

Research article

Timing of disturbance changes the balance between growth and survival of parent and offspring ramets in the clonal forest understory herb *Uvularia perfoliata*

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Abstract. Preformation of organs involves the initiation of vegetative and generative tissues at least one season before they are actually produced. It is a strategy to deal with environments characterized by predictable seasonality as it enables fast growth of plants at the onset of favorable conditions. However, early preformation also strongly restricts plants in their response to unpredictable environmental changes and disturbance. In this study we investigated the response of the clonal forest understory herb *Uvularia perfoliata* to disturbance and resource limitation. In *U. perfoliata* shoot characteristics, as well as vegetative and sexual reproduction are determined at the end of the previous growing season. Plants were grown under two light levels and the rhizome connection between parent and offspring ramets were severed at various times during the growing period. Disturbance did not affect total biomass accumulation but it did affect the relative allocation and survival probability of parents and offspring ramets. Early severing resulted in increased survival chance and future fitness of the parent ramet, while late severing resulted in a higher survival chance and increased fitness of offspring ramets. The response was mediated by plant size and resource availability. These results show that the life history of *U. perfoliata* includes the possibility to alleviate the effects of disturbance even though the species is characterized by strong developmental canalization through organ preformation.

Key words: clonal growth, developmental decisions, light, preformation, severing, trade-off

Introduction

Most woodland herbs in deciduous forests are perennials and the majority of them are also clonal (Kawano, 1975; Klimeš *et al.*, 1997; Shimizu *et al.*, 1998; Jolls, 2003). Clonal plants are characterized by two modes of reproduction, asexual by means of vegetative propagation, and sexual by means of flowering and seed production. The timing and amount of resources invested into survival and growth of the parent plant vs. asexual reproduction forms one of the most important life history decisions in clonal plants (Bierzychudek, 1982). There is evidence for a trade-off in the allocation of biomass between growth and reproduction (de Kroon *et al.*, 1991; Wijesinghe and Whigham, 1997).

However, the actual costs of reproduction and time when plants are actually experiencing costs are difficult to determine because plants allocate resources simultaneously to growth, survival and reproduction. In addition, in most clonal plants offspring ramets produce leaves and roots at an early developmental stage, thereby contributing to their survival and the survival of the parent ramet.

Most woodland herbs of deciduous forests produce buds that contain preformed organs determining the growth characteristics such as shoot size, leaf number, flowers or size and position of vegetative offspring of individuals in the next growing season (e.g., Sohn and Policansky, 1977). Preformation has thus a significant effect on resource uptake as well as the future demographic characteristics of populations. Preformation is common in habitats with a restricted period of favorable conditions such as light availability in forest understories (Whigham, 1974; Inouye, 1986; Geber *et al.*, 1997a, b; Worley and Harder, 1999; Meloche and Diggle, 2001, 2003). One benefit of preformed buds is that plants are able to begin growth as soon as appropriate environmental conditions are present, resulting in an efficient use of the favorable period (Inouye, 1986). In forest habitats many species emerge very early in the growing season, grow rapidly, and often produce seeds and asexual ramets before development of the forest canopy is complete (Whigham, 1974; Kawano, 1975; Wijesinghe and Whigham, 1997).

At the same time, early preformation restricts plants in their response to environmental conditions (Diggle, 1997; Geber *et al.*, 1997a; Worley and Harder, 1999). All plant parts to be produced in the coming growing season (e.g., number of leaves, presence or absence of flower primordia, number of asexual ramets) are determined in the previous growing season (Watson and Lu, 1999). The development of preformed buds may leave plants with little or no opportunity to change allocation patterns in response to disturbances or prevalent environmental conditions and the consequences of the present environment on growth and reproduction are manifested only one to several growing seasons later (Geber *et al.*, 1997a; Worley and Harder, 1999). The preformation of buds thus potentially results in developmental constraints.

Preformation may make plants especially vulnerable to herbivory and disturbance, as they have a very limited capacity to produce new tissues in order to replace any lost tissue. It has been shown that most woodland herbs do not produce new leaves in response to above ground herbivory resulting in decreased growth (e.g., Lubbers and Lechowicz, 1989; Whigham and Chapa, 1999). To date, however, there have been few studies of the effects of disturbance on current and future growth of woodland herbs, even though herbivory and physical disturbance are common in these environments. In Eastern North America, for example, increasing incidence and severity of disturbance caused by expanding populations of White-tailed deer (*Odocoileus virginianus*) have

had severe consequences on woodland herbs (Tilghman, 1989; McShea and Rappole, 1992; Rooney, 1997; Waller and Alverson, 1997).

Models of clonal growth of woodland herbs have primarily focused on growth dynamics in the absence of physical disturbance to individual plants (e.g., Wijesinghe and Hutchings, 1997; Cain and Damman, 1997). Other than a few herbivory studies, there have been few studies of the direct effects of disturbance on the ecology of woodland herbs (Bierzychudek, 1982; Whigham and Chapa, 1999; Gilliam and Roberts, 2003). The objective of this experiment was to test specific predictions (see below) of how a clonal woodland herb characterized by preformation of vegetative and reproductive tissues responds to physical disturbance of the connection between parent plants and developing ramets. We were especially interested in the effects of disturbance at different times during the growing season as this can provide novel information about the 'temporal window of opportunity' within which plants are able to change or partly reverse life-history decisions in response to their environment. We were also interested in the question to what extent and in what way resource availability and the timing of disturbance affect the trade-off between growth and survival of the parent and the offspring ramet, respectively. In general we predict that early disconnection between parents and ramets diminishes clonal reproduction and has a negative impact on total biomass accumulation of parents and offspring.

The specific questions asked in this study were as follows: (1) How flexible is the allocation pattern to parent and offspring? Can plants respond to disturbance by changing their allocation patterns through initiating new offspring ramets or increase allocation to the rejuvenation of the parent ramet? (2) When does offspring production confer costs to the parent? (3) How long should the offspring be connected to the parent in order to survive? (4) Does resource availability affect trait integration and the response of plants to severing? (5) How does storage affect future growth and the response of plants to resource availability and disturbance?

Materials and methods

Species description

Uvularia perfoliata L. (Liliaceae) is one of five species in a genus that is endemic to deciduous forests of Eastern North America. It typically occurs in patches composed of a single or multiple genets (Kudoh *et al.*, 1999). Whigham (1974) and Wijesinghe and Whigham (1997) have shown that plant performance (e.g., growth, flowering, ramet production) is influenced by light. Plants in high light conditions (e.g., tree gaps) are larger and produce more and larger ramets.

Successful seed production only occurs under relatively high light conditions (Kudoh *et al.*, 1999).

Ramets are produced at the ends of slender rhizomes and ramets do not produce leafy shoots in the growing season that they are formed (Fig. 1). Thus, ramets depend completely on parent plants during the time that they are developing. Before the onset of winter each viable ramet consists of 2–10 thickened storage roots, a shoot bud and 0–4 rhizome buds. The number of leaves and flowers are preformed in the shoot bud. In addition, number and position of rhizome buds which will eventually give rise to new ramets in the next growing season are preformed as well and rhizomes begin to grow very early in the growing season. By the time that the forest canopy has developed, rhizomes have reached their maximum length and ramets have started to form at the end of each rhizome (Whigham, 1974). Offspring ramets become independent of parent plants when the rhizome connections disintegrate by the end of the growing season.

Uvularia perfoliata occurs in deciduous forests in patches varying in light availability from 10–60% of full sun before the tree canopy develops to 1–10% of full sun following canopy development (Neufeld and Young, 2003). In deciduous forests disturbance is common and environmental conditions are largely unpredictable between seasons. Disturbance agents in these environments include fall of branches, trampling by large mammals and above as well as belowground herbivory by small mammals.

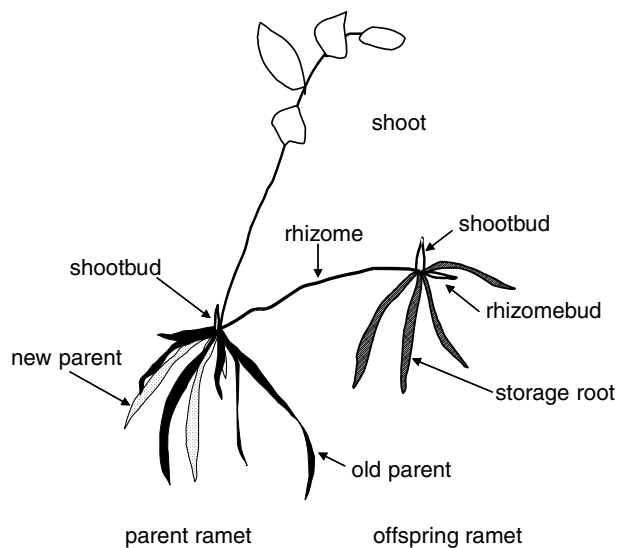


Figure 1. Schematic drawing of *U. perfoliata*, indicating allocation to parent and offspring ramet, as well as the location of preformed buds.

Experiment

At the beginning of September 1999, 60 ramets were collected in each of six populations within a mature forest of the Smithsonian Environmental Research Center (38°53' N, 76°33' W) near Edgewater, Maryland (USA). At the time of collection, the annual shoots of the parent ramets had already died. However, all connections between parent and offspring ramets were still intact. This enabled us to determine whether each individual was a parent or an offspring ramet. We used only offspring ramets in this study to prevent eventual effects of ramet age on growth and survival. We collected ramets that had one shoot bud and one bud (hereafter called a rhizome bud), which would give rise to a ramet during the next growing season. Ramets were washed, carefully dried and individually weighed, the number of storage roots (see Fig. 1) was counted and the length of the shoot and the rhizome bud was measured using digital calipers. At the time of collection ramets weighed between 170 and 1210 mg and contained 3–7 storage roots. Thereafter plants were planted at a depth of 3–5 cm into beds filled with potting soil. The distance between ramets was 25 cm. The beds were inoculated with a 50:50 mixture of water and soil collected from natural populations. The inoculum was used to increase the probability that the plants would develop mycorrhizal associations with appropriate fungi.

For each population, plants were divided into two weight classes and three plants per population per weight class were randomly allocated to each treatment. Treatments included two light treatments and five severing treatments. A total of 360 plants (6 populations \times 2 weight classes \times 2 light treatments \times 5 severing treatments \times 3 replicates) were used for the experiment. In spring 2000 we scored emergence of plants every other day until all plants had emerged. On June 2nd 2000, we measured the size of shoots, as well as the number of fully expanded leaves and the length and width of the longest leaf on each shoot.

The light treatments were imposed by means of covering the beds with layers of neutral shade cloth at a height of 2 m. The light levels were 7–10% of the ambient radiation for the high light treatments and around 1% of ambient radiation for the low light conditions. These light levels covered the range of light conditions inhabited by *Uvularia* under natural conditions (Wijesinghe and Whigham, 1997). High light conditions were comparable to small gap sites while the low light conditions simulated the light conditions found under an intact tree canopy. The light treatments were placed over the beds in April (2000) when shoots emerged above the soil surface.

Severing treatments were employed at four different times during the growing period. Plants chosen for each severing treatment and controls were randomly selected at the beginning of the experiment. At the time of severing

soil was carefully removed near each plant to expose newly formed rhizomes that connected parents with offspring ramets. The rhizomes were severed with a sharp knife at 1 cm distance from the parent ramet. The rhizome was followed to its end and, if present, the position of the offspring ramet was marked with a plastic label to facilitate its retrieval at the end of the growing season. Controls, here after referred to as C, were marked also but rhizomes were not severed. Severing was imposed on April 7 (S1), May 18 (S2), June 28 (S3), August 10 (S4). At each severing, rhizomes of three randomly chosen plants were excavated per population, size class and light treatment. After severing, two of the plants were covered with soil and allowed to continue growth, while the third plant was harvested and used to measure seasonal biomass allocation patterns.

In October 2000 all remaining plants were harvested and care was taken to excavate parent, as well as offspring ramets. At the time of harvest most shoots of the parent ramets had died and started to disappear and the rhizome connections between parent and offspring ramets had started to disintegrate. Harvested plants were divided into shoots, old and new roots on the parent ramet, the rhizome and the roots on the offspring ramet. The number of roots was counted and the dry-weight of all plant parts determined. At the final harvest we additionally counted the number of rhizome buds and measured the lengths of the rhizome and shoot buds. The number of leaves in the shoot buds was determined by making vertical sections through shoot buds. The sections were stained with 0.2% Aniline Blue Black mixed with 7% Acidic Acid and the number of leaves was counted using a binocular microscope at 25-fold magnification.

Statistical analysis

Data were analyzed by means of Analysis of Covariance, using severing time, light treatment and population as main effects and initial plant size and time of emergence as covariates. The main effects, the covariates as well as the interactions among light treatment, severing time and initial plant size were included into the model. As there was no significant effect of population, plants from the six populations were pooled before proceeding with the analysis. We used a top-down approach during the analysis. Plants were defined as surviving if either parent or offspring ramets had produced a root cluster containing a new shoot bud. The shoot and leaf size, total weight, as well as the relative biomass allocation pattern to the different structures were analyzed for this whole group of plants. The weight of the ramets as well as the number of storage roots and rhizome buds, lengths of shoot buds, and number of leaves within shoot buds was analyzed for surviving parent and offspring ramets separately. There was no significant three way interaction between light, severing time and initial weight. Therefore, the three way interactions were

excluded from all analyses. Data were transformed prior to analyses to match the assumptions of analysis of variance. The effects of severing time and light treatment on plant survival, the production of parent and offspring ramets, as well as the number of storage roots and rhizomes initiated were analyzed with categorical analysis using logistic regressions.

The pattern of trait integration was analyzed with path analyses using AMOS (Arbuckle and Wothke, 1999). Path analysis is a method to identify the structures of dependency among variables (Shipley, 1997). Basically it is a more general form of multiple regressions that allows consideration of complicated causal structures with more than one dependent variable on one another (Mitchell, 1993). This statistical procedure deals with intertrait correlation in the same way as does multiple regression, thus providing statistical control. We used a path analysis to determine direct and indirect effects among plant traits and to show which traits were the most significant determinants of the allocation to parent vs. offspring ramets in the two light treatments. We analyzed the effects of initial traits on growth traits and their effects, as well as the effect of severing on final biomass distribution for the two light treatments separately. We report the standardized regression coefficients, which allow for direct comparisons of the individual trait correlations as well as of the two path diagrams.

Results

Survival

Plants grown under high light conditions and plants that were initially larger had a significantly higher chance of survival than plants grown under low light availabilities (Tables 1 and 2). Higher initial weight increased the chance that surviving plants produced a new parent ramet, but did not affect the likelihood of offspring ramet production (Tables 1 and 2). Severing did not significantly affect plant survival nor did it alter the likelihood of surviving plants to produce a new parent. However, later severing resulted in a significant increase in offspring ramet production. (Table 1)

At the time of harvest, plants grown under high light conditions and initially bigger plants had a significantly higher old root biomass and gave rise to significantly greater root biomass on parents (Figs. 2 and 3; Table 2). The size of offspring was positively affected by high light availability, but not by initial weight (Figs. 2 and 3; Table 2). Severing time significantly affected weight and relative allocation to parent vs. offspring (Fig. 2; Table 2). At early severing time, parent ramets became significantly heavier, while severing connections later favored biomass allocation to offspring ramets.

Table 1. Percentage plant survival (i.e., whether a parent had produced a viable new parent and/or offspring ramet) and percentage of surviving plants producing a new parent or a new offspring

	High light			Low light		
	Plant	Parent	Offspring	Plant	Parent	Offspring
S1	83	90	10	42	100	0
S2	83	85	65	25	100	0
S3	92	77	86	58.3	28.6	78.6
S4	87.5	67	85.7	33	12.5	87.5
C	62.5	40	93	21	0	100

Table 2. ANCOVA results (*p*-values) for biomass and growth parameters

	Light	Severing	Initial weight	Light* Severing	Initial weight *		Emergence
					Light	Severing	
<i>Survival</i>							
Whole plant	0.001	0.340	0.029	0.791	0.495	0.397	0.126
Parent	0.989	0.757	0.027	0.999	<i>0.075</i>	0.416	0.189
Offspring	0.138	0.035	0.991	0.269	0.541	0.725	0.711
<i>Biomass</i>							
Total dryweight	0.001	0.957	0.001	0.852	0.166	0.715	0.376
Old parent	0.001	0.773	0.001	0.754	0.592	0.636	0.160
New parent	0.007	0.004	0.002	0.746	0.646	0.223	0.176
Offspring	0.010	0.001	0.516	0.149	0.566	0.795	0.641
<i>% Allocation</i>							
Shoot	0.002	0.428	0.003	0.839	0.782	0.214	0.445
Old parent	0.001	0.540	0.005	0.592	0.025	0.744	0.059
New parent	0.236	0.001	0.903	0.001	0.516	0.599	0.505
Offspring	0.461	0.001	0.305	<i>0.051</i>	0.933	0.769	0.268
<i>Shoot characteristics</i>							
Length	0.439	0.433	0.001	0.586	0.025	<i>0.098</i>	0.117
Leaf number	<i>0.078</i>	<i>0.059</i>	0.001	0.001	0.725	0.771	0.011
Leaf length	0.257	0.321	0.001	0.958	0.509	0.011	0.382
Leaf width	0.229	0.351	0.001	0.165	0.563	0.337	0.459
<i>Parent</i>							
Root number	0.549	<i>0.085</i>	0.001	0.205	0.411	<i>0.075</i>	0.175
Shootbud length	0.270	0.102	0.010	0.516	0.542	0.340	0.939
Preformed leaves	0.102	0.112	0.018	0.779	0.705	0.260	0.718
Rhizome number	0.974	0.386	<i>0.054</i>	0.994	0.671	0.425	0.864
Rhiz. bud length	0.157	0.007	0.114	0.137	0.222	0.012	0.910
<i>Offspring</i>							
Root number	0.001	0.006	0.007	0.789	0.197	0.358	0.521
Shootbud length	0.017	0.001	0.009	0.793	0.524	0.760	0.389
Preformed leaves	0.042	0.002	0.002	0.090	0.614	0.139	0.415
Rhizome number	0.175	0.224	0.826	0.509	0.274	0.244	0.777
Rhiz. bud length	0.923	0.050	0.106	0.576	.	0.302	0.624

Significant effects are highlighted in bold and italics, marginally significant effects in italics.

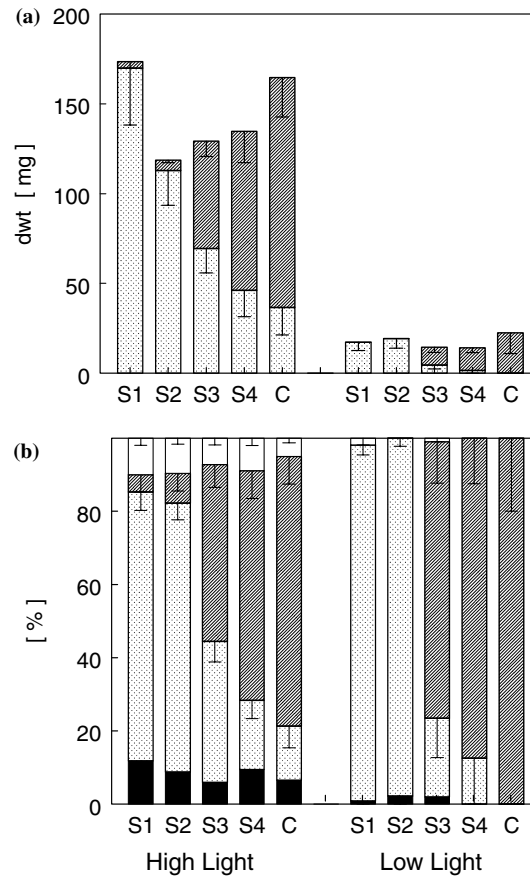


Figure 2. Absolute weight of new parent (light bars) and offspring ramet (dark bars) at the end of the growing season (a), and (b) percentage allocation to old parent (black), new parent (light bar), offspring ramet (dark bar) and aboveground structures (white bar). Severing treatment abbreviations: S1 – severing on April 7th, S2 – severing on May 18th, S3 – severing on June 28th, S4 – severing on August 10th, C – no severing applied. For significances of the effects see Table 2.

There was a significant interaction between light availability and severing on the relative allocation to parent and offspring ramets (Fig. 2; Table 2). This was due to a more gradual response to the timing of severing under high light conditions as compared to low light conditions. Under low light conditions almost all resources were allocated to the surviving parent if severing occurred early (S1, S2) while more than 80% of the resources were allocated to the offspring if severing was applied later (S3, S4, C). There was a significant interaction between light availability and initial weight on the relative weight of the old parent ramet (Table 2). Under low light conditions the relative allocation to the old parent ramet was independent of initial size whereas under high light conditions the relative allocation to the storage roots of the old

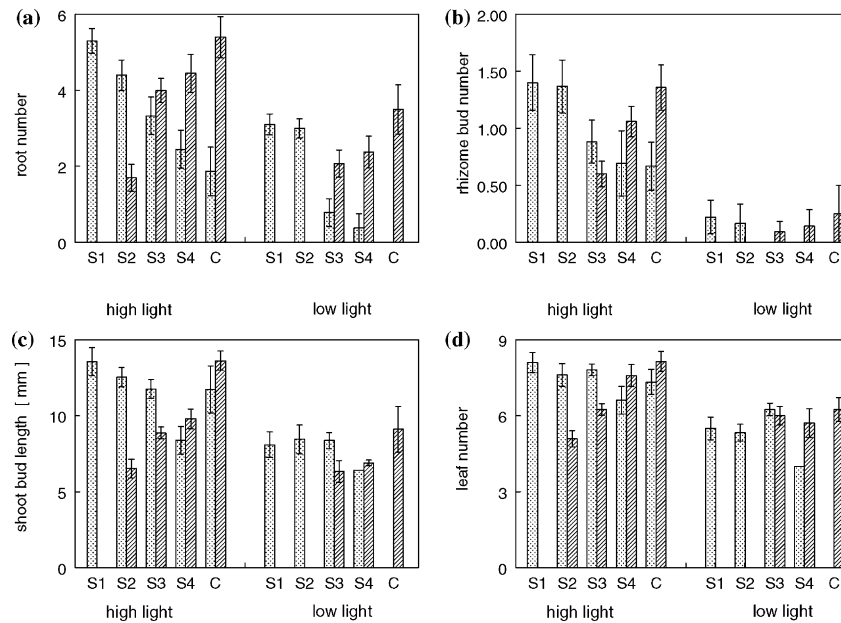


Figure 3. Allocation parameters predicting the fitness in the coming season: (a) number of storage roots, (b) number of rhizome buds, (c) length of the shoot bud, and (d) number of leaves preformed in the shoot bud. Left (stippled) bars indicate new parent ramets, while right (hatched) bars indicate offspring ramets. For explanations of treatment abbreviation see Figure 2. For significances of the effects see Table 2.

parents of initially larger ramets was higher than allocation to old storage roots of initially lighter ramets at the harvest in October.

Shoot characteristics

Initial weight significantly affected shoot size and morphology (Table 2). Ramets that were initially larger gave rise to larger shoots with more and larger leaves. There was a significant interaction between light and severing on leaf number. The timing of severing had a stronger impact on leaf number in low as compared to high light conditions. There was also a significant interaction between initial weight and severing on leaf length. In plants severed early in the growing season leaf length was more affected by initial size as compared to plants severed later in the growing season.

Effects on future plant performance

Severing time had a slight, though not significant, effect on the number of storage roots of the new parent which tended to decrease if severing occurred later ($p = 0.085$) and an interaction between initial weight and severing time on the

number of storage roots of new parent ramets ($p = 0.075$). Rhizome buds were shorter if severing occurred later in the growing season (Table 2). Neither light availability nor severing time significantly affected traits predicting future fitness of the new parent ramets. Initial weight significantly affected plant traits predicting future fitness of the new parent ramets (Table 2; Fig. 4). Parent ramets produced by initially bigger ramets had a higher number of storage roots, larger shoot buds, a higher number of preformed leaves and a marginally higher number of initiated new offspring ramets.

Light availability, timing of severing and initial weight significantly affected most traits characterizing the future fitness of offspring ramets (Table 2; Figs. 3 and 4). Offspring originating from ramets grown under low light had fewer roots, shorter shoot buds and fewer preformed leaves. Early severing significantly decreased the number of storage roots, the lengths of shoots and rhizome buds as well as the number of leaves preformed in the shoot buds of offspring ramets (Fig. 3). Higher initial weight positively affected the number of storage roots, the length of shoot buds as well as the number of leaves preformed in shoot buds of offspring ramets (Fig. 4).

Trait integration

Analysis of the pattern of trait integration revealed a strong negative correlation between offspring and parent size, indicating significant costs of reproduction (Fig. 5). Severing did not affect total biomass production, but the allocation of resources to offspring vs. parent ramets. Initial weight affected total biomass directly as well as via other correlated traits such as leaf number and initial shoot bud size. Trait integration (i.e., number and strength of trait correlations) was much stronger under low light conditions than under high light conditions. Especially under resource poor conditions growth and reproduction depended strongly on initial weight and the size of the preformed structures. In contrast to high light conditions, many negative trait correlations were expressed under low light conditions. Under low light conditions, initial number of storage roots and the number of leaves produced negatively affected biomass production. Shoot length negatively affected the size of new parent and offspring ramets. Leaf length positively affected biomass accumulation, but negatively affected the size of offspring. Initial size of the rhizome bud did not predict size of the offspring. Size of the shoot bud did predict size of the new parent under low light availability.

Discussion

The main aim of this study was to gain insight into the life history responses of a clonal woodland herb with strong preformation of vegetative and repro-

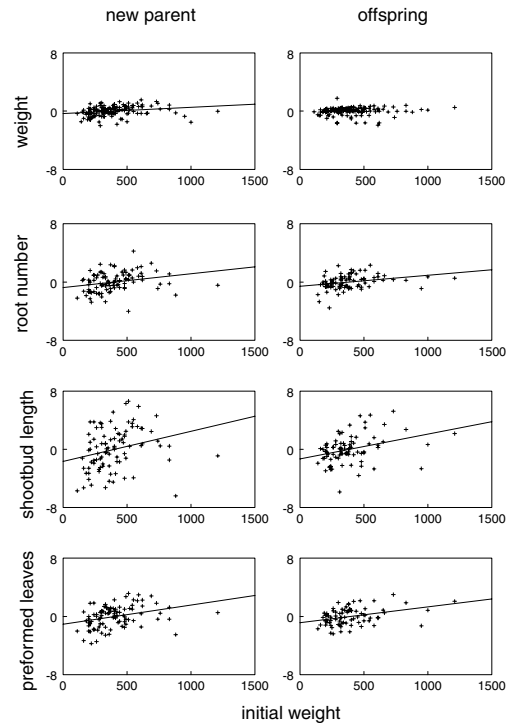


Figure 4. The effect of initial weight on traits predicting future fitness. 1st row: dry weight of the ramets, 2nd row: number of storage roots; 3rd row: shoot bud length; 4th row: number of leaves performed in the shoot bud. On the x -axis initial weight is depicted, on the y -axis the residuals of the respective traits after correcting for the effects of severing, light availability and emergence time. Regression lines indicate significant ($p < 0.05$) association among initial weight of plants and traits expressed at the end of the growing season.

ductive tissues to disturbance, and how the timing of disturbance, carbohydrate storage, and resource availability affects these responses. The study species, *U. perfoliata* is representative of many clonal woodland herbs that produce ramets without aboveground structures during their first growing season (e.g., Cook, 1988; Lubbers and Lechowicz, 1989; Whigham and Chapa, 1999) and which are characterized by predominant resource allocation to offspring ramets (Wijesinghe and Whigham, 1997). *U. perfoliata* is characterized by strong organ preformation which, in addition to the size of the storage roots, is a source of carry over effects from one generation to the next, as past conditions impose developmental canalization of growth and performance in the coming growing season and ramet generation (Geber *et al.*, 1997a, b).

An unexpected result of the experiment was that severing did not affect survival and biomass accumulation of the whole plant (e.g., parent and offspring combined), indicating that plants were able to successfully reallocate

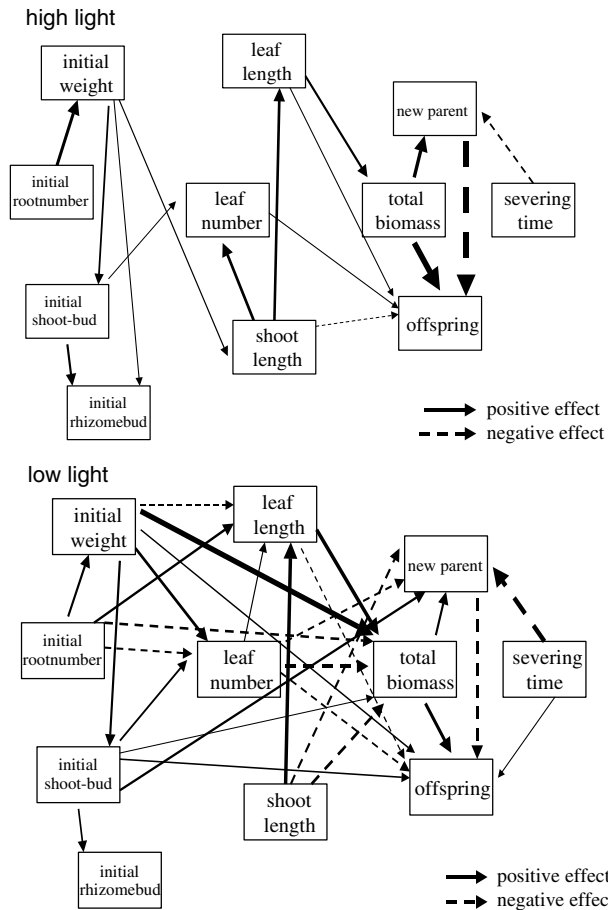


Figure 5. Path diagram showing the effects of initial size and morphology on shoot characteristics and biomass allocation as well as the effect of timing of severing on biomass production and allocation under high light and low light conditions. Dashed lines indicate negative path coefficients. Only significant paths are shown, the thickness of the lines reflects the strength of trait integration, as indicated by the standardized path coefficients, ranging from 0.1 (thinnest line) up to 0.9 (thickest line); variation due to error is not included for simplicity.

resources; thereby preventing the loss of assimilates through severing. This result is clearly different from the responses of woodland herbs to aboveground herbivory. Removal of leaf tissue in woodland herbs appears to always result in decreased present and future growth (e.g., Primack and Hall, 1990; Whigham, 1990; Rockwood and Lobstein, 1994). Despite the strong preformation of plant organs in *U. perfoliata*, a life history trait that could limit responses to disturbance, the potentially negative effects of severing on total biomass allocation were buffered by a flexible seasonal allocation pattern. In control plants most of the resources were invested into the production of one large offspring

and many of the parent ramets died, especially under low light conditions. In response to disturbance early in the growing season (treatments S1 and S2) most resources were invested into the rejuvenation of the parent ramet. By the middle of the growing season (S3), however, resources were about equally divided between parents and offspring ramets. Severing at that stage resulted in the production of more, but smaller ramets. Under unpredictable and resource poor conditions (i.e., low light) ramet size may be one of the strongest determinants of plant survival. This was also reflected by the stronger effect of initial ramet size on the size of newly produced ramets in low as compared to high light conditions. If ramets are big enough they may be able to endure more than one unfavorable year, perhaps supported by mycorrhizal interactions (Widden, 1995; Whitbread *et al.*, 1996; Shefferson *et al.*, 2001; Watson *et al.*, 2002) while 'waiting' for an improvement of environmental conditions (e.g., Gill, 1996).

Our study clearly demonstrates that the production of offspring ramets has priority over the survival of the parent ramets. Similar early allocation of resources to vegetative reproduction has been found for other forest herbs (e.g., Bell, 1974; Kawano, 1985). Surprisingly, offspring ramets that were disconnected from the parents at an early stage (S1 and S2) were able to survive. Small belowground ramets may be able to survive because of low maintenance costs of such systems, which lack all above ground structures and which possess a small root system consisting of storage roots only (young ramets of *U. perfoliata* do not have fine roots; D. Whigham, personal observation). Small ramets are also likely to develop mycorrhizal relationships that help with resource acquisition and survival (Brundrett and Kendrick, 1990; deMars and Boerner, 1995; Watson *et al.*, 2002). If no disturbance occurred, however, investment into the renewal of parent ramets started relatively late in the growing season and the main growth of the parent's storage roots took place after the offspring ramet finished development. Resource poor conditions strengthened this pattern. The low survival chance of undisturbed parent ramets indicates that allocation of resources to the offspring ramet was prioritized and that only a surplus of resources was invested into the rejuvenation of the parent.

Varying the timing of disturbance resulted in altered allocation patterns. Disturbance triggered earlier and higher investment into the parent ramet as compared to the undisturbed treatment. Such an increased proportional allocation to one function need not necessarily indicate a strategic emphasis on that function, but may merely result if that function is most able to accommodate surplus resources (Worley and Harder, 1999). In our experiment this was clearly the case for the increased survival of parent ramets after severing. If no severing occurred, parent ramets mainly invested into their own survival after the offspring ramets had finished development and were no longer a

strong sink for resources. As offspring ramets of *U. perfoliata* are completely dependent on resource support from the parent ramet, their survival chance and future fitness increased with later occurrence of disturbance. After severing, parent ramets neither continued to invest resources into the offspring, nor could they initiate new rhizomes to produce additional ramets as the number and position of offspring ramets was already determined the previous growing season. The post-disturbance surplus of resources in the parent led to an increased investment of resources into the renewal of the parent ramets, resulting in a higher survival chance and higher future fitness.

Based on previous studies of the same species (e.g., Wijesinghe and Whigham, 1997) we had anticipated that varying light levels would influence patterns of resource allocation. Under low light conditions the survival of parent vs. offspring ramets responded more strongly to timing of severing. Resource mediated trade-offs among different life history functions are often less pronounced in benign than in stressful environments (Wijesinghe and Whigham, 1997; Arntz *et al.*, 2002). Resource limitation thus strengthens internal trait integration thereby increasing the expression of trade-offs. Wijesinghe and Whigham (1997) found that in non-gap habitats the investment into clonal offspring resulted in higher costs for survival and future reproduction of parent ramets of *U. perfoliata* than in gap populations. We found that under low light availability early severing triggered virtually sole survival of parents whereas late severing resulted in virtually sole survival of offspring ramets. Under high light conditions plants showed a comparable, but much less pronounced response. These results indicate that the cost of reproduction was much higher under low than under high light conditions. Our pattern of trait integration thus confirmed the notion of a stronger canalization of plant growth and response to severing in plants subjected to low as compared to high light conditions. Similarly, Cheplik (2001) also found that the pattern and strength of integration among parameters describing resource allocation was stronger under low as compared to high nutrient availability for *Amaranthus albus*.

Severing also affected the number and weight of storage roots. In *U. perfoliata* each ramet consists of 3–10 thickened roots, which serve as a storage organ (Whigham, 1974). Stored resources can be used for winter survival, support of increased assimilate need during shoot growth in spring and reproduction, buffer adverse conditions or enabling plants to survive and respond to herbivory (Whigham, 1990; Zimmerman and Whigham, 1992; Rockwood and Lobstein, 1994; Wyka, 1999, 2000; Meloche and Diggle, 2003). Under high light conditions the root dry mass stayed constant throughout the whole growing period and decreased only when the roots started to die in October (data not shown). Under low light conditions, on the contrary, the root weight steadily decreased throughout the growing period (data not shown) leading to a significantly lower weight of the old root cluster of parent ramets

subjected to low light as compared to high light conditions. For other species (e.g., *Oxytropis sericea*, Wyka, 1999) shading leads to a remobilization of otherwise unused carbohydrates to support reproduction. Stored carbohydrates can thereby buffer the negative impact of adverse environmental conditions and maintain genet survival and reproduction. The presence of storage organs may relax the developmental canalization and enable plants to respond in a plastic way by means of serving as short term storage of assimilates until the allocation pattern has been changed in response to environmental conditions or by providing plants with essential resources under very resource limited conditions. In order to answer this hypothesis, experiments are needed which specifically study the fate of stored carbohydrates under different environmental conditions, such as herbivory, severing and low light.

Conclusions

Preformation of organs is a strategy to deal with environments characterized by predictable seasonality, where relatively short periods of favorable conditions are alternated with relatively long periods of unfavorable conditions. High degrees of preformation enables plants to optimally use the short favorable period, as preformed organs can rapidly expand and mature. Disturbance and other unpredictable changes in environmental conditions, however, may offset the advantages of organ preformation as it restricts the plants in their short-term response to their environment. This study clearly demonstrates that the timing of disturbance has a significant influence on patterns of resource allocation by affecting the relative amount of biomass invested into parent as compared to offspring ramets. The responses, however, are modified by initial plant size and resource conditions (i.e., light levels). Our results demonstrate that the developmental canalization characterizing plants with organ preformation can be relaxed through storage and flexible resource allocation in response to environmental conditions, thereby alleviating the effects of disturbance on growth and survival of *U. perfoliata*. The most surprising result, however, was that the timing of disturbance had no effect on overall plant size, even though future performance (i.e., growth and propagation in the next growing season) was affected. Additional research is needed to determine the generality of our findings in other woodland herbs and it would be especially useful to know how important mycorrhizal interactions are in controlling overall plant responses. There is some evidence that mycorrhizal interactions, while common, may be facultative in woodland herbs (Watson *et al.*, 2002) and one response to disturbance may be an increase in the allocation of resources to the establishment of mycorrhizal interactions that will increase survival and minimize the losses of biomass.

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