

Patterns of defensive chemical production in wild parsnip seedlings (Apiaceae: *Pastinaca sativa* L.)

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Summary. To ascertain patterns of allocation between growth and defense in seedlings, we measured plant biomass and the amount of six furanocoumarin defensive chemicals in wild parsnip roots and shoots (Apiaceae: *Pastinaca sativa* L.) in sequential harvests for sixty days following emergence and compared them to previous studies on mature plants. Furanocoumarins were present from the first day of emergence and were actively synthesized from the onset of seedling growth. Although initial amounts of each furanocoumarin species differed, they were produced at the same rate. Furanocoumarin production was not commensurate with biomass accretion, and fluctuations in concentration varied dramatically between roots and shoots. Concentrations of furanocoumarins in seedlings are far lower than in adult plants, perhaps because the selective regime of seedlings differs from that of mature plants, and inter-seedling competition favors investment in growth rather than defense.

Key words. Apiaceae – furanocoumarins – *Pastinaca sativa* L. – resource partitioning – seedlings

Introduction

The precarious seedling stage of a plant's ontogeny necessitates optimal allocation between growth and defense. Early investment of resources in growth may greatly influence a seedling's future resource-gathering capability and competitiveness, since small differences in emergence time and physical space occupied by seedlings become accentuated during establishment, setting up a dominance hierarchy in which the largest plants outcompete their smaller neighbors (Ross & Harper 1972; Gaudet & Keddy 1988). Aggregation of seedlings in some species can accelerate the onset of inter-plant competition.

However, the young, tender foliage of seedlings can be nutritionally attractive to herbivores. Numerous studies have shown that insect herbivores generally prefer new foliage to older leaves because of their

higher relative nitrogen content (*e.g.* Feeny 1970; Coley 1980; Raupp & Denno 1983). Entire seedlings could be vulnerable unless chemically defended. While a tiny, inconspicuous seedling may be overlooked by herbivores, aggregations of seedlings would be more easily located while simultaneously increasing interplant competition.

Investing resources in defense rather than growth during this precarious life stage could compromise competitive ability. Implicit in theories of defense allocation is the assumption that investment in defensive chemicals sequesters resources that would otherwise be used for growth or reproduction (Bazzaz *et al.* 1987). Such trade-offs have been difficult to document, and the results of some studies difficult to interpret (Simms 1992).

In the present study, growth and the production of a suite of furanocoumarin defensive chemicals was measured in wild parsnip (Apiaceae: *Pastinaca sativa* L.), an introduced biennial common in old-fields and waste places in eastern North America (Baskin & Baskin 1979). Furanocoumarins are well-characterized plant defensive chemicals which are repellent or toxic to many insect herbivores (Berenbaum 1990). The photoactive effects of linear furanocoumarins are toxic to a wide variety of organisms including microbes and insect herbivores; angular furanocoumarins are less toxic except to specialist herbivores (Berenbaum & Feeny 1981).

Several studies have documented a physiological cost of defense at the expense of growth and allocation to reproductive tissue in wild parsnip (Berenbaum *et al.* 1986; Zangerl and Berenbaum 1997; Zangerl *et al.* 1997). Further, biochemical pathway analysis by Gershenson (1994) has estimated that 3.39 g of glucose are used to produce one gram of the furanocoumarin psoralen. Bergapten, isopimpinellin, imperatorin, and xanthotoxin (all measured in this study) are all produced from subsequent enzymatic modification of psoralen, and are therefore likely to be even more costly. In addition to these costs of production, specialized storage and delivery systems are likely to contribute to the cost of defense. Based on this evidence that furanocoumarin production incurs a cost to growth, and that furanocoumarin concentrations in wild parsnip show heritable variation on which natural selection can act

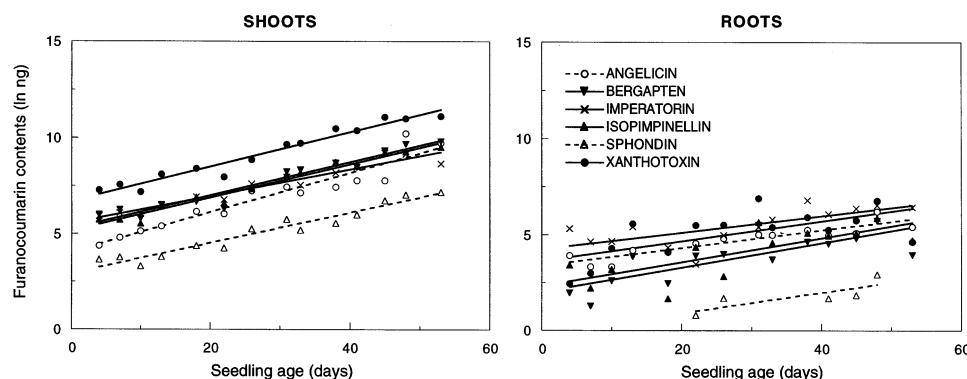


Fig. 1 Furanocoumarin contents (ln ng) in root and shoot tissues of parsnip seedlings, throughout a 53-day growth period. Angular furanocoumarin species are designated with dotted lines, linear species with solid lines. Regression lines are model I linear regressions

(Zangerl *et al.* 1989), further information was sought on the allocation of resources to growth and defense in wild parsnip.

Trade-offs between growth and defense have been investigated primarily in mature plants; considerably less attention has been paid to resource allocation throughout the beginning of an herbaceous plant's development (but see Simms 1992, Ohnmeiss & Baldwin 1994, Bryant & Julkunen-Tiitto 1995). Selective pressures acting on this age class may differ from those on adults, causing hitherto unknown patterns of allocation between growth and defense in roots and shoots (Kearsely & Whitham 1989). It is well documented that wild parsnip seeds contain furanocoumarins (Berenbaum *et al.* 1984). Seedlings may initially incorporate at least some of these seed defenses into their tissues, but the onset of defense production has been unexplored.

We measured rates of furanocoumarin and biomass accumulation in the roots and shoots of wild parsnip seedling in the absence of resource limitation and herbivory for two months following germination to address the following set of questions: When does production of plant defenses begin? Do different species of furanocoumarin defenses accumulate at different rates? Do angular and linear furanocoumarins accumulate at different rates? Do furanocoumarins (total, and as individual species) accumulate in root and shoot tissues at similar rates? Do patterns of furanocoumarin accumulation in seedlings differ from those reported for mature plants? Finally, what can be inferred about tradeoffs between growth and defense in seedlings?

Materials and methods

Wild parsnip seeds were collected at the Philips Tract Research Area located 3 km northeast of Urbana, IL, and stratified for germination by placing them in moist storage at 5°C. Immediately after the seeds began to sprout, 4 seeds were placed in each of thirty 4-inch pots containing a 1:1:1 mixture of soil, sand, and perlite. Baldwin (1988) found differences in defensive chemical production between plants grown in the field and plants grown in a greenhouse, an effect which he attributed to the plants becoming "pot-bound". The volume of soil used in our pots was sufficient to prevent pot-binding, as confirmed by visual inspection of the roots and the continued increase in

root growth to the end of the experiment. Pots were evenly spaced on a greenhouse bench in the plastic-paned Biosphere III Greenhouse at Bradley University and were periodically repositioned at random. The seedlings were fertilized with 11 ml of 8 g/l Peter's 20:20:20 NPK fertilizer solution per pot on the day of planting and weekly thereafter, to give a total of 0.616 g/pot fertilizer over the course of the experiment. No herbivores or evidence of herbivory were apparent during the course of this experiment.

The first harvest was taken on 24 October 1994, four days after planting, when the first seedlings began to emerge from the soil. Harvests were made approximately every three days (range = 2–5 d) until 11 December 1994, for a total of fourteen harvests. To harvest the plants, their pots were immersed in water, and the soil and plant gently dumped out. Care was taken to minimize breakage of fine root hairs. Plants were dried in an oven at 25°C for 24 h, and then stored at room temperature. Five plants were harvested initially to obtain the minimum sample mass required for high performance liquid chromatography (HPLC) analysis, gradually decreasing to one plant/harvest as the seedlings grew. Seedlings were thinned to one plant per pot on day 15 when all seedlings had emerged. The roots and shoots of each dried plant were massed separately and a mean shoot and root mass per plant were calculated for each harvest. The dried tissue was then ground to a powder in a mortar and pestle and placed in Eppendorf tubes with ethyl acetate. Amounts of each of six different furanocoumarins in each sample (angelicin, bergapten, imperatorin, isopimpinellin, sphondin, and xanthotoxin) were determined by HPLC analysis using the method of Berenbaum *et al.* (1984), and mean quantities and concentrations per plant calculated.

The per plant and per structure (root vs. shoot) biomass (ln μ g) and furanocoumarin contents (individual furanocoumarin species, total angular furanocoumarins, total linear furanocoumarins, and total furanocoumarins; ln ng), and per structure furanocoumarin concentration (mg/g) were plotted versus seedling age (Figs. 1, 2). Allometric plots of root versus shoot, biomass (ln μ g), and furanocoumarin contents (individual furanocoumarin species, total angular furanocoumarins, total linear furanocoumarins, and total furanocoumarins; ln ng) were also constructed (Fig. 3). Best-fit model I linear regressions proved an adequate fit in most cases (Figs. 1A, B, 2C, 3A, B). In some cases, however, the relationships were appreciably curvilinear (Figs. 2A, B, 3C). For those relationships, we evaluated model I linear regression models including first-, second-, and third-order polynomial terms in order to determine the most appropriate models for each relationship (Data Desk v.5.0). The ln shoot mass vs. seedling age model included a significant second-order term (Fig. 2A, $F_{1,11} = 28.199$, $P = 0.0002$); the remaining relationships in Figure 2A were adequately described by either linear or second-order polynomial models. Furanocoumarin concentrations in shoots vs. seedling age included significant second- and third-order terms (Fig. 2B, $F_{1,10} = 9.0286$, $P = 0.0132$ and $F_{1,10} = 9.2314$, $P = 0.0125$, respectively); the furanocoumarin concentration in root tissue vs. seedling age relationship was adequately described by either linear or second-order polynomial models. The ln root vs. ln shoot mass model included a significant second-order term (Fig. 3C, $F_{1,10} = 13.744$,

$P = 0.0041$); the \ln furanocoumarin content in root tissue vs. that in shoot tissue relationship was adequately described by either linear or second-order polynomial models. Accordingly, we employed second-order polynomial regressions to the following relationships: root and shoot biomass vs. seedling age, total furanocoumarin contents in roots and in shoots vs. seedling age, and furanocoumarin concentration in roots vs. seedling age (Figs. 2A, B, 3C). Furanocoumarin concentration in shoots vs. seedling age was described by a third-order polynomial regression (Fig. 2B). In cases in which linear regression proved an adequate fit to the data, slopes and intercepts (*i.e.*, of

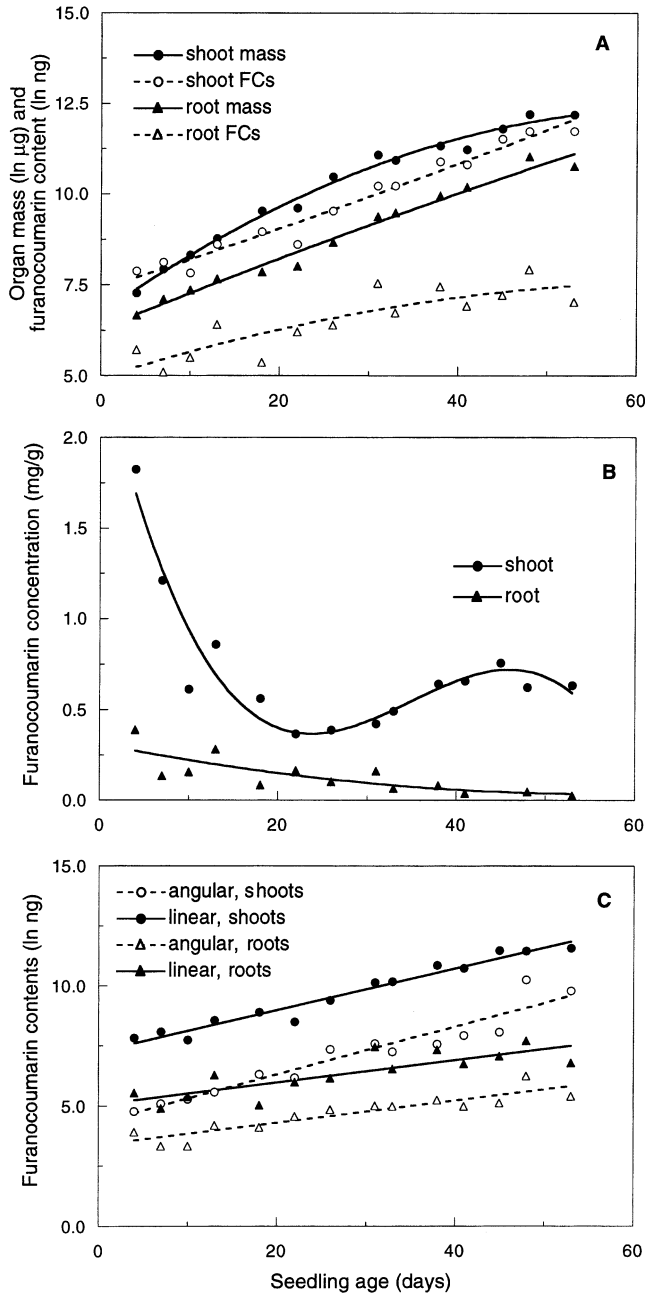


Fig. 2 (A) Organ mass (ln µg, closed symbols and solid lines) and furanocoumarin contents (ln ng, open symbols and dotted lines); (B) furanocoumarin concentrations (mg/g); and (C) linear (closed symbols and solid lines) and angular (open symbols and dotted lines) furanocoumarin contents (ln ng) for parsnip seedling shoot (circles) and root (triangles) tissues, throughout a 53-day growth period. Regression lines are linear (C), second - (A, roots in B) or third-order polynomial (shoots in 2B) model I regressions

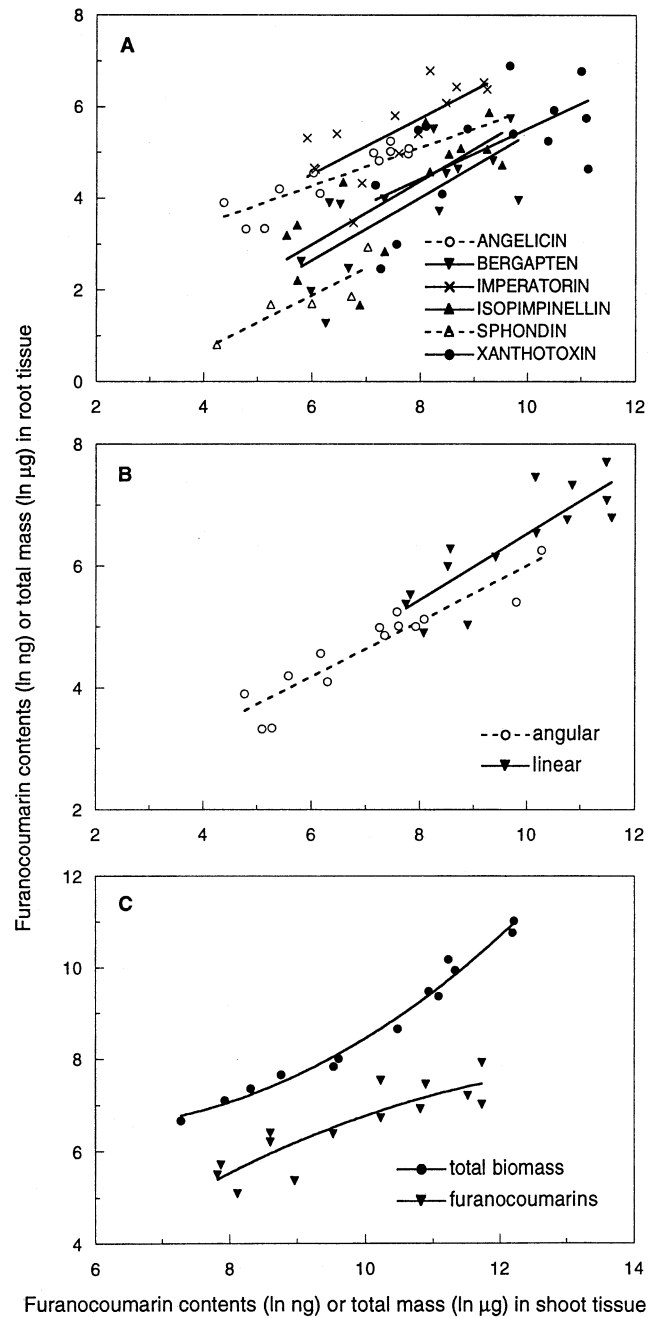


Fig. 3 Furanocoumarin contents (ln µg) and total biomass (ln µg) in root vs. shoot tissue of parsnip seedlings, throughout a 53-day growth period. In all panels, dotted lines refer to angular furanocoumarin species, solid lines refer to linear furanocoumarin species. Regression lines are linear (A, B) or second-order polynomial (C) model I regressions

individual furanocoumarin species, or of total angular versus linear furanocoumarins) were compared via ANCOVA (Data Desk v.5.0); higher order polynomial curves were compared graphically.

Results and discussion

From the first harvest (day 4), wild parsnips contain furanocoumarins in above- and below-ground tissues.

Five of the six furanocoumarins which we assayed – angelicin, bergapten, imperatorin, isopimpinellin, and xanthotoxin – were found in the roots and shoots of wild parsnip during the first and subsequent harvests. The sixth furanocoumarin, sphondin, was found in roots at the sixth harvest (day 22) and subsequent harvests but was present in shoots from the first harvest (Fig. 1). Although rates varied slightly, all furanocoumarins increased in amount after the first harvest indicating that these chemical defenses were being synthesized and were not merely residual defenses from the seeds. Individual species of furanocoumarins accumulated at roughly the same rates within roots (ANCOVA homogeneity of slopes test, $P = 0.8627$; model $r^2 = 0.74$) and within shoots (ANCOVA homogeneity of slopes test, $P = 0.0688$; model $r^2 = 0.97$; Fig. 1), but roots accumulated chemical defenses at a lower rate than shoots (Fig. 2A). Collectively and individually, the amount and concentrations of furanocoumarins were always higher in shoots than in roots (Figs. 1, 2, and 3).

The higher furanocoumarin concentrations in the shoots relative to roots of the older seedlings is consistent with trends seen in adult plants. Several studies on mature parsnips have shown that above-ground structures (*i.e.* leaves, stems, and reproductive structures) are better defended than their roots (Simsová & Blazek 1967; Berenbaum 1981). This disparity between roots and shoots is consistent with optimal defense theory and the probability of attack, which is lower in roots, as articulated by Zangerl and Bazzaz (1992).

When angular and linear furanocoumarin species are considered separately, roots and shoots show similar patterns of accumulation. Within shoots and within roots, angular furanocoumarins accumulated at the same rate as linear furanocoumarins (ANCOVA homogeneity of slopes test, $P = 0.4542$; model $r^2 = 0.96$), but linear furanocoumarins were present in larger amounts in both structures (ANCOVA linear vs. angular contrast, $P < 0.0001$; Fig. 2C). Further, shoots had higher amounts of both linear and angular furanocoumarins than did roots (ANCOVA root vs. shoot contrast, $P < 0.0001$; Fig. 2C) and accumulated furanocoumarins at a faster rate (ANCOVA homogeneity of slopes test, $P < 0.0001$; Fig. 3B).

During the harvest period, root and shoot mass increased logarithmically, with the average seedling dry mass increasing from 0.0022 g to 0.243 g (Fig. 2A). However, biomass accumulation was not commensurate with furanocoumarin accumulation, causing divergent patterns of defense concentration between roots and shoots. Root concentrations steadily decreased while concentrations in shoots fluctuated throughout the harvest period (Fig. 2B). Growth rates of shoots decreased compared to roots during the course of the harvest period while rates of shoot furanocoumarin accumulation outstripped that of roots at approximately the same time (Fig. 3C). Initially high concentrations of certain furanocoumarin species in both roots and shoots seem to be

the result of initially high maternal investment in seed concentrations; subsequent decline in concentration is the result of divergent rates of biomass and furanocoumarin accumulation. The disparity between fluctuations in root and shoot furanocoumarin concentrations seems to be most parsimoniously explained as the result two physiological processes acting independently: furanocoumarin production and biomass accretion. Differences in these two decoupled functions between roots and shoots result in defense concentration fluctuations as growth progresses.

Concentrations of defensive chemicals in seedlings are lower than in mature plants. This conclusion is bolstered by the similar findings of Simsová and Blazek (1967). In their study of furanocoumarin ontogeny in *Pastinaca sativa eusativa* over its entire life span, they also found that furanocoumarin concentrations in adults were much greater than those found in seedlings. Allocation of dry mass to furanocoumarins – a measure of relative defense cost between life stages – constitutes less than 0.20% in seedlings. This proportion is far lower than for adult plants grown in the field (Maksyutina & Kolesnikov 1965; Beyrich 1966; Fedorin & Georghieyevsky 1975; all cited in Berenbaum 1981; Zangerl & Bazzaz 1992) or in the greenhouse (Zangerl & Berenbaum 1987; Zangerl 1990).

Previous investigations of seedling defense on herbaceous plants have also found less concentrated defense chemicals in seedlings. Iridoid glycoside production in *Plantago lanceolata* is low shortly after germination, and monoterpene production in mint shows a similar pattern (cited as personal communication from D. Bowers and J. Gershenson in Bryant & Julkunen-Tiitto 1995). Bowers and Stamp (1993) report that young *Plantago lanceolata* were more defended by iridoid glycosides than old plants against specialist and generalist insects, though this study compares young and old genets (clones) which may not undergo ontogenetic changes typical of newly germinated seedlings. In contrast to the pattern shown by herbaceous seedlings, woody plant species seedlings and saplings have generally higher levels of chemical defenses than mature plants (Bryant *et al.* 1991).

Kearsely and Whitham (1989) suggested that the effectiveness of plant defenses to different herbivores changes during development. Changes in the herbivore fauna associated with a particular species of plant may similarly track ontogenetic changes in plant visibility, primary and secondary chemistry, and microhabitat. Throughout its range, wild parsnip is primarily fed upon by the parsnip webworm, *Depressaria pastinacella*, which feeds almost exclusively on its reproductive structures (Hodges 1974; Thompson 1978), and is also commonly eaten by caterpillars of the black swallowtail, *Papilio polyxenes* (Tietz 1972). It is unlikely that adult females of these two lepidopteran species would oviposit on a wild parsnip seedling, because the seedlings are both inconspicuous and not large enough to provide forage for even a single caterpillar. Wild

parsnip seedlings therefore may not be susceptible to attack from the specialists adapted to the adult stage; generalist feeders such as slugs and mobile insect herbivores may be their most significant enemies. Given the toxicity of linear furanocoumarins (Berenbaum 1978; Murray *et al.* 1982), concentrations of defensive chemicals lower than those in adult plants may be sufficient to deter these generalist enemies.

The patterns of linear vs. angular furanocoumarin production observed in this study, however, are similar to those in adult plants. Linear furanocoumarins are toxic to an array of herbivores and pathogens, while angular furanocoumarins have a deterrent effect on specialist herbivores adapted to detoxifying linear furanocoumarins (Berenbaum & Feeny 1981). The mere presence of angular furanocoumarins in seedlings and the similarity to adult plants in their abundance relative to linear species suggests that the production of angular furanocoumarins is either genetically canalized or physiologically linked to the production of linear furanocoumarins, or that production of angular furanocoumarins is not costly enough to merit fine-tuning during the seedling stage when attack by specialists is highly unlikely.

The competitive microenvironment of most parsnip seedlings would seem to select for optimal allocation between growth and defense during this stage of their ontogeny. The dispersal mechanism of parsnip seeds leads to aggregations of seedlings in the spring (Baskin & Baskin 1979; M.R. Berenbaum pers. comm.), and competition between these seedlings is likely to be intense; in the population that they studied, Baskin and Baskin (1979) found that fewer than one percent of seedlings lived to reproduce. Since these two selective pressures ostensibly require mutually exclusive resource investments, the seedlings must partition their resources between defense and resource foraging structures. The true dynamics of allocation between growth and defense in the face of competition and herbivory are likely to be much more complex, as there is evidence that furanocoumarins leached from seeds may mediate competition between wild parsnip and other germinating seedlings, including conspecifics (Fukushi 1960; Kato *et al.* 1978; M.R. Berenbaum pers. comm.), complicating predictions of competitive outcomes and the assessment of defense cost to seedlings. An investigation of the effects of seedling competition on defensive chemical production may prove useful in elucidating the dynamics of seedling resource partitioning between growth and defense in seedlings. Additional field studies correlating changes in herbivore composition with these changes in allocation might lead to a better understanding of changes in herbivore selection pressure and its consequences throughout a plant's life.

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