

Costs of producing clonal offspring and the effects of plant size on population dynamics of the woodland herb *Uvularia perfoliata* (Liliaceae)

DUSHYANTHA K. WIJESINGHE* and DENNIS F. WHIGHAM

Smithsonian Environmental Research Center, PO Box 28, Edgewater, MD 21037, USA

Summary

1 Clonal propagation is an important means of population increase in many temperate woodland herbs. The production of vegetative propagules is often limited by the patchy availability of light in the understorey. A field study and a greenhouse experiment investigated the patterns of clonal growth under different light conditions in the shade-tolerant herb species *Uvularia perfoliata*.

2 In the field study, vegetative propagation in four populations, two growing under closed canopy and two in gaps, was compared. A significantly higher proportion of plants in gap populations produced clonal offspring than plants from closed-canopy populations, possibly because of higher light availability. The cost to plants of producing clonal offspring was seen as a significantly lower probability of survival and reduced capacity of the survivors for future clonal propagation.

3 In the greenhouse experiment, offspring ramets of three size classes (small, medium and large) from both closed-canopy and gap sites were grown under low and high light conditions. Plants grown from larger ramets from both sites produced more clonal offspring and invested more biomass in reserves and clonal propagation than plants grown from small ramets. Counter to our expectations, plants did not produce more clonal offspring in high light than in low light. However, plants invested more biomass in clonal propagation in high light, especially if they were grown from larger ramets. The only evidence for adaptation to conditions at the site of origin was that increased reserve allocation in high light was more marked in plants from gaps. The effect of ramet size on performance was stronger than the effect of light level or site of origin of plants, although plants grown from larger ramets also benefited more from high light.

4 Unless plants have sufficient biomass and morphological capacity their positive response to high light is delayed. Although clonal propagation is always costly, costs are less severe in gaps where plants have the potential to produce clonal offspring repeatedly in consecutive seasons. Our results also show that plant size has a potential long-term effect on population dynamics of this species, with the advantages of large size expressed over several generations.

Keywords: canopy gaps, reproductive costs, reserve formation, shade tolerant, storage roots, vegetative propagation

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Introduction

The phenology of temperate woodland herbs is intimately linked to the annual cycle of abiotic factors such as temperature and light (Vézina & Grandtner

1965; Bierzychudek 1982; Hicks & Chabot 1985; Kawano 1985). These species largely limit their activities to periods when temperature and light levels under forest canopy are above some critical level (Kawano 1985). However, even during optimal periods for growth, woodland herbs function under relatively low light conditions. Leafless tree canopies can intercept as much as 30% of the incident radiation

(Collins, Dunne & Pickett 1985). Below the completely closed canopy photosynthetically active radiation may be as low as 1–5% of that in the open (Anderson 1964; Chazdon & Pearcy 1991). However, the light environment of the understorey is not homogeneous, but a mosaic of relatively low and relatively high light patches. For example, in deciduous forests of north-eastern United States, on average between 1% and 2% of the canopy in any one year consists of gaps that allow increased light penetration into the understorey (Runkle 1985). Depending on canopy height and gap diameter, the photon flux density (PFD) of light within such gaps can be between 10% and 90% of ambient light (Collins *et al.* 1985).

Despite being adapted to the extremely low light conditions found under closed canopies, many woodland species can respond to moderate increases in light levels caused by canopy gaps. For example, increases in PFD up to 10% of ambient light can enhance population growth in a number of species (Reader & Bricker 1992) and significantly higher rates of flowering and seed production have been observed in populations of woodland species growing in gaps (Barkham 1980; McCall & Primack 1987; Whigham & O'Neill 1988; Whigham, O'Neill & Cipollini 1993). Clonal herbaceous species respond to higher light levels in gaps by increasing the production of vegetative propagules (Barkham 1980; Pitelka, Stanton & Peckham 1980; Ashmun & Pitelka 1984). Thus, it appears that disturbances in the canopy are important for the growth of woodland herb populations.

Although light conditions in gaps are favourable for growth, there may be physiological constraints limiting the responses of woodland species to large increases in light levels. Leaves of shade-tolerant species appear to be particularly vulnerable to heat damage caused by excessive light. Shade-tolerant plants are also prone to photoinhibition at high light levels, which can reduce the capacity for light-saturated and light-limited photosynthesis and can destroy the photosynthetic apparatus (Boardman 1977; Demmig-Adams & Adams 1992; Long, Humphries & Falkowski 1994). Therefore, these species may show positive responses to light increases only in gaps of small to moderate size. There is evidence that gaps larger than 10 m in radius have a negative impact on population density of some woodland herbs (Reader & Bricker 1992).

In this paper we report a field study and a greenhouse experiment investigating the patterns of population flux due to clonal propagation of the woodland herb *Uvularia perfoliata* L. (Liliaceae) growing in different light environments. *U. perfoliata* is a spring-blooming shade-tolerant deciduous perennial herb, which occurs as patches under completely closed canopy and in gaps. *U. perfoliata* shows increased growth in response to light increases in small to moderately sized canopy gaps (Whigham 1974). In the field study, we compared vegetative propagation in four

U. perfoliata populations, two growing under closed canopy and two growing in small gaps, to determine how heterogeneity in light availability influenced clonal propagation. Our first hypothesis was that *U. perfoliata* populations in gaps would produce more clonal offspring than those growing under closed canopy.

The clonally produced offspring ramet of *U. perfoliata* is totally dependent on its parent for photosynthates while the two ramets remain physically connected. The offspring ramet can photosynthesize only when it has grown a leafy shoot after separating from its parent. It is possible that the parent bears a cost by providing photosynthates (and mineral nutrients) to fuel the growth of the offspring. We therefore tested the hypotheses that in all sites, the risk of mortality would increase and future productivity would decrease in parents producing offspring ramets (hypothesis 2), and that the costs would be larger in populations growing under closed canopy than in those growing in gaps (hypothesis 3).

Within a single patch of *U. perfoliata*, the sizes of clonal offspring vary widely, with sometimes as much as a 20-fold range in weight (D.K. Wijesinghe, personal observation). The population dynamics of clonal species can be influenced by ramet size because the number of clonal propagules and allocation of biomass to them can increase with increasing ramet or plant size (Antlfinger, Curtis & Solbrig 1985; Ashmun & Pitelka 1985; Pitelka, Hansen & Ashmun 1985; Méndez & Obeso 1993; Worley & Harder 1996). We designed a greenhouse experiment to investigate the effects of initial size on the performance of *U. perfoliata* ramets collected from sites in the field study. In addition, the experiment attempted to distinguish between purely environmental effects, e.g. those due to differences in light availability, and more site-specific effects, e.g. those due to genetic effects. The experiment was a three-way factorial design, with ramet size, site of origin and light level as the three main factors. Offspring ramets of three size classes (small, medium and large) were collected from one closed-canopy and one gap site from the field study and were grown in the greenhouse. The ramets were provided with either low or high light that corresponded to the light levels at the site of origin. We tested (hypothesis 4) whether larger ramets from both sites, irrespective of light conditions, would produce more clonal offspring and invest more biomass in reserves (parent storage roots) and propagation (offspring ramets) than smaller ramets. We also predicted (hypothesis 5) that all ramets, irrespective of size and site of origin, would produce more clonal offspring and invest more biomass in reserves and propagation in high light than in low light.

Site-specific responses can be manifested, for example, if ramets from the closed-canopy site are better adapted to low light conditions and are more tolerant of low light than ramets from the gap site. In addition,

the ability of a *U. perfoliata* ramet to respond to its environment is to some degree predetermined early in its development. Leaf meristems are initiated and the number of leaves within shoot buds of newly produced ramets preset while they are still attached to their parents (D.F. Whigham, personal observation). It is possible that the number of leaves on an independent ramet, and to some extent its ability to harvest light, could be influenced by the light environment experienced by its parent in the previous season. Consequently, ramets from the closed-canopy site may show a more limited response to high light than ramets originating from the high-light environment of the gap. Site-specific responses can be detected by examining the main factor site and the site \times light level interaction in the factorial design. We therefore determined (hypothesis 6) whether low light would be more detrimental to ramets from the gap site than to ramets from the closed-canopy site, and (hypothesis 7) whether ramets from the closed-canopy site would perform less well in high light than ramets from the gap site.

Materials and methods

THE SPECIES

U. perfoliata is one of five spring-flowering perennial herb species in a genus endemic to eastern North America (Wilbur 1963). It forms patches in the understorey of mature deciduous forests. Apical buds of *U. perfoliata* elongate and emerge through the leaf litter in late winter to early spring (Whigham 1974). Each plant bears a single shoot and a cluster of fleshy storage roots that arise from a short caudex (<1 cm long). Perfoliate leaves are arranged alternately on the usually unbranched stem, which forms a single short sympodial branch only when the plant is flowering. In this study shoots bore between two and six leaves. Flowering occurs in spring before complete closure of the forest canopy (Whigham 1974), with each shoot bearing a single, pale yellow flower. The mature capsule contains, on average, about four seeds (range 1–13) that are shed in late summer and dispersed by ants (Whigham 1974). The shoots die back in autumn, leaving only the below-ground structures to over-winter.

U. perfoliata propagates clonally by producing one or two offspring ramets per season. Each offspring ramet consists of a shoot bud and a cluster of fleshy storage roots borne at the tip of a slender subterranean stolon (<2 mm in diameter). The stolons grow centrifugally from the caudex of the parent plant and are, on average, 20 cm in length. In addition to the shoot bud, each offspring ramet also bears up to two lateral buds that can develop into third generation ramets in subsequent seasons (Whigham 1974; Fig. 1). The offspring ramet is fully dependent on the parent plant for photosynthates during the season of its

birth, since its shoot bud develops into an aerial shoot only in the following season. It is also likely that the offspring ramet depends on the parent plant, while still connected to it, for providing at least a part of its mineral and moisture requirements. The offspring ramet continues to develop below-ground until the aerial shoot of the parent dies back in autumn. At this point, the offspring ramet is capable of surviving if physically separated from the parent. Usually, it becomes naturally separated from its parent sometime during winter, when the stolon connecting it to the parent decays. The shoot bud of the independent offspring ramet elongates in the following spring to produce an aerial shoot and it can produce offspring ramets even in its first year of independent life.

THE FIELD STUDY

The field study was carried out in summer and autumn of 1993 and 1994 at the Smithsonian Environmental Research Center (38°53'N, 76°33'W) in Edgewater, Maryland, USA. The study area was a deciduous secondary forest in the northern coastal plain bordering the Chesapeake Bay. Patches of *U. perfoliata* are common in the understorey herbaceous layer. In July 1993, four populations of *U. perfoliata* were located; two growing under completely closed canopy (sites 1 and 2) and the other two growing in gaps (sites 3 and 4). The gaps were small, created by one or two fallen trees, and the light levels within the gap sites were on average 10% of ambient light, compared to between 4% and 5% of ambient light in the closed-canopy sites. The sites were at least 500 m from each other.

Seventy-seven, 76, 73 and 47 shoot-bearing plants, respectively, from the populations at sites 1, 2, 3 and 4 were chosen at random and their positions marked with coloured plastic flags. Site 4 had the smallest population and all of its plants were marked. The soil around each marked plant was excavated to locate any offspring ramets. The presence of a shoot bud on the parent ramet was noted, as was the number of offspring ramets whose positions were then marked with flags. The plants were covered with soil and leaf litter and left to over-winter. In September 1994, the soil around the shoots of all surviving plants marked in 1993 (both parents and offspring from the previous year) was removed in order to expose the roots. The presence of a shoot bud and the number of offspring ramets produced by each surviving individual were noted. In 1994, only 45, 40, 65 and 27 of all marked individuals, in sites 1, 2, 3 and 4, respectively, emerged. The area around all marked individuals that did not emerge was also excavated. In these cases, their roots were decomposed and they did not appear to be alive. No marked plants flowered at any site in either year of this study.

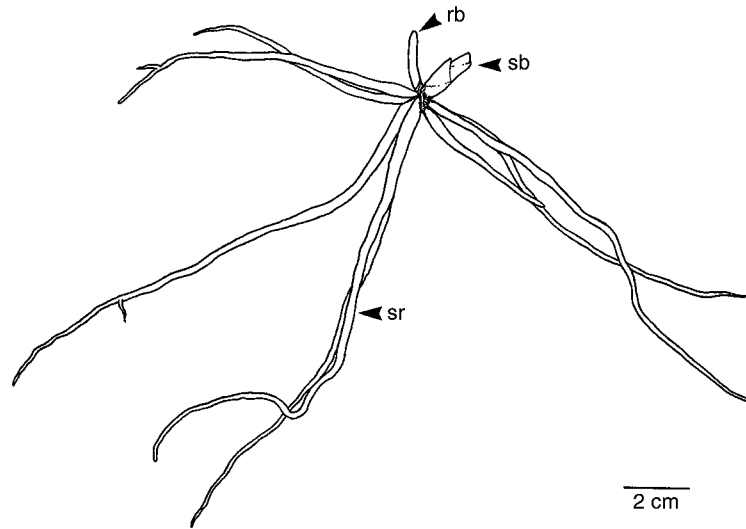


Fig. 1 The offspring ramet of *U. perfoliata*. The subterranean ramet consists of a cluster of thickened storage roots (sr) with a shoot bud (sb) and ramet buds (rb) at the centre of the cluster. It is connected to the parent ramet by a slender stolon (not shown).

THE GREENHOUSE EXPERIMENT

The experiment was conducted in a greenhouse at the Smithsonian Environmental Research Center. In October 1994, ramets of *U. perfoliata* were collected from the closed-canopy site 1 and gap site 3. From each population 69 offspring ramets, newly produced that season by shoot-bearing parent plants, were selected at random. At this time the offspring ramets were mature and capable of surviving independently. The ramets were weighed fresh in the laboratory and the frequency distribution of ramet weight from each site was determined. The distributions were not statistically different from each other (ANOVA of log-transformed data: $F_{1,136} = 0.27$, $P = \text{NS}$). Twelve each of small-, medium- and large-sized ramets were chosen from each of these distributions ($n = 72$). As far as possible, the small-sized ramets were selected from the 1st–15th percentile, the medium-sized ramets from the 50th–60th percentile and the large-sized ramets from the 85th–100th percentile of the two distributions. It was desirable to choose ramets from the distribution in this manner because a random selection might not have represented adequately the size range observed in the natural populations (Hicks 1982). The mean (\pm SE) weights of the small, medium and large ramets respectively were 154 mg (± 7), 333 mg (± 5) and 592 mg (± 16) from the closed canopy population and 149 mg (± 8), 331 mg (± 10) and 602 mg (± 18) from the gap population. There was no statistical difference between sites in the weights of the three ramet size classes (ANOVA of log-transformed data: $F_{1,70} = 0.0006$, $P = \text{NS}$).

The selected ramets were planted singly in plastic pots (15 cm in diameter) filled with a 1 : 2 mixture of sand and peat-based potting compost. The pots were lowered up to their rims into holes excavated in the ground of an outdoor common garden and were cov-

ered with a layer of mulch approximately 5 cm deep. The ramets were left to over-winter from October 1994 to March 1995. On 1 March 1995 the pots were uncovered. They were taken to the greenhouse on 29 March and placed on four benches shaded with shade cloth. To mimic natural shoot emergence, pots were placed under shade only after the majority of the shoots had emerged. There were then two light treatments, low and high. The low light treatment provided 5% and the high light treatment provided 9% of ambient light in the greenhouse, corresponding, respectively, to average light levels measured in closed-canopy site 1 and gap site 3 where the ramets were collected. Two of the four greenhouse benches used for the experiment were assigned to the low light treatment and the other two to the high light treatment. Six pots were selected randomly from each size class from each site and were placed in low light and the remaining pots were placed in high light. Every second week after the experiment was set up, pots were randomly transferred between the two benches earmarked for the same light treatment. The pots were watered as necessary without removing the shades. The experiment was terminated on 6 July 1995 when the plants were harvested. Each plant was separated into leaves, stem, parent storage roots, stolons and offspring ramets. The total leaf area of each plant was measured using a LiCor Model Li 3000 leaf area meter. Each plant part was dried at 80°C and weighed separately.

DATA ANALYSIS

Most relationships were tested using the *G*-test of independence. In the field study, the relationship between site and clonal offspring production in both years was tested using two-factor (4×3) contingency

tables corresponding to site \times number of offspring (none, one or two) produced by the parents. The costs incurred by parents due to offspring production were tested using three-factor ($4 \times 2 \times 2$) contingency tables. One table corresponded to site \times number of offspring ramets produced by parent \times the fate of parent (survivorship for 1993 and bud production for 1994) for testing the effects of the number of offspring ramets produced on the subsequent survival and growth of the parent. Another corresponded to site \times number of offspring ramets produced by parents in 1993 \times number of offspring ramets produced by parents in 1994 for testing the effect of offspring ramet production in 1993 on offspring ramet production by the same parent in the following year. In the greenhouse experiment, offspring ramet production was analysed using a four-factor ($3 \times 3 \times 2 \times 2$) contingency table with site, light level, ramet size class and offspring ramet number produced as the four factors.

The weight of plant parts in the greenhouse experiment was analysed using multivariate analyses of variance. Leaf number, leaf area, specific leaf area and the weight of individual offspring ramets were analysed using univariate analyses of variance. In all cases, the experimental design was a fixed-model three-way factorial with site, light level and ramet size class as the three main sources of variation. The factor site was considered as fixed because the two sites were chosen from the four in the field study. Light level was also a fixed factor because the two levels were set by us to match the observed light levels in the field sites. Similarly, ramet size class was considered a fixed factor because the three levels (small, medium and large) were selected from the extremes and the centre of the offspring weight distribution (Hicks 1982). Data were transformed, when necessary, using the appropriate transformations to correct for non-normality and heteroscedasticity.

Results

THE FIELD STUDY

In both years, significantly more *U. perfoliata* parent plants produced clonal offspring in the populations

in gaps than in the populations under closed-canopy (4×3 contingency table; for 1993, d.f. = 6, $G = 16.72$, $P < 0.01$; for 1994, d.f. = 6, $G = 30.99$, $P < 0.0001$; Fig. 2). In 1993, between 62% and 72% of the parents in the two gap sites produced one or two offspring ramets, whereas no more than 48% of the parents growing in the two closed-canopy sites produced offspring ramets (Fig. 2). In all sites, the majority of the parents propagating vegetatively produced only one offspring ramet. A higher proportion of parents produced two offspring ramets in the gap sites than in the closed-canopy sites (Fig. 2).

The production of clonal offspring was costly to the parents. In all sites, fewer parents that produced offspring ramets in 1993 survived until the following growing season, than parents that did not propagate clonally (Table 1). In the closed-canopy sites, over 60% of the parents that did not produce offspring remained alive until 1994, while 48% or fewer of the parents that produced offspring survived. In the gap sites survivorship was higher, with 92% of the parents that did not produce offspring remaining alive until 1994, and up to 58% of the parents that produced offspring surviving. The magnitude of costs associated with clonal growth was even higher in 1994 (Table 1). For example, in closed-canopy site 1 none of the parents producing offspring in 1994 formed shoot buds for growth in 1995, compared to over 80% of the parents that did not produce clonal offspring (Table 1).

The production of offspring ramets in 1993 also affected the capacity of surviving plants to propagate clonally in 1994. In all sites, clonal offspring production in 1993 resulted in a drop in offspring production by the parents in the following year (Table 2). However, this negative effect was significantly more pronounced in the populations under closed canopy than in those occurring in gaps (there was a significant interaction between site and offspring production in 1993; Table 2). For example, in closed-canopy site 2, none of the surviving parents that produced clonal offspring in 1993 propagated clonally in 1994, whereas in gap site 4, 50% of the surviving parents that produced offspring in 1993 succeeded in producing clonal offspring as well in 1994 (Table 2).

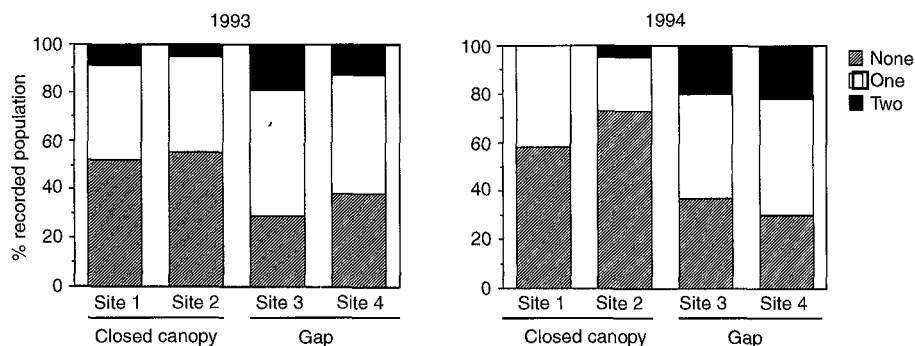


Fig. 2 Offspring ramet production by *U. perfoliata* plants growing in closed-canopy and gap sites in the field study in 1993 and 1994. The percentages of plants producing no offspring ramets, one and two offspring ramets are given for each site.

Table 1 The fate of *U. perfoliata* plants that produced either no offspring ramets or one or more offspring ramets in closed-canopy and gap sites. For 1993, fate is given as the percentage of plants that remained alive or died in the following year (1994). For 1994, fate is given as the percentage of plants that did or did not produce a shoot bud for following year's (1995) growth. Three-way ($4 \times 2 \times 2$) contingency tables were analysed using the *G*-test for each year separately. For 1993, the percentage of plants that were dead or remained alive the following year did not differ between sites (sites \times fate: d.f. = 3, $G = 2.62$, $P = \text{NS}$). In contrast, offspring number and the interaction between site and offspring number had a significant effect on the fate of plants (offspring number \times fate: d.f. = 1, $G = 10.16$, $P < 0.001$; site \times offspring number \times fate: d.f. = 10, $G = 30.11$, $P < 0.001$). For 1994, both site and offspring number and their interaction had a significant effect on the fate of plants (site \times fate: d.f. = 3, $G = 30.76$, $P < 0.0001$; offspring number \times fate: d.f. = 1, $G = 101.23$, $P < 0.0001$; site \times offspring number \times fate: d.f. = 10, $G = 147.95$, $P < 0.0001$)

Site/offspring number	1993		1994	
	Dead (%)	Alive (%)	Bud absent (%)	Bud present (%)
Closed-canopy sites				
Site 1: none	27	73	15	85
\geq one	52	48	100	0
Site 2: none	39	61	0	100
\geq one	55	45	54	46
Gap sites				
Site 3: none	8	92	17	83
\geq one	42	58	90	10
Site 4: none	8	92	50	50
\geq one	56	44	79	21

Table 2 The relationship between offspring ramet production in successive years by *U. perfoliata* plants in the four sites. There are two offspring ramet production categories, i.e. none and one or more (\geq one) offspring ramets, for 1993 and 1994. The percentage of plants in each offspring production category in 1993 that survived to produce no offspring ramets or one or more offspring ramets in 1994 is given. A three-way ($4 \times 2 \times 2$) contingency table was analysed using the *G*-test, with site, offspring production in 1993 (none or \geq one) and offspring production in 1994 (none or \geq one) as the three factors. There was a significant difference between sites in offspring production in 1994 (site \times offspring production in 1994: d.f. = 3, $G = 13.65$, $P < 0.01$). The two offspring production categories for 1993 did not differ significantly in productivity in 1994 (offspring production in 1993 \times offspring production in 1994: d.f. = 1, $G = 2.51$, $P = \text{NS}$). However, there was a significant interaction between site and offspring production in 1993 for productivity in 1994 (site \times offspring production in 1993 \times offspring production in 1994: d.f. = 10, $G = 26.49$, $P < 0.01$)

Site/number of offspring ramets produced in 1993	Number of offspring ramets produced in 1994	
	None (%)	\geq one (%)
Closed-canopy sites		
Site 1: none	59	41
\geq one	75	25
Site 2: none	78	22
\geq one	100	0
Gap site		
Site 3: none	42	58
\geq one	58	42
Site 4: none	27	73
\geq one	50	50

THE GREENHOUSE STUDY

Neither site nor light level had a significant effect on the capacity of plants to produce offspring ramets. In contrast, ramet size significantly affected offspring ramet production (Table 3 and Fig. 3). Forty-two per cent of the plants grown from small ramets did not produce any offspring, whereas only 12% and 8%, respectively, of the plants grown from medium and large ramets did not produce any offspring (Fig. 3). Size not only affected the capacity to produce off-

spring but also the actual number of offspring ramets produced. The majority (58%) of the plants grown from large ramets produced two offspring ramets while the majority (67%) of the plants grown from medium ramets produced only one offspring ramet. Only 8% of the plants grown from small ramets produced more than one offspring ramet (Fig. 3). The effect of ramet size on offspring ramet production also appeared to be responsible for the significant interactions between factors seen in the contingency table, i.e. the interaction between site and light level

Table 3 Analysis of the four-way ($3 \times 3 \times 2 \times 2$) contingency table for the production of offspring ramets by *U. perfoliata* plants in the greenhouse experiment. Plants were grown under two light levels (low and high) from ramets of three size classes (small, medium and large), collected from a closed-canopy and a gap site. There were three categories for the number of offspring ramets produced by the plants; none, one and two (see Fig. 3). For each test, the degrees of freedom (d.f.), the *G*-statistic and probability (at $P < 0.05$ level) are given

Test	d.f.	<i>G</i>	<i>P</i>
Site \times offspring number	2	3.43	NS
Light level \times offspring number	2	0.23	NS
Ramet size \times offspring number	4	20.88	<0.0001
Site \times light level \times offspring number	7	3.38	NS
Site \times ramet size \times offspring number	12	38.68	<0.0001
Light level \times ramet size \times offspring number	12	29.04	<0.01
Site \times light level \times ramet size \times offspring number	29	48.08	<0.05

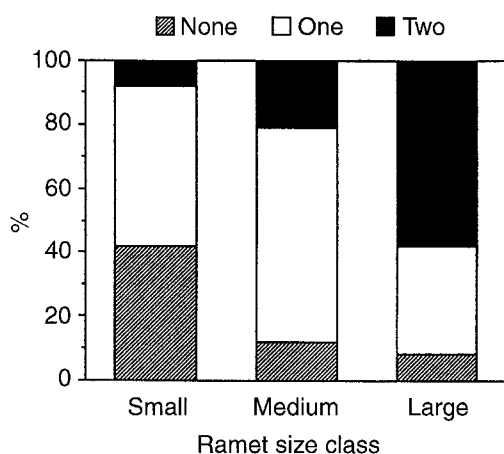


Fig. 3 Offspring ramet production by *U. perfoliata* plants in the greenhouse experiment. Offspring ramet production is given as the percentage of plants grown from small-, medium- and large-sized ramets producing no offspring ramets, one and two offspring ramets.

was not significant, whereas all interactions involving ramet size were significant (Table 3). For example, in high light all plants grown from large ramets produced one or two offspring ramets, with 75% producing two, while in low light 17% of the plants grown from large ramets did not produce any offspring and only 42% produced two.

Site, light level and ramet size, either as single factors or as interactions between factors, significantly affected total biomass production and biomass investment in reserves (parent storage root weight) and propagation (total offspring ramet weight) by the plants (MANOVA; Table 4a). Overall, ramet size had the greatest impact on biomass production by plants. Ramet size influenced all three parameters, with plants grown from large ramets weighing more and investing more in reserves and propagation than those grown from small and medium ramets (Table 4b and Fig. 4). Plants grown from large ramets were able to respond relatively more effectively to increased availability of light than those grown from ramets belonging to the smaller size classes (see the significant light level \times ramet size class interactions in the MANOVA and in the univariate tests for total weight and off-

spring weight; Table 4). In high light, plants grown from large ramets invested a disproportionately large amount of biomass in offspring compared to plants in the other size classes (Fig 4 and Table 4b).

By the end of the experiment, parent ramets from the gap site had gained significantly more storage root biomass than parent ramets from the closed-canopy site (mean parent storage root weight \pm SE of $0.12 \text{ g} \pm 0.01$ vs. $0.10 \text{ g} \pm 0.01$; Table 4b). Although light as a main effect was not significant, there was a significant site \times light level interaction (Table 4b). In plants originating from the gap site, over 38% more biomass was invested in parent roots when growing in high light compared to when growing in low light (mean \pm SE of $0.14 \text{ g} \pm 0.02$ vs. $0.10 \text{ g} \pm 0.01$), whereas in plants originating from the closed-canopy site there was no difference in biomass investment in parent roots when growing in high light or when growing in low light ($0.10 \text{ g} \pm 0.01$ in both cases). This outcome appears to be entirely due to site and the site \times light level interaction as there was no significant variation between sites in the starting weight of ramets used in the experiment (see the Materials and methods). Site had no direct effect on biomass investment in offspring ramets (Table 4b).

The size of individual offspring ramets was affected significantly by the size of ramets from which the parent plants were grown (Table 5 and Fig. 5). The mean (\pm SE) weight of individual offspring ramets produced by plants grown from large ramets ($0.05 \text{ g} \pm 0.004$) was over 1.5 times and twice as much, respectively, as those produced by plants grown from medium ($0.03 \text{ g} \pm 0.01$) and small ramets ($0.02 \text{ g} \pm 0.004$). Neither site nor light level had a direct effect on individual offspring ramet weight (Table 5). However, in conjunction with ramet size, light level had a significant indirect effect (see the significant light level \times ramet size interaction in Table 5), i.e. plants grown from medium ramets showed a larger positive response to high light than plants grown from ramets belonging to the other two size classes (Fig. 5).

Ramet size had a significant effect on the number of leaves produced by plants (Table 5 and Fig. 6). Plants grown from larger ramets produced more

Table 4 Multivariate analysis of variance of total weight, weight of parent storage roots and total weight of offspring ramets of *U. perfoliata* plants in the greenhouse experiment. Total weight of offspring ramets is the sum of weights of all offspring ramets produced by a plant. The design was a three-way factorial. Ramets of three size classes (small, medium and large), collected from a closed-canopy and a gap site, were grown under low and high light levels. (a) Multivariate test statistics, and (b) the corresponding univariate test statistics, are given for the test of each factor and the interactions between factors. The degrees of freedom (d.f.), the *F*-statistic and significance (at $P < 0.05$ level) are reported for each test. The data were $\log(1+n)$ transformed prior to analysis

(a)				
Source	Wilks' Lambda	d.f.	<i>F</i>	<i>P</i>
Site	0.829	3, 58	3.977	<0.05
Light level	0.658	3, 58	10.030	<0.0001
Ramet size	0.101	6, 116	41.389	<0.0001
Site × light level	0.926	3, 58	1.534	NS
Site × ramet size	0.859	6, 116	1.530	NS
Light level × ramet size	0.795	6, 116	2.348	<0.05
Site × light level × ramet size	0.928	6, 116	0.737	NS

(b)							
Source	d.f.	Total plant weight		Parent root weight		Total offspring ramet weight	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Site	1	7.326	<0.01	4.616	<0.05	0.162	NS
Light level	1	25.396	<0.0001	3.116	NS	10.411	<0.01
Ramet size	2	204.620	<0.0001	47.718	<0.0001	22.598	<0.0001
Site × light level	1	2.428	NS	4.690	<0.05	1.444	NS
Site × ramet size	2	0.750	NS	1.395	NS	3.784	<0.05
Light level × ramet size	2	3.497	<0.05	0.038	NS	4.793	<0.05
Site × light level × ramet size	2	0.632	NS	1.861	NS	0.793	NS
Error	60						

leaves than plants grown from smaller ramets, with a mean (\pm SE) of 5.6 (\pm 0.1), 4.9 (\pm 0.1) and 3.9 (\pm 0.1) leaves produced by plants grown from large, medium and small ramets, respectively. Neither site nor light level affected leaf number directly (Table 5). Site and ramet size had a significant effect on total leaf area produced by plants. Total leaf area of plants originating from the gap site was significantly larger, with a mean (\pm SE) total leaf area of 20.15 cm² (\pm 1.71), compared to 17.02 cm² (\pm 1.45) of plants originating from the closed-canopy site (Table 5). The effect of ramet size was even greater (Table 5 and Fig. 6). The mean (\pm SE) total leaf area of plants grown from medium and large ramets was more than twice as much (18.34 cm² \pm 0.88) and more than three times as much (29.03 cm² \pm 1/19), respectively, as the total leaf area (8.39 cm² \pm 0.59) of plants grown from small ramets. Light level had no effect on total leaf area produced by plants (Table 5 and Fig. 6). In contrast, light level had a highly significant effect on specific leaf area (Table 5 and Fig. 6). The mean (\pm SE) specific leaf area of plants grown in low light was 6.57 cm² mg⁻¹ (\pm 0.08), which was significantly larger than the mean value, 5.59 cm² mg⁻¹ (\pm 0.09), of plants grown in high light. Intriguingly, ramet size also had a highly significant effect on specific leaf area (Table 5 and Fig. 6). Plants grown from small ramets had a significantly larger specific leaf area (6.47 cm² mg⁻¹) than plants grown from medium and large ramets (5.88 cm² mg⁻¹ in both cases; Table 5 and Fig. 6).

Discussion

All three hypotheses tested in the field study were confirmed in full. *U. perfoliata* populations produced more clonal offspring in the high-light environment of gaps than under closed canopies. In all sites, parents produced clonal offspring at a significant cost to themselves. These costs were manifested in two ways. First, the probability of survival of reproductive plants was reduced compared to that of non-reproductive plants. Second, the capacity for future clonal propagation of surviving reproductive plants was diminished compared to that of non-reproductive plants. The magnitude of costs, especially of those expressed as reduced future propagation, was significantly higher for plants growing under closed canopies than for plants growing in gaps.

Of the hypotheses tested by the greenhouse study, hypothesis 4, that initial ramet size has a significant effect on plant performance was verified fully. Plants grown from larger ramets from both sites produced more clonal offspring and invested more biomass in reserves and clonal propagation than plants grown from smaller ramets. Hypothesis 5, that plants perform better in high light than in low light, was verified only partially. Although plants did not produce more clonal offspring in high light, they invested more biomass in clonal propagation, especially if they were grown from larger ramets. Although at the end of the greenhouse experiment plants from the gap site were

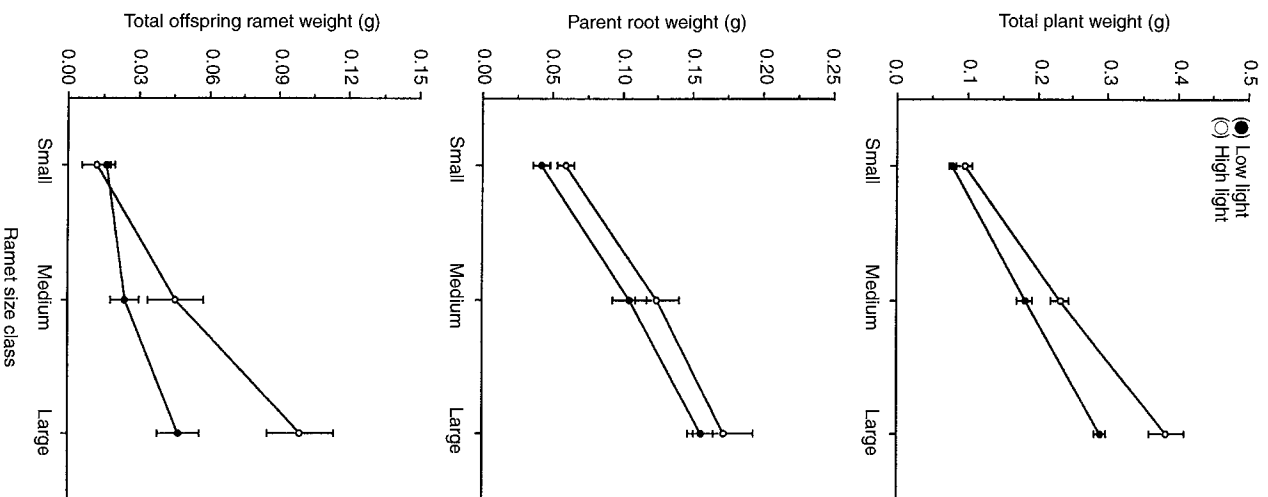


Fig. 4 Mean (± 1 SE) total weight of plants, weight of parent storage roots and total weight of offspring ramets of *U. perfoliata* plants grown in low or high light from ramets belonging to three size classes in the greenhouse experiment. Total weight of offspring ramets is the sum of weights of all offspring ramets produced by a plant. Interactive effects of light level and ramet size are shown. See Table 4 for statistical analyses.

larger, with more biomass and more leaf area, than plants from the closed-canopy site, neither of the two hypotheses testing for site-specific effects (6 and 7) was proved conclusively. There was no evidence that ramets from the closed canopy site were more tolerant of low light than ramets from the gap site. Closed-canopy plants responded less well to high light than gap plants in only one measure of performance, i.e. the increased investment in reserves in high light was marked in plants from the gap site while plants from

Table 5 Analyses of variance of individual offspring ramet weight, number of leaves, total leaf area (cm^2) and specific leaf area ($\text{cm}^2 \text{mg}^{-1}$) of *U. perfoliata* plants in the greenhouse experiment. The experimental design was a three-way factorial. Ramets of three size classes (small, medium and large) collected from a closed-canopy and a gap site were grown under low and high light levels. The degrees of freedom (d.f.), the *F*-statistic and significance (at $P < 0.05$ level) are given for each source of variation. The individual offspring ramet weight data were log transformed prior to analysis

Source	Individual offspring ramet weight			Leaf number			Total leaf area			Specific leaf area		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Site	1	0.198	NS	1	2.571	NS	1	9.802	<0.01	1	3.541	NS
Light level	1	0.742	NS	1	0.286	NS	1	1.549	NS	1	113.213	<0.0001
Ramet size	2	6.430	<0.01	2	90.929	<0.0001	2	141.978	<0.0001	2	18.098	<0.0001
Site \times light level	1	1.620	NS	1	0.001	NS	1	0.958	NS	1	2.610	NS
Site \times ramet size	2	0.706	NS	2	2.786	NS	2	0.561	NS	2	0.762	NS
Light level \times ramet size	2	3.176	<0.05	2	4.357	<0.05	2	1.750	NS	2	7.063	<0.01
Site \times light level \times ramet size	2	0.770	NS	2	0.214	NS	2	0.264	NS	2	0.287	NS
Error	45			60			60			60		

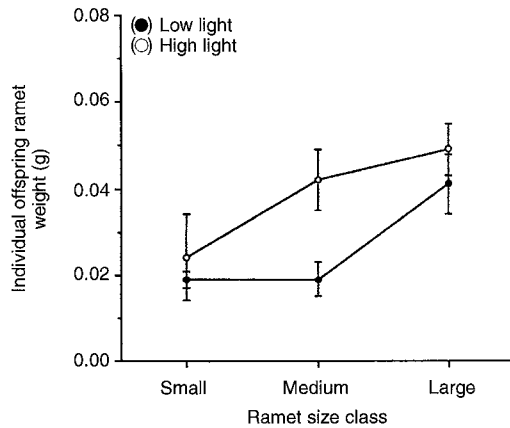


Fig. 5 Mean (+1 SE) weight of individual offspring ramets produced by *U. perfoliata* plants grown in low or high light from ramets belonging to three size classes in the greenhouse experiment. Interactive effects of light level and ramet size are shown. See Table 5 for statistical analyses.

the closed-canopy site invested the same amount of biomass in reserves in both high and low light. This may be because of the greater capacity of gap plants to harvest light as these plants possessed more leaf tissue. Although gap plants did not produce more leaves as expected, they produced larger leaves resulting in more overall leaf area than the closed-canopy plants (Table 5). Leaf number was affected only by ramet size, with larger ramets producing plants with more leaves. Overall, the effect of ramet size on performance was greater than the effect of light level or site of origin of plants. Also, plants grown from larger ramets benefited more from high light than did those grown from smaller ramets, as they produced more clonal offspring and invested more biomass in clonal offspring in high light than did the latter.

Studies of other woodland species suggest that light is the most critical factor limiting clonal growth (Whigham 1974; Pitelka *et al.* 1980; Jurik 1983; Ashmun, Brown & Pitelka 1985). However, the results of our greenhouse study imply that increased availability of light alone may not be sufficient to overcome this limit, especially in species such as *U. perfoliata* whose performance is influenced by their past history (Geber, de Kroon & Watson 1997). Plants must possess the capacity for building additional resource-acquiring structures, i.e. leaves and roots, if they are to be able to respond immediately to increased levels of resources. In *U. perfoliata*, the parent endows its clonal propagule with both carbohydrates and leaf meristems, which can be mobilized in response to the quality of the offspring's habitat. The option of producing extra leaves and increasing leaf area in order to exploit favourable light conditions is available only if plants have a sufficiently large initial parental investment, e.g. plants grown from larger ramets produced more leaves (Fig. 6). Consequently, plants grown from larger ramets are more responsive to high light than plants grown from smaller ramets. The main positive response to high light is shown not as

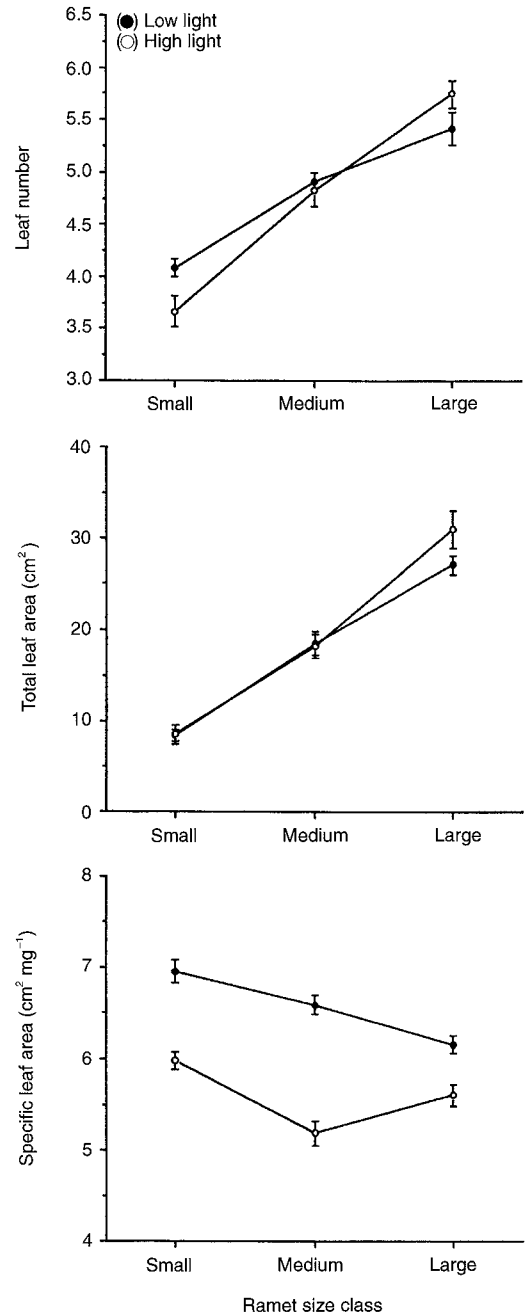


Fig. 6 Mean (+1 SE) number of leaves, total leaf area and specific leaf area of *U. perfoliata* plants grown in low or high light from ramets belonging to three size classes in the greenhouse experiment. Interactive effects of light level and ramet size are shown. See Table 5 for statistical analyses.

the production of *more* propagules but as the production of *larger* propagules (Table 3 and Figs 4 and 5). Thus increased population growth as a response to favourable light conditions in gaps appears to be a two-step process, with the production of larger offspring in the first growing season followed by a consequent increase in propagule production in the next season. In other woodland species increased population growth in response to high light was also seen only about two growing seasons after a gap was created (Reader & Bricker 1992).

Although allocation of resources to sexual reproduction has been found to be at the expense of growth or vegetative propagation (e.g. Sohn & Policansky 1977; Law 1979; Snow & Whigham 1989; Primack & Hall 1990; Primack, Miao & Becker 1994), few studies have investigated the costs associated with clonal propagation (Jurik 1985; Pitelka *et al.* 1985; Reekie 1991). For clonal plants, such costs can be expressed as a negative functional relationship between present and future clonal propagule production. This relationship is analogous to that for costs associated with sexual reproduction (Gadgil & Bossert 1970; Antonovics 1980). In *U. perfoliata*, costs in terms of reduced survivorship as well as reduced future vegetative propagation were expressed in parents in both low-light and high-light environments. Fewer parents producing offspring ramets survived in all sites and fewer surviving parents produced clonal propagules in the following growing season. These costs, especially the latter, were more severe in the closed-canopy populations, indicating that low availability of light here imposes even larger costs on *U. perfoliata* parents that produce clonal offspring. These costs are high for several reasons. The propagules are leafless, therefore they cannot contribute photoassimilates towards their own upkeep, in contrast to woodland herbs such as *Fragaria vesca* that produce numerous leafy offspring ramets that can become self-sufficient early in the growing season (Jurik 1985). *U. perfoliata* plants do not produce an extensive physiologically integrated ramet system within which resources can be translocated between nodes. For example, *Clintonia borealis* maintains a large underground system of rhizomes that remain connected and physiologically functional for many years (Pitelka *et al.* 1985). *C. borealis* also produces numerous green shoots during the growing season. Therefore, both light and nutrients can be acquired from several different positions within the habitat by the intact clone. In this species, offspring ramet production does not appear to be costly to the clone (Pitelka *et al.* 1985). In contrast, an intact *U. perfoliata* clone has only one point at which light can be acquired and between one and three points at which water and nutrients can be acquired, provided that the roots of offspring ramets are fully functional within the first season of their birth. Offspring ramets of *U. perfoliata* often become as large as their parents and have a large proportion of the biomass produced during the season allocated to them. Therefore, investment in offspring is possible only if large reserves of stored carbon and improved access to resources are available to the parents.

The results of the greenhouse study give some indication why the costs of producing offspring are low for parents from at least one of the gap sites (gap site 3). In the experiment, plants from the gap site invested more biomass in parent roots (reserves) in favourable light conditions than the plants from the closed-canopy site. This implies that the larger parent root clus-

ters of the gap plants could have a higher probability of survival through the winter and subsequent clonal offspring production than the parent root clusters of the closed-canopy plants. The gap plants had more leaf area and owing to this they could have harvested more light and consequently could have allocated more biomass to reserves in favourable light conditions than the closed-canopy plants. Although plants from both sites had similar numbers of leaves, the leaves of gap plants were larger (Table 5). It is possible that this difference was due to genotypic differences between plants from the two sites. Alternatively, gap plants may have had higher relative growth rates with quicker expansion of leaves than the closed-canopy plants. In *U. perfoliata* there seems to be a conflict between reserve formation and clonal propagation that is more acute when light conditions are less than optimal for growth. Reserves accumulated by a plant may enable it to propagate clonally in consecutive seasons. However, in closed-canopy populations such repeated episodes of vegetative reproduction seem to be limited. In contrast, reduced costs of clonal propagation contribute to the higher rate of population increase observed in gaps, because a significant proportion of the parents can produce clonal offspring a second time.

Although *U. perfoliata* plants perform better in the relatively high light environment of small gaps, they appear to have the capacity to make as much use as possible of the available light, however low, under closed canopies. *U. perfoliata* plants can distribute biomass within leaves economically to maximize the area of the photosynthetic surface even in unfavourable light conditions. For example, in the plants in the greenhouse experiment, the same absolute amount of leaf biomass was spread over a larger area producing thinner leaves with greater specific leaf area in low light than in high light (Fig. 6). Thinner leaves are more economical to produce than thicker leaves because, by increasing specific leaf area, a plant can increase the amount of light harvested without a concomitant increase in biomass investment in leaf tissue (Poorter & Remkes 1990; Shipley 1995). Also, the maintenance costs of thinner leaves are low because they have fewer mesophyll cells than thicker leaves (Boardman 1977; Chabot, Jurik & Chabot 1979). Thicker leaves do exhibit higher photosynthetic rates than thinner leaves. However, in order to sustain a positive carbon balance in light conditions sub-optimal for photosynthesis the more economical option for plants is to produce thinner leaves (Chabot *et al.* 1979). Intriguingly, specific leaf area of *U. perfoliata* was also affected by ramet starting size. Plants grown from smaller ramets produced significantly thinner leaves than those grown from larger ramets, particularly in low light (Fig. 6). It appears that *U. perfoliata* plants with a small starting capital produce leaves that are cheaper to maintain during the growing season. However, these plants are unable to invest in

sufficient amounts of leaf tissue to take advantage of high light levels to the same extent that larger plants do.

Our results confirm the importance of canopy gaps for the population dynamics of *U. perfoliata*. However, our results also suggest that increased clonal propagation in response to increased light availability in gaps is delayed. Unless plants have sufficient biomass and morphological capacity, i.e. enough leaf meristems, they do not show a positive response immediately to high light. Clonal propagation is costly to plants in both more favourable and less favourable environments. A significant proportion of the parent plants are unable to survive through to another season and their capacity for clonal propagation a second time is reduced if they produce one or more offspring. However, in high light environments these costs are less and plants have the potential to produce clonal offspring repeatedly in consecutive seasons. Our results show that plant size has a long-term effect on the population dynamics of this species. Larger plants not only produce more but also larger clonal offspring. Therefore, the advantages of large size are expressed not only in a single growing season but are also carried over to subsequent generations of ramets.

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