# Size dependency of sexual reproduction and of clonal growth in two perennial plants

**Bernhard Schmid, Fakhri A. Bazzaz, and Jacob Weiner**

**Abstract**: We compared the size dependency of sexual reproduction and clonal growth in two clonal perennials that inhabit old fields, *Aster lanceolatus* and *Solidago canadensis*. In both species there was a threshold size required for sexual reproduction to occur, and above that threshold reproductive output increased linearly with vegetative mass. Biomass allocated to clonal growth was also highly correlated with vegetative mass in both species, but there was no evidence of a threshold size for clonal growth. The absence of a clear size threshold for clonal growth emphasizes the similarity between clonal growth (vegetative reproduction) by rhizomes and growth of other vegetative parts, as opposed to sexual reproductive allocation. In both species there were differences in the allocation patterns of plants derived from seeds and those derived from rhizomes. Although seed- and rhizome-derived plants did not differ in phenology and size, the latter allocated more biomass to sexual reproduction and clonal growth in both species.

*Key words*: clonal growth, size dependency, reproduction, *Aster lanceolatus, Solidago canadensis*, size threshold.

**Résumé** : Les auteurs ont étudié l'influence de la grosseur des plants sur la reproduction sexuelle et la croissance des touffes chez deux plantes clonales pérennes habitant de vieilles prairies, l'*Aster lanceolatus* et le *Solidago canadensis*. Chez les deux espèces, il y une dimension critique qui doit être atteinte pour qu'il y ait reproduction sexuelle, et au dessus de ce seuil l'effort reproductif augmente linéairement avec la masse végétative. La biomasse allouée à la croissance clonale est aussi fortement corrélée avec la mase végétative chez les deux espèces, mais il n'y a pas de preuve du besoin d'une dimension critique pour la croissance clonale. L'absence d'une dimension critique précise pour la croissance clonale souligne la similitude entre la croissance clonale (reproduction végétative) par des rhizomes et la croissance des autres parties végétatives, contrairement à l'allocation pour la reproduction sexuelle. On observe des différences dans les patrons d'allocation des plantes provenant de graines et celles provenant de rhizomes, chez les deux espèces. Bien que les plantes provenant de graines et de rhizomes ne diffèrent ni phénologiquement ni en dimensions, ces dernières allouent plus de biomasse à la reproduction sexuelle et à la croissance clonale, chez les deux espèces.

*Mots clés* : croissance clonale, effet de la dimension, reproduction, *Aster lanceolatus, Solidago canadensis*, dimension critique.
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## Introduction

Many perennial plants multiply by both sexual reproduction and clonal growth. While the size dependency of sexual reproduction is well established (Samson and Werk 1986; Shipley and Dion 1992), little is known about the size dependency of clonal growth. Since the demographic processes of birth and death are mediated by growth, the relationship between the biomass of vegetative plant parts and the biomass allocated to sexual and clonal structures provides a basis for understanding the relationship between growth and reproduction in plant species.

From a simple constraints model, Weiner (1988) predicted that plants should have a minimum size for sexual reproduction and a linear relationship between size and reproductive output above that minimum (Crawley's (1983) "non-linear (sic) fecundity/size relationship"; Samson and Werk's (1986) model B). This pattern was observed in a number of species (Hartnett 1990; Thompson et al. 1991; Aarssen and Taylor 1992; Aarssen and Clauss 1992; Schmid and Weiner 1993; Méndez and Obeso 1993), although some species do not show evidence of a significant minimum size requirement for reproduction (Klinkhamer and de Jong 1987; Rees and Crawley 1989). Size–fecundity relationships show significant genotypic variation and phenotypic plasticity (Schmid and Weiner 1993; Clauss and Aarssen 1994*b*).

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We know of no clear theoretical expectation for the size dependency of allocation to clonal growth (but cf. Armstrong 1982, 1983; Sackville Hamilton et al. 1987). Hartnett (1990) found only weak positive relationships between plant size and rhizome mass in *Solidago canadensis* and *Pityopsis graminifolia*, with no evidence of a minimum size for rhizome production. *Potentilla anserina* rosettes grown at three densities showed no significant differences in percent allocation to clonal growth, which implies a simple linear relationship between size and clonal growth with no minimum size for allocation to clonal growth (Eriksson 1985). The probability of *Clintonia borealis* ramets showing evidence of clonal growth in the field increased with size under natural (Pitelka et al. 1985) and experimental (Ashmun and Pitelka 1985) conditions, and larger plants tended to produce more and larger rhizomes. The number of daughter tubers produced increased with size in *Arum italicum*, but even the smallest plants produced some daughter tubers (Méndez and Obeso 1993).

We investigated the relationships between size, reproduction, and clonal growth in two old-field perennials, *Aster lanceolatus* Willd. and *S. canadensis* L. under a range of conditions, using the simple model (Loehle 1987; Weiner 1988) for the mass of sexual structures

$$[1] \quad r = b_{\mathrm{r}} \cdot (v - a_{\mathrm{r}})$$

and the mass of clonal structures

$$[2] \quad c = b_{\mathrm{c}} \cdot (v - a_{\mathrm{c}})$$

where $v$ is the vegetative mass or size of the primary ramet, $a_{\mathrm{r}}$ and $a_{\mathrm{c}}$ are the minimum sizes required for sexual reproduction and clonal growth, respectively, and $b_{\mathrm{r}}$ and $b_{\mathrm{c}}$ are the slope parameters for the two relationships.

We test the following hypotheses: (*i*) both sexual reproduction and clonal growth show a positive linear relationship with plant size ($b_{\mathrm{r}} > 0$, $b_{\mathrm{c}} > 0$); (*ii*) both sexual reproduction and clonal growth require an initial investment, measurable as a positive minimum size for the two processes ($a_{\mathrm{r}} > 0$, $a_{\mathrm{c}} > 0$).

Conditions predicted to favor clonal growth (highly localized risk of mortality, low competition) are thought to occur during the early development of a genet; developmentally, seed-derived plants represent young genets, whereas rhizome-derived plants represent old genets (Zangerl and Bazzaz 1983; Schmid and Bazzaz 1990; Schmid and Weiner 1993). Therefore we tested the additional hypothesis (*iii*) plants derived from seeds allocate more biomass to clonal growth and less biomass to sexual reproduction than do plants derived from rhizomes.

## Methods

*Aster lanceolatus* and *S. canadensis* commonly colonize abandoned fields through dispersal of their small seeds and subsequently grow clonally. In spring, the perenniating rhizome system produces a cohort of aerial shoots that flower and fruit in late summer to early autumn and die back thereafter. Rhizome connections decay after 1 year in *Aster lanceolatus* and after more than 2 years in *S. canadensis*. All plant material used in the experiment was collected from old-field sites in eastern Massachusetts. Seedlings and rhizome cuttings of the test species were raised to a similar size in a heated glasshouse. When they had reached the rosette stage (15–16 May 1985) they were planted out to the experimental garden at Harvard University, Cambridge, Mass. There were 24 plots measuring 60 × 80 cm, each with 12 test individuals. Experimental factors that varied among plots were fertilizer application and presence or absence of background species. Experimental factors that varied within plots were species and mode of propagation (seed-derived versus rhizome-derived). Detailed descriptions of the experimental procedures are reported in Schmid and Bazzaz (1992).

The phenological status (rosette, bolting, branching, beginning to flower, flowering, fruiting), height, and basal stem diameter of all plants were recorded on 13 and 27 July, 10 and 23 August, 14 September, and 10 October 1985 (Julian days 194, 208, 222, 235, 257, 283). Stem volume was calculated from the measurements of diameter and height, assuming that the stem was a cone tapering off to half the diameter at the apex. On 7–19 November 1985 the plants were harvested to determine the dry mass of vegetative structures (roots, stems, leaves), sexual structures (seeds, flower heads, subtending leaves, and branches), and clonal structures (new rhizome buds and new primary and secondary rhizomes). The number of rhizomes per plant was counted and their length determined. To determine root mass, plants were excavated with the soil blocks, soaked, then hand washed for 30–60 min per individual.

The fertilizer application and background species are sources of controlled environmental heterogeneity, leading to a large variation in plant size. We analyze the resulting relationships among biomass components for seed- and rhizome-derived plants. Because all variables had error variation associated with them we used the errors in variables model to estimate the parameters (Kendall and Stuart 1973).

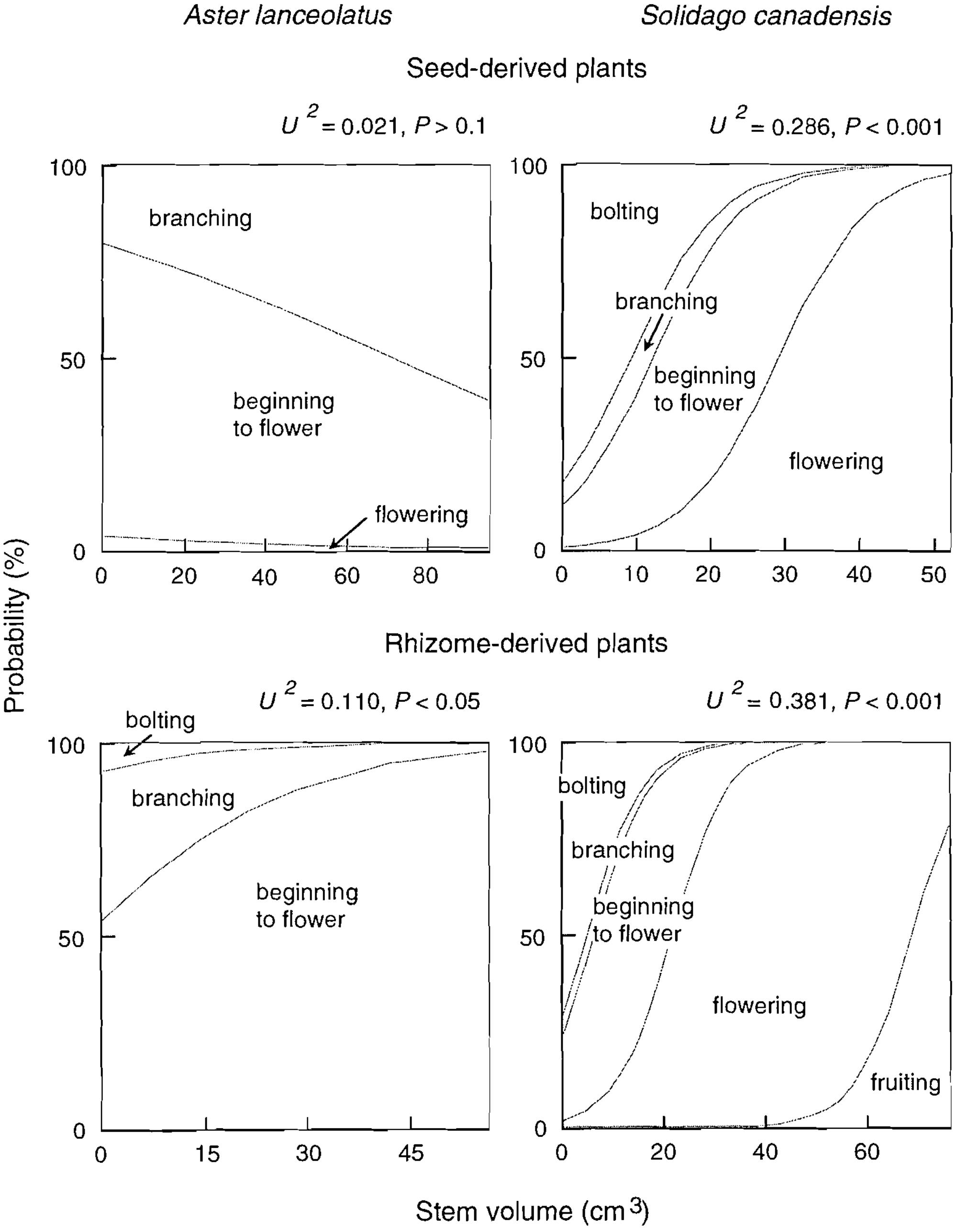
## Results

Fifty percent of the *S. canadensis* plants had started to flower by 12 August, whereas the *Aster lanceolatus* individuals did not reach this level of flowering until 2 September. The phenological development was strongly influenced by plant size in *S. canadensis*: for example, the probability that a plant was flowering at a given date increased with the stem volume it had reached (Fig. 1). In *Aster lanceolatus* this dependency was only visible in rhizome-derived plants and was weak even in this case.

At harvest, seed- and rhizome-derived plants of both species had similar total biomass (mean ± SE): 54.37 ± 8.86 g and 63.46 ± 9.19 g in *Aster lanceolatus* and 48.54 ± 3.62 g and 39.81 ± 3.62 g in *S. canadensis*. Variation in the mass of vegetative structures (leaves + stems + roots) accounted for a large proportion of the variation in the mass of sexual structures (inflorescences with seeds) and clonal structures (new rhizomes) using the simple linear model (Fig. 2; Table 1). However, the regression lines for the size dependency of sexual reproduction and clonal growth differed in their $x$-intercepts. The data suggest that a positive minimum plant size had to be attained for sexual reproduction to begin, but there is no evidence of a minimum size for clonal growth (Table 1).

The relationship between clonal growth and size was only

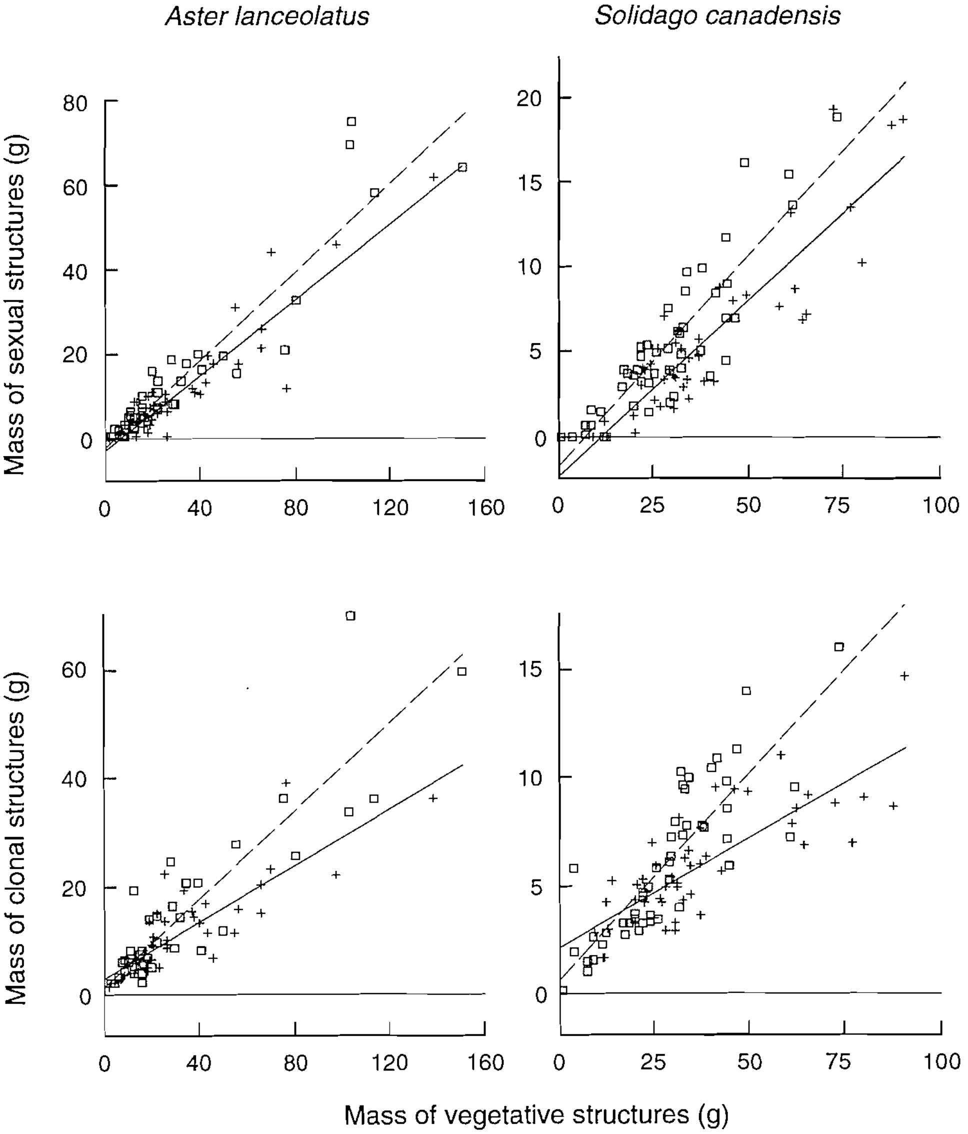
**Figs. 1.** Relationship between phenological status and stem volume on 23 August (day 235) for seed- and rhizome-derived plants of *Aster lanceolatus* and *Solidago cànadensis*; the *y*-axis represent the expected proportions of plants in a given phenological state (calculated by logistic regression, $U^2$ is a measure for the proportion of variance explained by the model and $P$ is the significance of the relationship; see SAS Institute Inc. (1989)).



slightly weaker than that between sexual reproduction and size ($r^2$ in Table 1). Because of the minimum size for sexual reproduction but not clonal growth, the ratio of reproductive mass to clonal structure mass increased with plant size from less than 1 to about 1.5 ($P < 0.05$ for all except rhizome-derived plants of *Aster lanceolatus*; cf. Fig. 2).

The allocation of total biomass to vegetative, sexual, and clonal structures differed between seed- and rhizome-derived plants in both test species (Fig. 2; Table 1): seed-derived plants tended to allocate less biomass to sexual reproduction than did rhizome-derived plants ($P < 0.1$ in *Aster lanceolatus* and $P \approx 0.1$ in *S. canadensis* for comparison of regression slopes), and this tendency was significant for biomass allocation to clonal growth ($P < 0.01$ in *Aster lanceolatus* and $P < 0.001$ in *S. canadensis* for comparison of regression slopes). Seed-derived plants still allocated a comparatively large proportion of biomass to roots and leaves at harvest, whereas rhizome-derived plants allocated a particularly large proportion of biomass to clonal structures (new rhizomes); with respect to stems, however, there was no difference.

**Fig. 2.** Relationship between the mass of sexual or clonal structures and the mass of vegetative structures at harvest for seed-derived (+, solid line) and rhizome-derived (□, broken line) plants of *Aster lanceolatus* and *Solidago canadensis* (linear regression with errors in variables, the errors in mass of vegetative structures were assumed to have half as much variation as the errors in mass of sexual or clonal structures; see Methods).



## Discussion

The linear size-dependent model worked well for both clonal growth and sexual reproduction in both species. However, the data suggest that a minimum plant size must be reached for sexual reproduction, but there is no evidence for such requirement for clonal growth (Table 1). There are two possible types of evidence that can support the hypothesis of a minimum-size requirement for sexual reproduction. The first type of evidence is an increasing probability of flowering with increasing size (Fig. 1). This was observed previously in several species with a relatively determinate growth of genets (e.g., biennials: Werner 1975; Gross 1981; Silvertown 1983) or shoots (Bradbury 1981; Primack and Hall 1990; Schmid and Weiner 1993). It appears that many perennial plants require a long period of vegetative growth before they first reach a size at which they can produce sexual structures (Harper 1977) and a similar situation may occur in clonal animals (Harvell and Grosberg 1988). The second type of evidence is a positive $x$-intercept in the relationship between reproductive output ($y$) and size ($x$). This was found in several plant species, both annuals and perennials (e.g., Hartnett 1990; Klinkhamer et al. 1992; Ridder 1990; Thompson et al. 1991) and is here evident in both *Aster lanceolatus* and *S. canadensis* (Table 1).

Whether or not a plant reproduces is a function of several factors, of which size is only one. The developmental stage of a plant is influenced by age, environmental factors such as nitrogen levels, and photoperiod, as well as size. When a plant does reproduce, however, the amount of reproduction (e.g., the number of flowers and seeds produced) is primarily determined by size (Schmid and Weiner 1993). During

**Table 1.** Parameter estimates for the relationship between the mass of sexual or clonal structures and the mass of vegetative structures at harvest for seed- and rhizome-derived plants of *Aster lanceolatus* and *Solidago canadensis.*

| | Minimum size ($x$-intercept ± SE) | Slope (± SE) | $n$ | $r^2$ |
|---|---|---|---|---|
| | **Sexual structures** | | | |
| *Aster lanceolatus* | | | | |
| Seed-derived plants | 5.48±2.50 | 0.45±0.03 | 42 | 0.85 |
| Rhizome-derived plants | 3.95±2.74 | 0.53±0.03 | 39 | 0.88 |
| *Solidago canadensis* | | | | |
| Seed-derived plants | 11.57±2.36 | 0.21±0.02 | 48 | 0.80 |
| Rhizome-derived plants | 7.33±2.04 | 0.25±0.02 | 48 | 0.78 |
| | **Clonal structures** | | | |
| *Aster lanceolatus* | | | | |
| Seed-derived plants | −12.04±5.09ns | 0.26±0.03 | 43 | 0.72 |
| Rhizome-derived plants | −4.39±4.05ns | 0.40±0.03 | 39 | 0.80 |
| *Solidago canadensis* | | | | |
| Seed-derived plants | −21.26±6.87ns | 0.10±0.01 | 48 | 0.64 |
| Rhizome-derived plants | −3.18±3.29ns | 0.19±0.02 | 48 | 0.71 |

**Note:** Linear regression with errors in variables is based on the assumption that the errors in mass of vegetative structures have half as much variation as the errors in mass of sexual or clonal structures (see Kendall and Stuart 1973). ns, not significant ($P > 0.05$).

the course of reproduction, resources are being transferred into reproductive structures, so reproductive output will be underestimated unless the plants have completed the reproductive episode (Thompson et al. 1991; Clauss and Aarssen 1994*a*). Rather than looking at single factors that may be confounded, we should now be able to model plant reproduction more fully as a function of more than one factor, as has been done for animals (Kooijman 1993). We hypothesize that for many plants in nature, the onset of reproduction will be determined primarily by an interaction between age and size, and the amount of reproduction will be determined primarily by size.

Although our data support the hypothesis of a threshold size for sexual reproduction, there was no evidence of a threshold size for clonal growth (rhizome formation). Of course, there may be a very small threshold size for clonal growth that we could not detect. The absence of a threshold for clonal growth in both species confirms observations made by Hartnett (1990) on two other perennial composites (*S. canadensis* var. *scabra* Torr. & Gray = *Solidago altissima* L. and *Pityopsis graminifolia*). Immediate allocation to clonal growth may be a general feature of clonal plants and animals (Hughes 1989; Salisbury 1942). The threshold size for sexual reproductive allocation but not clonal growth has important implications for allocation decisions. For example, *C. borealis* ramets can flower and (or) produce one or two rhizomes. While the probability of flowering and of rhizome production generally increases with ramet size, larger individuals are more likely to flower than to produce a second rhizome (Ashmun and Pitelka 1985; Pitelka et al. 1985). This suggests that plants will put resources into clonal growth, but if they have sufficient resources to reproduce sexually, they will do so and pay a cost in rhizome production.

Why does one form of propagation, sexual reproduction, clearly require the achievement of a threshold size, while the other form, clonal growth (vegetative reproduction), does not? One possible explanation is that clonal growth, the making of new shoots, is not fundamentally different from vegetative growth of a shoot and is therefore governed by similar rules. Clonal growth is vegetative growth of a genet, and in this sense is similar to vegetative growth of a ramet (shoot). Rhizome growth in a clonal perennial species is parallel to branch growth in a highly branched species, and there may be no threshold size for these activities if they are part of a single growth process. All these structures show large plasticity in size. They can be initiated by the parent organs at a very small size and can grow as much as environmental conditions allow. Reproductive structures, on the other hand, are fundamentally different. Flowers, carpels, and seeds are among the least plastic structures produced by plants (Schmid and Bazzaz 1992). Thus, a plant cannot commit itself to producing these structures until it has achieved a certain size, i.e., until it has accumulated a certain amount of resources (Weiner 1988). Reproductive output is plastic because the number of flowers produced by a plant can vary greatly, but many nonreproductive structures can vary greatly in size as well as number. This model leads to two specific testable hypotheses: (*i*) species with more deterministic growth forms should have relatively larger minimum sizes for reproduction (relative size at onset of maturity; Charnov 1991; Thomas, submitted[3]); (*ii*) plants with relatively large flowers or relatively fixed inflorescence size should have larger minimum size for reproduction. Our data provide some support for the first hypothesis, i.e., the species that showed a lower minimum size for sexual reproduction and a more size-independent flowering behavior, *Aster*

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[3] Thomas, S.C. 1995. Relative size at onset of maturity in rain forest trees; a comparative analysis of 37 Malaysian species. Submitted for publication.

*lanceolatus*, has a less deterministic growth form than does the other species, *S. canadensis* (Schmid and Bazzaz 1990).

Contrary to our hypothesis, seed-derived plants allocated less biomass to both sexual reproduction and clonal growth than did rhizome-derived plants. Thus, it appears that much of the biomass of seed-derived plants that could have been allocated to either of these functions is left in the vegetative parts that die back in the autumn. So why do seed-derived plants appear to waste resources that could be used for reproduction or clonal growth? One possible explanation is based on the different selection pressures facing plants growing from seeds and those produced by rhizomes. In nature, shoots from rhizomes are part of an established clone, and the risk of mortality is not as great as that facing an individual growing from a seed (Hartnett and Bazzaz 1985). Because shoots that are parts of clones can receive resources from other parts of the clone, they are somewhat buffered against many hazards (Bazzaz 1984). Therefore, the risk of mortality will be higher for a seed-derived shoot than for a shoot of the same size that is part of a clone. The reluctance of plants growing from seeds to allocate resources to propagation may be the result of a bet-hedging strategy, which minimizes the risk of mortality, rather than maximizing average fitness (Stearns 1992). The resources that a seed-derived plant could use for propagation and that appear to be wasted at the end of the growing season are held as insurance against hazards such as herbivory. According to this hypothesis, a clone shifts away from the conservative bet-hedging strategy towards more reproduction and clonal growth as it spreads.

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