately from the areas designated as patches 1, 2, and 3 in each treatment (see Fig. 1). Biomass samples were dried at 80°C to a constant mass.

Data analysis—For each species, biomass, architectural traits, and estimators of fitness were analyzed using one-way analyses of covariance (ANCOVA) with the soil heterogeneity treatment as the main factor. Architectural traits were analyzed only for the two clonal species, and the traits used were stolon length for *U. perfoliata* and the number of branches and internode length for *U. sessilifolia.* Estimators of fitness used were genet size for *U. perfoliata* and the size of the bud bank for *U. sessilifolia* and *U. puberula.* These are suitable measures of fitness because the number of independent ramets comprising a clone is an indicator of its capacity for risk spreading and persistence (Cook, 1979), while the size of the bud bank is a measure of the future capacity of plants to respond to environmental heterogeneity (Wat-

TABLE 1. ANCOVA of architectural traits, root numbers, and biomass of *Uvularia perfoliata*, *U. sessilifolia*, and *U. puberula* plants in the four experimental treatments (see Fig. 1). For each species, fresh biomass of the material used to set up the experiment in 1993 (ramet, rhizome segment, or root cluster) was used as the covariate. The mean (± 1 SE) for each variable is given, together with the ANCOVA results (at $P < 0.05$ level). For some variables, the test gave a significance level $0.05 > P < 0.1$ (indicated by *). Unplanned means comparisons were carried out using the Bonferroni multiple means comparison test (at $P < 0.05$ level). Means with the same superscript are not significantly different from one another. In some cases, data were log transformed prior to analysis (indicated by #).

Variable	Experimental treatment				*P*
	A	B	C	D	
U. perfoliata					
Stolon length (cm), 1994	7.19 (± 0.60)	6.64 (± 0.69)	8.68 (± 1.31)	6.09 (± 0.47)	n.s.
Stolon length (cm), 1995	11.01 (± 1.14)	10.14 (± 0.57)	13.58 (± 1.13)	10.84 (± 0.78)	n.s.*
Root number, 1995	25.60 (± 3.22)	25.10 (± 3.73)	34.20 (± 3.89)	29.56 (± 3.98)	n.s.
Total biomass (g)	0.65 (± 0.09)	0.69 (± 0.14)	0.75 (± 0.11)	0.89 (± 0.15)	n.s.
Shoot biomass (g)	0.24 (± 0.04)	0.24 (± 0.04)	0.31 (± 0.05)	0.32 (± 0.05)	n.s.
Belowground biomass (g)	0.41 (± 0.06)	0.45 (± 0.09)	0.47 (± 0.06)	0.58 (± 0.10)	n.s.
U. sessilifolia					
Internode length (cm), 1994	7.25 (± 0.61)	7.16 (± 0.64)	8.21 (± 0.43)	8.24 (± 0.55)	n.s.
Internode length (cm), 1995	10.09 (± 0.83)	8.59 (± 0.77)	7.84 (± 1.04)	8.30 (± 1.13)	n.s.
Branch number, 1994#	1.30 (± 0.15)^{b}	2.00 (± 0.15)^{ab}	2.60 (± 0.27)^{a}	1.90 (± 0.28)^{ab}	<0.01
Branch number, 1995#	4.89 (± 0.72)	5.30 (± 0.40)	5.50 (± 0.56)	4.10 (± 0.61)	n.s.
Root number, 1994	6.50 (± 0.87)^{c}	10.70 (± 1.07)^{ab}	12.30 (± 1.11)^{a}	8.30 (± 1.07)^{bc}	<0.0001
Root number, 1995	34.11 (± 4.34)	33.40 (± 3.98)	38.20 (± 6.22)	25.40 (± 3.69)	n.s.
Total biomass (g)	1.91 (± 0.23)	1.69 (± 0.22)	1.92 (± 0.41)	1.25 (± 0.29)	n.s.
Shoot biomass (g)	0.45 (± 0.06)	0.44 (± 0.05)	0.51 (± 0.10)	0.38 (± 0.08)	n.s.
Belowground biomass (g)	1.43 (± 0.17)	1.25 (± 0.17)	1.41 (± 0.31)	0.91 (± 0.22)	n.s.
U. puberula					
Root number, 1994#	5.40 (± 0.37)^{ab}	7.10 (± 0.75)^{a}	6.90 (± 0.53)^{ab}	5.10 (± 0.31)^{b}	<0.05
Root number, 1995#	13.00 (± 2.92)	19.40 (± 2.61)	13.50 (± 1.75)	13.50 (± 3.59)	n.s.*
Total biomass (g)#	0.83 (± 0.29)	1.43 (± 0.24)	0.96 (± 0.25)	0.64 (± 0.14)	n.s.*
Shoot biomass (g)#	0.45 (± 0.16)	0.67 (± 0.12)	0.45 (± 0.12)	0.28 (± 0.07)	n.s.
Belowground biomass (g)#	0.38 (± 0.13)^{b}	0.76 (± 0.13)^{a}	0.52 (± 0.13)^{ab}	0.36 (± 0.08)^{ab}	<0.05

son, Hay, and Newton, 1997). The distribution of belowground structures of *U. perfoliata* and *U. sessilifolia* in patches 1, 2, and 3 (see Fig. 1) was analyzed using one-way multivariate analysis of covariance (MANCOVA). Fresh biomass of the material used to set up the experiment in 1993, i.e., ramet, root cluster, or rhizome segment, was used as the covariate for tests of each species. Data were transformed, when necessary, using log or angular (in the case of proportions) transformations to correct for non-normality and heteroscedasticity.

The preferential location of roots (foraging) in the three species was examined in greater detail using the distribution of roots of each species in patches 1, 2, and 3 of the heterogeneous treatments A and B. Only the 1995 data were used since the belowground structures of two of the species (*U. perfoliata* and *U. sessilifolia*) had not extended as far as patch 3 in 1994. The nonparametric Mann-Whitney *U* test was used to compare the proportion of the total number of roots and of root biomass distributed in each patch in the two treatments. Patch 1 in both treatments is nutrient rich (Fig. 1). In treatment A, patch 3 is also nutrient rich and foraging roots have to traverse the nutrient-poor patch 2 to reach it. In treatment B, patch 3 is nutrient-poor and foraging activity should be more confined to the inner nutrient-rich area of patches 1 and 2 (Fig. 1). Thus, if plants are actively foraging, placement of roots in patches 1 and 3 should be significantly greater in treatment A than in treatment B. The analyses of root number and of root biomass gave similar results, therefore only the former are presented.

Foraging abilities of the three species were compared by examining the overall distribution of roots in rich patches in treatment A. The proportion of the total number of roots distributed in rich patches (patches 1 + 3) of treatment A was compared between the three species using the nonparametric Kruskal-Wallis test. In addition, the pattern of patch use by each species was examined. A ''patch use ratio'' (PUR) was calculated for each species as follows:

$$\text{PUR for patch 1} = \frac{p_{i(1)}}{X_{(1)}} \quad \text{and} \quad \text{PUR for patch 3} = \frac{p_{i(3)}}{X_{(3)}},$$

where $p_{i(1)}$ (or $p_{i(3)}$) is the proportion of the total number of roots in patch 1 (or patch 3) of each replicate in treatment A and $X_{(1)}$ (or $X_{(3)}$) is the mean proportion of the total number of roots in patch 1 (or patch 3) for all replicates in treatment B. The ratios were compared between species using the Kruskal-Wallis test. A PUR > 1 and a PUR < 1 indicate, respectively, overutilization and underutilization of the patch in treatment A relative to the same patch in treatment B, while PUR = 1 denotes a similar patch use pattern in the two treatments.

RESULTS

Hypothesis 1: selective placement of roots—In *U. perfoliata*, there was no significant difference between treatments in the total number of roots produced by clones (Table 1). However, the placement of roots in the three patches differed between treatments A and B (Fig. 2a). Over 23% of the roots were in patch 3 of treatment A compared to only 9% in patch 3 of treatment B (Mann-Whitney *U* test: $U = 78$, $P < 0.05$). In both treatments nearly one-third of the roots were in patch 1 (Mann-Whitney *U* test: $U = 51$, $P =$ n.s.). Although not a statistically significant difference, 65% of roots in treatment B compared to only 48% in treatment A were distributed in patch 2 (Mann-Whitney *U* test: $U = 33$, $P =$ n.s.). In treatment B, 91% of the roots were located in the central nutrient-rich area (patches 1 + 2; Fig. 1) compared to only 77% in the same area of treatment A (Mann-Whitney *U* test: $U = 22$, $P < 0.05$).

Results for 1994 indicate that overall root proliferation in *U. sessilifolia* clones was affected by total patch quality (Table 1). In 1994, the clones extended only as far as patch 2, which in treatments C and B was of high quality. Significantly greater numbers of roots were produced in these treatments than in

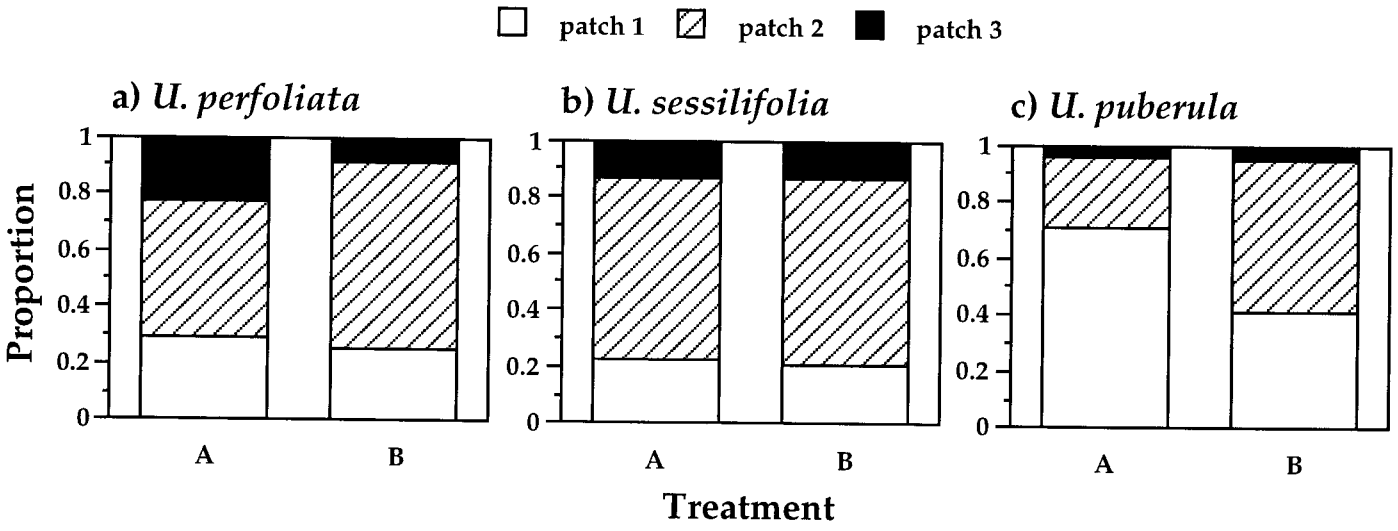

Fig. 2. The proportion of the total number of roots located in patches 1–3 of treatments A and B for (a) *Uvularia perfoliata,* (b) *U. sessilifolia,* and (c) *U. puberula.*

treatments A and D. In 1995, the clones had extended into patch 3. Although the differences in root proliferation between treatments were not significant for this year, treatment A was similar to B and C, while D produced on average between 24 and 34% fewer roots than the plants in the other three treatments (Table 1). However, there was no selectivity in the placement of roots. There were no differences between treatments A and B in the proportion of roots distributed in the three patches (Mann-Whitney U test: patch 1, $U = 51$, $P =$ n.s.; patch 2, $U = 38$, $P =$ n.s.; patch 3, $U = 45$, $P =$ n.s.; Fig. 2b).

In *U. puberula,* there were some differences in root proliferation between treatments, with plants in treatment D producing significantly fewer roots than plants in the other treatments in 1994 (Table 1). However, these differences had disappeared by 1995. In this year, root placement was significantly different between treatments A and B, indicating selectivity (Fig. 2c). In treatment A, >70% of the roots were located in patch 1 compared to only 41% in treatment B (Mann-Whitney U test: $U = 87$, $P < 0.01$). Conversely, in treatment B, 54% of roots were located in patch 2 compared to only 25% in treatment A (Mann-Whitney U test: $U = 10$, $P < 0.01$). Plants in both treatments mostly exploited the central area (patches 1 + 2) of the arenas, while there was very little exploration of patch 3. A similar proportion of roots was placed in this patch in both treatments (Mann-Whitney U test: $U = 48$, $P =$ n.s.; Fig. 2c).

Hypothesis 2: facilitatory morphological changes—In both 1994 and 1995, *U. perfoliata* stolon length did not differ between treatments (Table 1). For 1994 this was the predicted result, since the parent ramets occupied nutrient-rich patch 1 in all cases. However, by 1995 the majority of parent ramets in treatments A and D were occupying nutrient-poor patch 2, whereas the majority of their counterparts in treatments B and C were occupying nutrient-rich patch 2 (Fig. 1). The expectation that stolons of *U. perfoliata* in treatments B and C should be shorter than stolons of A and D was not confirmed for 1995. The distribution of ramets also did not conform to the predictions. If ramets are positioned in nutrient-rich patches to maximize acquisition, the expected distributions should be D > A > B ≥ C for patch 1, B ≥ C > A ≥ D for patch 2, and A > C > D ≥ B for patch 3. However, ramet distribution in the three patches was essentially similar for all treatments (MANCOVA of the proportion of ramets in patches 1, 2, and 3 in 1995: Wilks' Lambda = 0.68, $F_{9,78} = 1.51$, $P =$ n.s.; for univariate tests see Table 2).

In *U. sessilifolia,* there was no difference in internode length between treatments (Table 1). In 1994, the total number of branches produced differed significantly between treatments. It was greatest in treatment C, in which rhizomes extended into nutrient-rich patches, and least in treatment A, in which rhizomes extended into nutrient-poor patches (Table 1). In 1995, there was no significant difference between treatments in the number of branches, although the trend was similar to that seen in 1994. The highest value was seen in treatment C, in which rhizomes continued to grow into nutrient-rich patches, and lowest in treatment D, in which rhizomes continued to grow into nutrient-poor patches (Table 1). However, there was no difference between treatments in the distribution of rhizome branches in the three patches (MANCOVA of the proportion of branches starting in patches 1, 2, and 3 in 1995: Wilks' Lambda = 0.72, $F_{9,78} = 1.24$, $P =$ n.s.; for univariate tests see Table 2). If resource acquisition is to be maximized, relationships similar to those given above for *U. perfoliata* ramet distributions are also expected for *U. sessilifolia* rhizome branch distributions.

Hypothesis 3: relative foraging abilities—The proportion of roots located in high-quality patches in treatment A was greatest in *U. puberula* and least in *U. sessilifolia,* with *U. perfoliata* in an intermediate position (Kruskal-Wallis test: the proportion of roots in nutrient-rich patches, $H = 10.79$, $P < 0.01$; Fig. 3a). However, the PURs reveal that *U. puberula* and *U. perfoliata* made use of different favorable patches (Kruskal-Wallis test: PUR for patch 1, $H = 5.92$, $P < 0.05$; PUR for patch 3, $H = 6.69$, $P < 0.05$; Fig. 3b). *Uvularia puberula* overutilized patch 1 and *U. perfoliata* overutilized patch 3 in treatment A relative to their use of the same patches in treatment B. *Uvularia sessilifolia* used the two patches in a similar

TABLE 2. Univariate ANCOVA of the distribution of belowground structures in patches 1, 2, and 3 of the four experimental environments (see Fig. 1). For *Uvularia perfoliata* the proportion of ramets and for *U. sessilifolia* the proportion of branches starting and ending in each patch were used in the analyses. In 1994, the distributions of belowground structures of both species were analyzed using only univariate ANCOVA as the structures did not extend as far as patch 3. In 1994, all branches of *U. sessilifolia* started in patch 1. Thus, only the proportions of branches ending in patches 1 and 2 were analyzed. In 1995, the proportion of branches starting in each patch was analyzed using univariate ANCOVA for only patches 1 and 2 since no branches were initiated in patch 3. The other data were analyzed using MANCOVA (see text for results). The mean (± 1 SE) proportion is given together with the ANCOVA result ($P < 0.05$ level). The data were angular transformed prior to analysis.

Patch	Experimental treatment				*P*
	A	B	C	D	
U. perfoliata					
1994					
Patch 1	0.50 (± 0.06)	0.60 (± 0.07)	0.57 (± 0.08)	0.53 (± 0.07)	n.s.
Patch 2	0.50 (± 0.06)	0.40 (± 0.07)	0.43 (± 0.08)	0.47 (± 0.07)	n.s.
1995					
Patch 1	0.22 (± 0.10)	0.22 (± 0.05)	0.19 (± 0.02)	0.15 (± 0.07)	n.s.
Patch 2	0.53 (± 0.08)	0.68 (± 0.06)	0.46 (± 0.07)	0.58 (± 0.07)	n.s.
Patch 3	0.25 (± 0.07)	0.10 (± 0.06)	0.35 (± 0.08)	0.27 (± 0.09)	n.s.
U. sessilifolia					
1994 (ending)					
Patch 1	0.40 (± 0.15)	0.15 (± 0.11)	0.18 (± 0.06)	0.13 (± 0.10)	n.s.
Patch 2	0.60 (± 0.15)	0.85 (± 0.11)	0.82 (± 0.06)	0.87 (± 0.10)	n.s.
1995 (starting)					
Patch 1	0.24 (± 0.11)	0.02 (± 0.02)	0.09 (± 0.05)	0.18 (± 0.11)	n.s.
Patch 2	0.76 (± 0.11)	0.98 (± 0.02)	0.91 (± 0.05)	0.82 (± 0.11)	n.s.
1995 (ending)					
Patch 1	0.06 (± 0.03)	0.02 (± 0.02)	0.00 (± 0.00)	0.08 (± 0.06)	n.s.
Patch 2	0.69 (± 0.09)	0.80 (± 0.06)	0.49 (± 0.10)	0.49 (± 0.12)	n.s.
Patch 3	0.25 (± 0.10)	0.18 (± 0.06)	0.51 (± 0.10)	0.43 (± 0.13)	n.s.

manner in both treatments, confirming the earlier results obtained for the analyses of selective placement of roots (Fig. 2b).

Hypothesis 4: the effects of patch configuration—If patch configuration affects long-term performance of *Uvularia* spp., yield and estimators of fitness should show the relationship C > B > A > D. However, a significant treatment effect was detected only for belowground biomass of *U. puberula* (Table 1). Plants of this species in treatment B produced twice as much root biomass as plants in treatments A and D. However, the differences in root biomass did not translate into significant differences either in total or shoot biomass. The yields of both *U. perfoliata* and *U. sessilifolia* were not affected by treatment (Table 1).

There was no treatment effect in both years on the estimator of fitness, i.e., clone size measured as the total number of ramets comprising each clone, of *U. perfoliata* (ANCOVA: 1994, $F_{3,34} = 0.69$, P = n.s.; 1995, $F_{3,34} = 1.41$, P = n.s.; Fig. 4a). In 1994, clones in all treatments consisted of approximately two ramets. This number increased to 5–6 ramets at the end of 1995 (Fig. 4a). Although clones in all treatments were of similar size, there was a significant impact of treatment on the survivorship of older ramets. By the beginning of the growing season in 1995, 56 and 50% of the replicates in treatments D and A, respectively, had lost the original ramets used in the set-up of the experiment, while none of the replicates had lost these ramets in treatment C (4×2 contingency table: df = 3, $G = 11.91$, $P < 0.01$; Fig. 5). Thus, in treatment C, nearly all replicates consisted of three overlapping generations of ramets, i.e., the original first generation ramet, second generation ramets (the cohorts produced in 1994 and 1995 by the original ramet), and third generation ramets (those produced in 1995 by the 1994 cohort). In contrast, in 1995, the majority of the replicates in treatments D and A consisted of only second and third generation ramets (Fig. 5).

In *U. sessilifolia,* the estimator of fitness (size of bud bank) was significantly affected by treatment, but not in the manner predicted (Fig. 4b). In 1994, plants in treatment C produced the greatest number of shoot buds, while those in treatment A produced the least (ANCOVA: $F_{3,35} = 6.24$, $P < 0.01$). In 1995, plants in treatment A had caught up with those in B and C and plants in all three of these treatments produced nearly three times as many buds as plants in treatment D (ANCOVA: $F_{3,34} = 11.89$, $P < 0.0001$; Fig. 4b). In *U. puberula,* a treatment effect on the bud bank was apparent only in 1995 (ANCOVA: 1994, $F_{3,35} = 0.46$, P = n.s.; 1995, $F_{3,32} = 3.87$, $P < 0.05$; Fig. 4c). For this species too, the observed relationship was somewhat different from the expected, with plants in treatment B having the largest and those in treatment D the smallest bud bank.

DISCUSSION

Morphological plasticity and the facilitation of foraging—Our results support the view that plasticity in architectural traits of plagiotropic stems is not an important requirement for the expression of the foraging response (de Kroon and Hutchings, 1995). In *U. perfoliata,* selective placement of roots in high-quality patches occurred without accompanying changes in stolon length or ramet density. Some authors have suggested that plagiotropic stems should show little plasticity in response to resource availability compared to orthotropic stems (de Kroon and Hutchings, 1995; Huber, 1996; Stuefer, 1996). Pla-

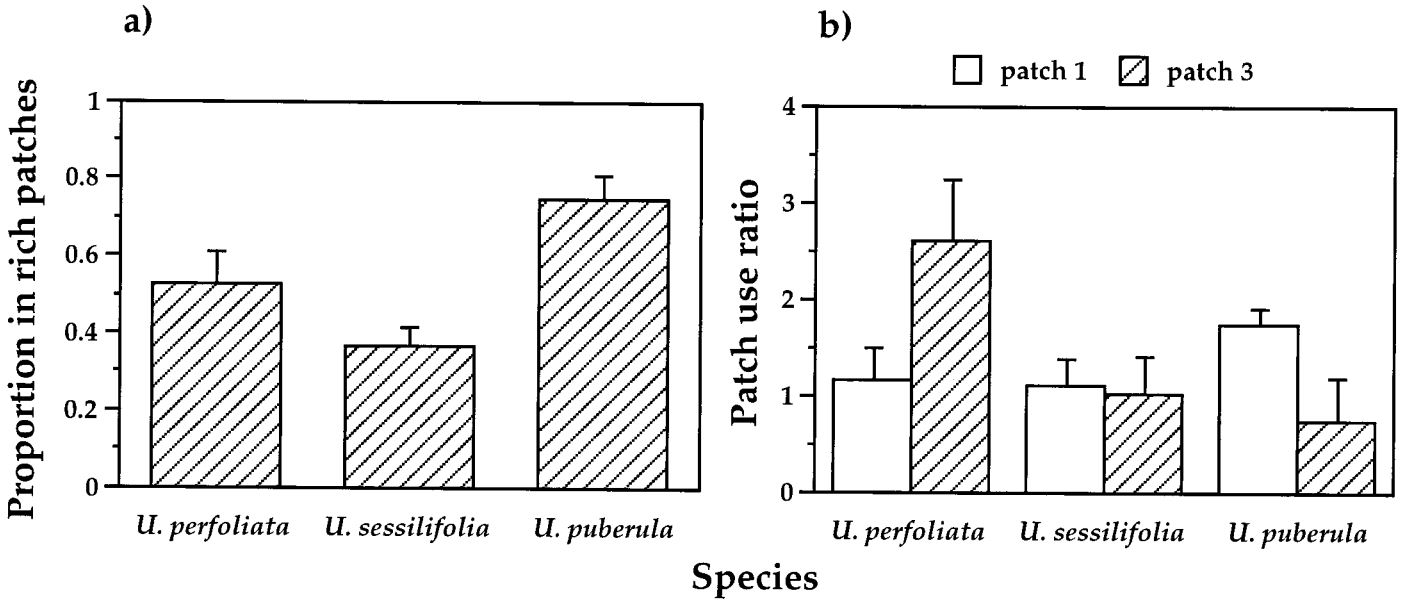

Fig. 3. Mean (+1 SE) proportion of the total number of roots located in (a) all nutrient-rich patches and (b) patch use ratio (see MATERIALS AND METHODS for computation) for patches 1 and 3 of the heterogeneous treatment A for the three *Uvularia* species.

giotropic stems growing in the horizontal plane would encounter both heterogeneously and unpredictably distributed light and edaphic resources, whereas the availability of light for orthotropic stems growing in the vertical plane would be, although heterogeneous, much more predictable (Huber, 1996; Stuefer, 1996). It is thought that plasticity is unlikely to be adaptive in heterogeneous environments if those environments are also unpredictable (Scheiner, 1993; Stuefer, 1996).

Relative foraging abilities—*Uvularia puberula* showed greater capacity than the other two species for positioning roots in high-quality patches of heterogeneous environments. However, this species exploited only those patches nearest to it (Fig. 3b). Although it was capable of producing roots of sufficient length to reach patch 3, it hardly explored this patch. In contrast, *U. perfoliata* exploited the more distant patches (Fig. 3b). *Uvularia perfoliata* is the most mobile of the three species and its greater mobility appears to enable clones to explore their environments more widely than individual plants of the nonclonal *U. puberula* whose exploration is spatially limited. The mobility of *U. perfoliata* may enable individual ramets to avoid patches previously or presently occupied by other members of the same genet (e.g., those in patch 1 in the experimental treatments), thus lessening the likelihood of establishing in patches depleted of resources. This is an effective form of ramet dispersal in a species that shows limited seed production. In contrast to *U. puberula* and *U. perfoliata*, *U. sessilifolia* clones, with their longer-lived physiologically integrated rhizome systems, did not show selective placement of roots in high-quality patches. Thus, our results provide evidence for the view that highly integrated clones are less effective than clones with physiologically more autonomous ra-

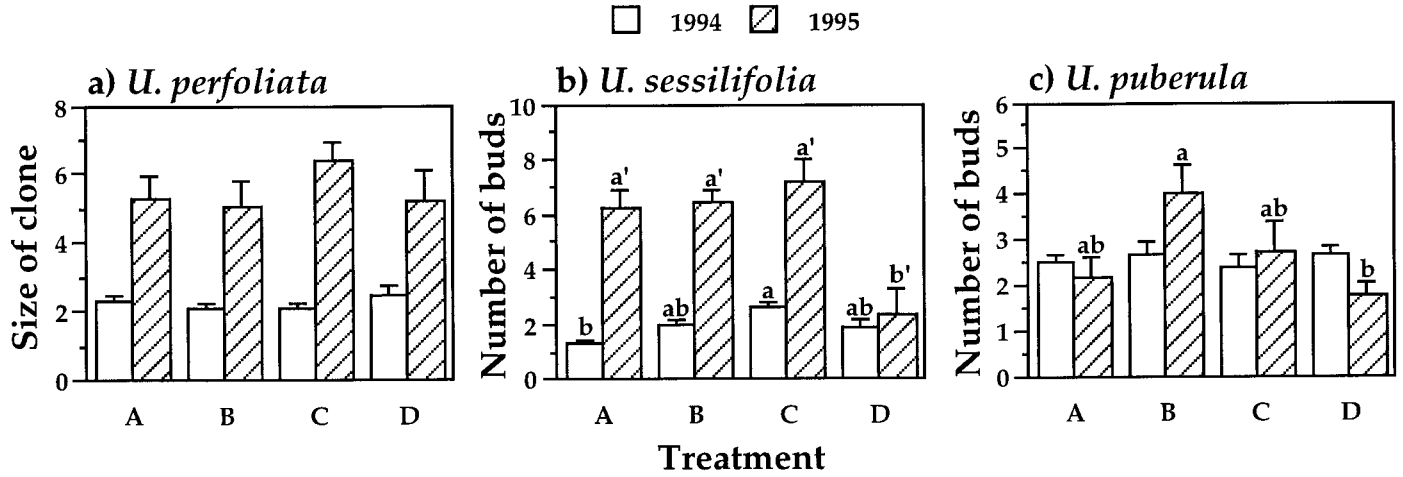

Fig. 4. Mean (+1 SE) values for estimators of fitness for 1994 and 1995. (a) For *Uvularia perfoliata*, the estimator was clone size measured as the total number of ramets produced by each clone. For (b) *U. sessilifolia* and (c) *U. puberula*, the estimator was the size of the bud bank. Means with different letters above the error bars differ significantly from one another (Bonferroni multiple-means comparison test, $P < 0.05$ level).

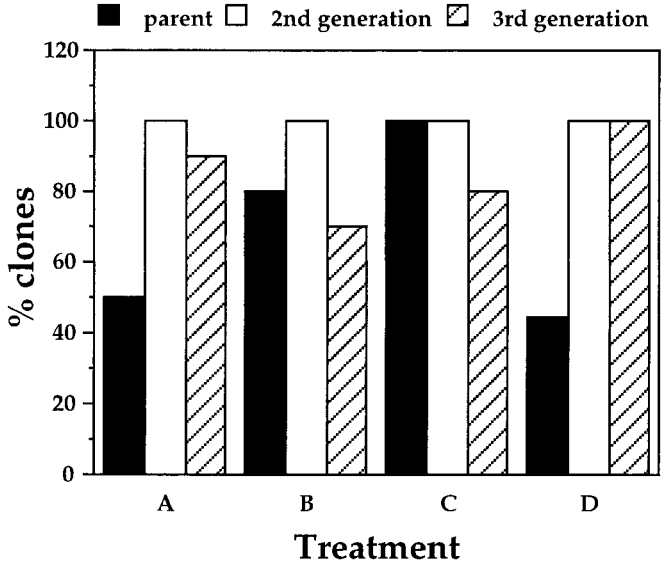

Fig. 5. The percentage of all clones of *Uvularia perfoliata* in each treatment with parent (the original first generation ramet), second generation (the cohorts produced in 1994 and 1995 by the original ramet), or third generation (those produced in 1995 by the 1994 cohort) ramets in 1995.

mets at selective exploitation of patches in heterogeneous environments (de Kroon and Schieving, 1990).

Integration vs. disintegration—Pitelka and Ashmun (1985) have suggested that physiological integration is adaptive in patchy environments where functional connections between ramets are necessary in order to grow across unfavorable patches, and to maintain links between ramets occupying favorable patches. Physiological integration enabled clones of *U. sessilifolia* to continuously explore the habitat while simultaneously sampling numerous patches of different quality. Thus, by 1995, when plants were able to sample all patches in the heterogeneous experimental environments, they produced clones of essentially similar biomass to those in the homogeneously favorable environment (Fig. 4b; Table 1). In contrast, disintegrators such as *U. perfoliata* can sample only a few patches at any one time. For these species the scope for ''averaging'' habitat heterogeneity should be limited and the capacity for active foraging by individual ramets should become more important. This argument can be extended to include nonclonal species and clonal species with restricted integration whose ramet systems consist of several small independent integrated physiological units (see Jónsdóttir and Watson, 1997). Active foraging by resource-acquiring organs should be particularly important when morphological adjustments cannot be made that promote the precise placement of ramets in patches, i.e., aggregation in high-quality patches and escape from low-quality patches. In highly integrated clones, the lack of precise placement of ramets and selective placement of organs can be compensated by transfer of resources between ramets occupying patches of different quality.

It has been suggested that despite the adaptive nature of physiological integration in heterogeneous environments, rapid decay of ramet connections, as seen in *U. perfoliata*, should be favored if the costs of maintaining connections are high (Pitelka and Ashmun, 1985; Eriksson and Jerling, 1990; Caraco and Kelly, 1991). There is evidence from an earlier study (Wijesinghe and Whigham, 1997) that the production and maintenance of offspring ramets are costly for *U. perfoliata* parent ramets. These costs were expressed as increased risk of mortality and reduced growth potential of the parents. The present study shows that the mortality risk for parents was greater when their offspring occupied lower quality patches, suggesting that the offspring in such patches acted as stronger sinks for nutrients than their counterparts in more favorable patches. However, clone size was maintained across a range of environments, with older ramets being sacrificed for the production of new ramets in the less favorable environments. These results show that the provisioning of new ramets by the old can maintain *U. perfoliata* genets in unfavorable environments for several seasons. Kudoh et al. (1999) have described this as a ''waiting strategy'' in which vegetative propagation prolongs the life of genets until more optimal conditions occur under which individual ramets can attain sizes conducive to seed production.

Responses to environmental heterogeneity—In common with other perennial species (Geber, de Kroon, and Watson, 1997), past experiences can exert a prolonged influence on future developmental events in all three species of *Uvularia*. In *U. perfoliata*, the type of shoot (flowering or nonflowering) and the maximum number of offspring produced by each ramet, and in *U. sessilifolia* and *U. puberula*, the type and maximum number of shoots produced by the plant in the following season are predetermined during the current growing season. Thus, responses to present environmental conditions can set an upper limit on the plant's capacity to respond to future conditions (Watson, Hay, and Newton, 1997). This could be a disadvantage if current conditions are less favorable than those that occur in the future, and the plant is constrained by the lack of means, e.g., meristems, to track precisely changes in resource availability. Thus the nature of consecutive, but also contiguous, patches should have an important influence on the overall performance of the plant. However, we did not find a significant effect of patch configuration on the performance of any *Uvularia* species, other than a reduced pool of buds in *U. sessilifolia* and *U. puberula* in treatment D where consecutive unfavorable patches were encountered (Fig. 4). For example, the bud bank of *U. sessilifolia* in 1994 was significantly larger in the homogeneously favorable treatment C than in the heterogeneous treatment A. However, in 1995, similar numbers of buds developed into shoots in both treatments, although the rhizome segments that bore these shoots occupied qualitatively different patches (see Table 1 for analysis of shoot biomass in patch 2). In addition, for *U. sessilifolia* and *U. puberula*, there was also at least a season's delay in emergence of differences in the size of the bud bank between the least favorable treatment (D) and the most favorable treatment (C; Fig. 4b, c).

A possible explanation for the above results is storage. Storage of carbon and minerals is expected to even out spatial and temporal variability in the availability of these essential resources (Chapin, Schulze, and Mooney, 1990; Eriksson and Jerling, 1990). Physiological integration on its own should buffer clones against short-term fluctuations in patch quality encountered during a single growing season, whereas storage coupled with physiological integration should have a longer term impact, spread over several growing seasons, on performance (Eriksson and Jerling, 1990). All three species of *Uvularia* store resources in belowground structures. However, the storage roots of each *U. perfoliata* ramet are replaced annually,

whereas the storage structures of *U. sessilifolia* and *U. puberula* persist for more than one season. While the long-term performance of *U. perfoliata* genets in heterogeneous environments is maintained by recycling of resources from parent to offspring ramets, the performance of plants belonging to the other two species may be regulated mainly by storage. Thus, *U. sessilifolia* and *U. puberula*, as well as *U. perfoliata*, can withstand fluctuations in the quality of the environment for at least one growing season.

Conclusions—The three species of *Uvularia* have different strategies for living in patchy environments. *Uvularia perfoliata* and *U. puberula* forage actively for nutrients in favorable patches in their habitats. However, the latter exploits only those patches in its immediate vicinity, while the more mobile *U. perfoliata* is able to move across its environment exploring new patches. *Uvularia sessilifolia*, on the other hand, appears to have a conservative strategy (sensu de Kroon and Schieving, 1990), which involves enhanced growth in response to high resource availability without active foraging in high quality patches. Unlike *U. perfoliata*, *U. sessilifolia* does not actively avoid unfavorable patches and seek favorable patches, but rather makes use of the latter as they are encountered. The conservative strategy of this species may be aided by a high degree of physiological integration coupled with storage, which enables clones to expand and occupy space. All three species can withstand unfavorable conditions for at least one growing season and are thus expected to be capable of surviving until conditions improve in their spatially and temporally patchy woodland habitat.

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