Physiological integration for carbon in mayapple (Podophyllum peltatum), a clonal perennial herb

Keith Landa, Barb Benner, Maxine A. Watson and Janna Gartner


The degree of physiological integration among compartments within modular plants and animals, as measured by the sharing of resources, can determine the response of such organisms to environmental variability. We used 14C tracer methods to determine distribution patterns for photoassimilate in mayapple, Podophyllum peltatum L., a rhizomatous perennial herb with a simplified clonal architecture. Over half of the carbohydrate fixed during mid May, 1988, ended up in older segments of the rhizome system by early autumn, 1988. Roots, rhizomes and nodes along the entire length of the rhizome system all contained labelled material. By the following spring, 1989, there was a proportionate increase in label in the newly developing segment. Increases in activity in new roots and shoot between autumn and spring were accompanied by steep declines in activity in nearby rhizomes. Autoradiograms showed support of damaged rhizome branches by carbohydrate from attached, undamaged branches and the presence of carbohydrate fixed in 1988 throughout all structures of the developing 1989 shoot. No differences were seen in this study in the allocation patterns of systems with sexual or vegetative shoots. Mayapples exhibit high levels of physiological integration for carbohydrate compared to other, similar clonal perennials. This translocation may serve several functions, including storage and remobilization to support new growth, maintenance of an extensive root system and maintenance of a bud bank.

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Clonal plant species vary greatly in the extent to which carbohydrate and other resources are transported among their component parts (Pitelka and Ashmun 1985). Some species, such as Dupontia fisheri (Allesio and Tieszen 1975), show extensive physiological integration, with sustained transport of resources between ramets. In other species, ramets become independent of each other soon after their production (e.g., Aster acuminatus: Ashmun et al. 1982). The level of carbohydrate translocation within clonal plants has been proposed to serve a number of potential functions, including storage (Callaghan 1976, Ashmun et al. 1982, Newell 1982), maintenance of old roots and rhizomes to buffer plants against spatial and temporal variation in soil nutrient levels (Callaghan 1980, Noble and Marshall 1983, Headley et al. 1985), maintenance of reserve meristems at old nodes to facilitate recovery of plants from damage to younger sections (Jónsdóttir and Callaghan 1988) and support for locally stressed regions of plants (Slade and Hutchings 1987). These functions of translocation may be important in allowing clonal plants to monopolize a local area or to explore a patchy environment (Pitelka and Ashmun 1985).

In this paper, we use 14C labelling to examine patterns of translocation for carbohydrate in mayapple, Podophyllum peltatum L., a forest herb with a persistent rhizome system. The simple architecture of mayapple aids the study of carbon flows in this clonal perennial. Most mayapples consist of a linear, sympodial rhizome system with a single terminal shoot (Fig. 1); a minority
of plants have branched rhizome systems, with a shoot at the end of each branch. Shoots are annual and are not replaced at old locations in subsequent years, resulting in the simplified aboveground architecture. There are two morphologically distinct shoot types. Vegetative shoots consist of a single leaf, while sexual shoots are a branch with two leaves and a single large flower. Rhizome systems can be divided into a number of segments, each of which represents an annual growth increment. Boundaries between annual segments are marked by thickened regions of the rhizome, where shoots arose in previous years. These regions have been termed “nodes” by Sohn and Policansky (1977) and Benner and Watson (1989), but actually consist of a number of nodes and short, vertical internodes. Roots persist in old segments along the length of the rhizome system, although root biomass decreases in older segments.

Based on the clonal morphology of mayapple, we address a number of specific questions about mayapple translocation patterns. 1) Where is current assimilate translocated? Does labelled carbohydrate remain primarily in the shoot and its associated segment of the rhizome system, or is it transported back to older segments or forward to newly-developing structures? 2) Do roots of old segments receive current assimilate, indicating that they may still be metabolically active? 3) Are there differences in allocation patterns between plants with sexual or vegetative shoots? 4) What levels of transport occur between branches in branched systems? Answers to these questions, and the level of physiological integration that they indicate, will be discussed in terms of mayapple response to environmental variability, both spatial and temporal. Also, differences in allocation patterns between systems with vegetative or sexual shoots may suggest physiological mechanisms for any potential cost of reproduction in mayapple (Sohn and Policansky 1977).

Methods

The basic experimental design of this study was to label 20 shoots (10 vegetative and 10 sexual) midway through the 1988 growing season. Plants were then randomly assigned to one of two harvest dates: autumn 1988 and spring 1989. This design allows comparisons of how the two shoot types allocate assimilate to different structures of the rhizome systems over long time periods, and how those distributions change between seasons. At each harvest, one vegetative and one sexual system were chosen haphazardly for autoradiography, to determine the qualitative distribution of labelled material. The remaining 16 systems were oxidized to quantify the distribution of labelled material (see below).

Our study site was located on a private farm in Greene county, in south central Indiana. Dominant trees at the site were beech, sugar maple and shagbark hickory; the shrub layer was poorly developed. Mayapples used in this study were from a single large colony, consisting of one or more genets, located on a wooded hillside with a northeast exposure. The selected shoots were at least of 80 cm apart to minimize the chance of double labelling a branched system.

Mayapples were labelled during the second wk of May, 1988. At this time mayapple leaves were fully expanded and sexual shoots were flowering. Canopy closure had not occurred yet, so that the mayapples were still exposed to intermittent direct sunlight. To label the plants, the single leaves of vegetative shoots or the larger leaves of the two-leaved sexual shoots each were exposed to 100 μCi of 14CO2 within clear plastic enclosures. We varied exposure time among individual shoots from 30 to 90 min, depending on temperature and cloud cover at the time of labelling, in order to facilitate maximum uptake of label by all systems. The high level of label (100 μCi) was chosen because mayapples are relatively large and this study was a preliminary experiment to see what levels of label would be needed to be detectable during the course of a subsequent multiyear labelling study. Additional plants were exposed to 300 or 500 μCi, but many of these plants displayed growth abnormalities the following spring (presumably due to the high exposure levels) and these treatments were thus not analyzed for this study.
Table 1. Repeated measures ANOVA for the distribution of biomass, total activity and specific activity within and between mayapple plants. Harvest date was taken as a between-individual treatment effect and the weights, total activities or specific activities of the individual segment by structure (node, roots, rhizome) combinations were the within-individual repeated measures. Shoot type had no significant main effect or interactions and was therefore omitted from the model. Specific activities could not be calculated for some segment by structure combinations lacking in some systems (recorded as 0 mg and 0 DPM for the analysis of biomass and total activity), resulting in lower degrees of freedom for the analysis of specific activity (dfw) than for weight or total activity (dfwt, dfw).

<table>
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<th>Effect</th>
<th>dfwt,dfw</th>
<th>Fwt</th>
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<td>12.48</td>
<td>0.0001</td>
<td>8.104</td>
<td>7.00</td>
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<td>0.10</td>
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Plants were left in situ, under undisturbed conditions, until the time of their respective harvests. Labelled shoots of all systems were collected in July, 1988, following shoot senescence, to determine how much label remained in them. The first harvest of rhizome systems occurred in early September, 1988, at which time the newly developing rhizome segment had completely elongated and had differentiated the overwintering bud containing the 1989 shoot. The second harvest occurred the following spring, in April, at the onset of expansion of the 1989 shoot. Entire rhizome systems were harvested by carefully excavating them from the surrounding soil. Harvested systems were washed, diagrammed, measured and then separated by annual segments into node, root and rhizome structures.

Autoradiography was used to examine the qualitative distribution of labelled material among and within structures of rhizome systems. Rhizomes were split in half longitudinally and nodes were cut into 4 or 5 sagittal sections, to expose their interiors, because $^{14}C$ is too weak a $\beta$-emitter to allow exposure through the epidermis of the rhizome. For the spring harvest plants, bud scales were dissected away from the developing shoots and the scales, stems and leaves were pressed flat. The prepared plants were then mounted on paper and exposed to Kodak XRP x-ray films overnight, which were developed using a Kodak XO-Mat M20 Processor.

Plants to be oxidized were dried to constant weight at 65°C and the individual pieces weighed. To aid combustion during the oxidizing process and to homogenize the material from each piece for subsampling, all materials were ground individually in a Wiley mill with a #20 mesh. For each plant part, two or three subsamples were weighed and then combusted at 900°C for 5.5 min in a Harvey Instrument Corporation biological oxidizer (model 4000), with the resulting CO$_2$ collected into separate scintillation vials containing 15 ml of C14 Cocktail (Harvey Instrument Corp.). After storage in the dark overnight, the vials were loaded onto a Beckman scintillation counter (model LS230) and their activity counted for 5 min.

The replicated scintillation counts and subsample weights were used to calculate mean specific activity (disintegrations per minute [DPMs] per mg dry weight) for each plant part. This mean value was multiplied by the total weight of the plant part to calculate the total activity present in each part. The total activity and weight measures for nodes, roots and rhizomes were summed within annual segments to give segment totals, which were then summed to give the total activity and total weight for each rhizome system. Specific activities of segments and whole rhizome systems were determined from the summed weight and total activity values.

The patterns of weight and activity distribution among segments and structures of rhizome systems were analyzed using a repeated measures ANOVA, where the weight or activity values for each segment by structure combination within a rhizome system represented repeated measures on individual plants. Weight and activity of the 1989 buds were combined with the 1989 nodes to keep the statistical design consistent across segments. Structure main effects test test whether nodes, rhizomes and roots differ in weight or activity, while segment effects test for weight or activity differences between annual segments. Significant structure-by-segment interactions indicate that the distribution of biomass or activity among nodes, rhizome and roots varies between segments. Shoot type (sexual vs vegetative) and harvest date (autumn 1988 or spring 1989) represented treatment effects between individuals. Interactions of within-individual effects and between-individual effects test for changes in biomass and activity distributions over time or due to shoot type.

**Results**

**Mayapple architecture**

The rhizome architecture of plants in our study colony was relatively uniform; almost 90% of the plants harvested were linear systems. Branched systems did not differ from linear ones in the distribution of biomass or...
activity along their labelled branches, and were therefore included in the statistical analyses presented below. Plants averaged 6.7 (±1.2) annual segments. This average length was unrelated to harvest date, shoot type or branching condition.

Total belowground weight did not differ significantly between sexual and vegetative rhizome systems or between harvest dates, and averaged 9.3 g per plant. Sexual shoots were 40% larger than vegetative shoots (ANOVA, p = 0.0151). As expected, there was no difference in senesced shoot weight between the two rhizome harvest treatments. The senesced shoots represented 15 to 20% of total plant biomass.

Rhizome system biomass was distributed unequally among structures and among annual segments (Table 1). Nodes were a smaller fraction of total weight than either roots or rhizomes (Fig. 2a-2c), while middle segments were heavier than both younger and older segments (Fig. 2d). Plant structures differed significantly in their distribution of biomass across segments (structure by segment interaction); node weights were relatively constant across segments, while roots and rhizomes mirrored the segment weights in having peak biomass in middle segments.

Harvest effect on biomass was not significant, indicating no overall differences in total belowground weight between the two harvests. Individual segments, however, differed significantly in their weight changes over time (segment by harvest interaction). The new 1989 segment gained weight while all other segments, especially the middle ones, lost weight (Fig. 2d). This resulted in a shift of biomass to more forward segments between autumn and spring. Structures differed marginally in their weight changes between the harvests (structure by harvest interaction); nodes lost the least weight while roots lost the most (Fig. 2a–2c). The interaction between segment, structure and harvest was not significant.

**Distribution of total activity**

Less than 10% of labelled material remained in the shoots after they senesced. There were no significant differences between senesced sexual and vegetative shoots in the amount of labelled material they contained. In addition, shoot type had no effect on the amount or distribution of activity in the belowground structures.

Significant amounts of labelled material were detected in all segments and within all structures of the rhizome system (Fig. 2e–2h). As with weight, total activity was distributed unequally among annual segments and among structures (Table 1). Total activity per segment increased toward younger segments (Fig. 2h). However, more than 50% of the belowground labelled material was in 1987 and older segments of the rhizome system. Only slightly more than 20% of the belowground activity remained in the 1988 segment that gave rise to the shoot that was labelled and the remainder was transported forward into the newly developing 1989 segment. Among structures, rhizomes contained the
most activity (Fig. 2c) and nodes the least (Fig. 2f), with roots intermediate (Fig. 2g). Structures differed in their distribution of labelled material across segments (significant segment by structure interaction). Node activity was fairly constant across segments, root activity peaked in the labelled 1988 segment and rhizome activity was highest in the new 1989 segment.

Total activity levels declined significantly between harvests (Table 1). Rhizome systems collected in the spring harvest contained roughly half the amount of activity of those from the preceding autumn (Fig. 2h). The distribution of activity among segments was not significantly different between the two harvests (segment by harvest interaction), although there was a shift in the proportion of labelled material to more forward segments. Rhizomes lost a greater proportion of activity between the two harvests than either nodes or roots (significant structure by harvest interaction). Finally, specific segment by structure combinations differed significantly in their changes in activity over time (segment by structure by harvest interaction). The node and roots of the new 1989 segment were the only compartments that increased their content of labelled material over time, while the 1986 through 1988 rhizomes showed the steepest percent declines.

Specific activity patterns

Although the distributions of biomass and total activity in rhizome systems showed many of the same general patterns, there were still significant differences in specific activity among structures and among segments (Table 1). Specific activity was highest in the young segments and lowest in middle segments (Fig. 2l), while roots tended to have lower specific activities than nodes and rhizomes (Fig. 2i–2k). Structures also differed in the patterns of specific activity across segments (segment by structure interaction). The specific activity of both nodes and rhizomes were highest in young segments, dropped in middle segments and then increased again in the oldest segments (Fig. 2i, 2j). Roots lacked the increases in specific activity in the oldest segments seen in nodes and rhizomes and had smaller differences in specific activity between forward and back segments (Fig. 2k).

The decline in overall specific activity between harvests was not significant and there were no changes in the patterns of specific activity among segments (segment by harvest interaction). Structures differed significantly in their changes in specific activity over time (structure by harvest interaction); nodes and rhizomes uniformly declined in specific activity over time while roots remained constant or increased. Finally, the magnitude of the changes in specific activity over time displayed by structures varied significantly among segments (segment by structure by harvest interaction). Forward segments showed the greatest changes in specific activity (declines for nodes and rhizomes, increases for roots), while back segments were more constant.

Transport to unlabelled branches

There were two branched systems among the plants analyzed quantitatively for the autumn harvest. In one, the branching occurred in 1986 while the other one branched in 1983. The unlabelled branches contained 5% and 10%, respectively, of the total activity in these systems. The labelled material present in the unlabelled branches was confined to newly developing terminal
segments, which had specific activities comparable to levels found in the labelled 1988 segments of the labelled branches. Activity in the other segments of the unlabelled branches was not significantly above background levels. Labelled material was transported across 6 segments in the plant that branched in 1986 (representing 3 yr growth) and across 12 segments in the one that branched in 1983 (6 yr growth).

Of the spring harvest systems that were oxidized, none were branched. However, one of the spring harvest systems used for autoradiography was branched. (See results below.)

Autoradiography

Autoradiograms of systems collected in the autumn harvest showed intense labelling of the newly developing 1989 segment (Fig. 3, top panel). Labelling was less intense in middle segments and then increased toward the back end of the belowground systems. These patterns seen in autoradiograms correspond to the quantitative data on specific activity reported above, confirming the validity of such autoradiographic observations. In addition, several nodes displayed localized areas of intense labelling within them (Fig. 3, top panel, 1987 and 1984 nodes).

Systems collected in the spring 1989 harvest showed incorporation of labelled material throughout all structures of the newly developing shoots: leaves, flowers, stems and bud scales (Fig. 3, bottom panel). Interestingly, the shoot developing on the unlabelled branch of this branched system was more intensely labelled than the shoot developing on the labelled branch. The unlabelled branch had been broken in 1988 and a new 1989 shoot was growing out of the 1986 node behind the break. Other areas of heavy labelling were the new 1989 roots on both branches, roots from the 1988 node that gave rise to the labelled shoot and the old rhizome and node behind the position at which the system branched.

Discussion

Segmental distribution of current assimilate

Mayapples labelled in this study transported a large amount of current assimilate to older segments of the rhizome system, compared to results from field studies of other species. We found that over 50% of the labelled carbohydrate was present in older mayapple segments by the end of the growing season. In contrast, less than 20% of the labelled carbohydrate was found in older segments of Carex bigelowii (Jónsdóttir and Callaghan 1988) and less than 10% in Clintonia borealis (Ashmun et al. 1982), two species with clonal architectures similar to mayapple. Ranunculus repens, a species with a more complicated clonal morphology, also transported less than 10% of labelled assimilate to older portions of a labelled stolon (Ginzo and Lovell 1973).

The relatively high amount of transport to old segments in mayapple compared to other species may be due to the fact that previous labelling studies have not examined distributions of carbohydrate over such long time periods as in this study. Additional labelling studies with mayapple indicate, however, that the extensive back translocation of assimilate from mid-May occurs within two wk after labelling, and possibly sooner (Landa and Vuorisalo, pers. obs.), suggesting that time between labelling and harvest does not account for the differences between species. More problematical for species comparisons is that these additional labelling studies in mayapple indicate a distinct phenology of storage, with plants labelled earlier or later transporting less carbohydrate to back segments of the rhizome.

Better understanding of the annual carbohydrate cycles of the species that have been used in labelling studies are needed before meaningful between-species comparisons of translocation patterns can be made.

Changes in the distribution of activity between the autumn and spring harvests suggest that some of the carbohydrate that was transported to old segments during summer 1988 was remobilized the following spring to support new growth at the apex of the rhizome system. The 1989 node and roots showed increased 14C-activity between the two harvests, unambiguous evidence of translocation into these structures. At the same time, rhizomes of nearby segments experienced steep declines in amount of label. Some of the decline in activity must be attributable to respiratory losses. These nearby rhizomes, however, lost a greater proportion of their activity than any other compartment within the plants. Either these nearby rhizomes respired at higher rates than other areas of the rhizome system, for as yet unknown reasons, or they transported newly stored carbohydrate to sinks in the rapidly growing regions of the apex. Additional support for the second hypothesis comes from preliminary rhizome severing experiments, which indicate that developing shoots which are separated from back segments grow to a smaller size than shoots from intact rhizome systems (Geber and Landa, pers. obs.).

Another possible function of carbohydrate stored in old rhizomes is to aid in recovery following damage to the forward portions of the rhizome system. Although old nodes typically do not branch or produce additional shoots in undisturbed situations, severing of the rhizome system leads to the release of meristems from nodes behind the point of severing, resulting in the production of new perennating branches in almost all cases (de Kroon et al. 1991). The performance of these released branches is correlated with the size of the rhizome system remaining behind the point of severing (Geber and Landa, pers. obs.), and thus presumably with the amount of stored carbohydrate available to the newly-developing branch. Rhizome damage appears to
be a common phenomenon in nature, as many may-apple rhizome systems in field samples from our populations show evidence of recovery from damage. Possible agents of damage include insect herbivores and winter frost heaving.

**Activity in old roots**
The patterns of biomass and labelled material in old roots support the idea that roots undergo a continual turnover, with some current assimilate incorporated each year into new root material in all segments. Labelled material was present in roots at all old segments. Although old roots lost a greater percentage of their biomass over winter than did old nodes or rhizomes, they maintained constant specific activities between the two harvests. Old nodes and rhizomes, meanwhile, uniformly declined in specific activity. The constant specific activity of roots is best explained by the incorporation of labelled current assimilate into both structural material and metabolizable pools, in proportion to unlabelled carbohydrate. Metabolism or physical loss of root biomass (as in attrition over winter) would then lead to weight loss but no decline in specific activity. If labelled material were primarily entering metabolizable or storage pools and all structural material were unlabelled, then respiratory losses or export of carbohydrate would lead to declines in specific activity, such as is seen in nodes and rhizomes.

The allocation of current assimilate to roots in old segments suggests that these old roots are physiologically active and may contribute nutrients and/or water to increase the performance of the forward shoot. Uptake of water, nitrogen and phosphorus by old roots and subsequent transport to growing sections of the rhizome has been demonstrated under field conditions for species with similar clonal architecture as mayapple (Headley et al. 1988a, b, Jónsdóttir and Callaghan 1990). Demonstration of such transport, however, does not prove that the amounts of nutrients transported have significant effects on the demographic performance of the plants. Root pruning studies in mayapple have shown that loss of uptake by old roots decreases current shoot performance (Landa, pers. obs.), but that the effects are slight.

**Shoot type effects**
This study found no significant differences in allocation patterns between systems with sexual or vegetative shoots. Partly, this may be due to the drought-induced lack of fruit formation by sexual shoots during summer 1988. However, results from additional labelling studies indicate that plants labelled at different times of the season than in this experiment do sometimes show differences between sexual and vegetative systems, even in the absence of fruit formation by the sexual shoots (Landa and Vuorisalo, pers. obs.). Additional experiments are currently being analyzed to detect differences in allocation patterns within sexual systems, with and without fruit development.

**Translocation in branched plants**
The amount of labelled material transported between branches in undamaged mayapples, 5% to 10%, is high compared to other values in the literature. For example, only about 1% of labelled material was transported between branches of undamaged systems in either *Clin tonia borealis* or *Aster acuminatus* (Ashmun et al. 1982). The labelled material transported between branches in mayapples is specifically transported to growing points, at distances up to a meter. Damage appears to substantially increase levels of physiological integration (Fig. 3, lower panel). Increases in levels of physiological integration in response to localized stress are common (Marshall and Sagar 1965, Gifford and Marshall 1973, Ashmun et al. 1982, Welker et al. 1985, Alpert and Mooney 1986). These conclusions concerning mayapple are based, however, on the few branched systems randomly selected in this experiment. More detailed studies on branched mayapples are needed to quantify the level of integration between undamaged branches, the magnitude of response to localized damage and the costs of between-branch integration.

Physiological integration within clonal plants, especially translocation of resources from healthy to stressed ramets, has been proposed to be advantageous for monopolizing space in stable habitats (Pitelka and Ashmun 1985). Support of locally stressed ramets can allow the maintenance of dense aggregates of ramets, which would then deter the invasion of one genet by another. Some mayapple colonies do form dense patches and appear to exclude other herbaceous plants. The increased levels of integration following localized damage in branched mayapples is consistent with the hypothesis that high levels of integration are important for space monopolization. However, the low frequency of branching in most colonies, the annual habit of above-ground shoots and the eventual decay of old segments results in a majority of mayapple plants being composed of disconnected linear rhizome systems, each with a single terminal shoot. Most stressed shoots, therefore, would not have a healthy sister shoot that could provide support. In mayapples, the relative costs and benefits of branching, and of maintaining old rhizome connections vs allowing them to decay, are so far still poorly understood.
Physiological integration and response to the environment

Mayapples display extensive physiological integration for carbohydrate, in terms of translocation both throughout linear systems and between branches. All of the functions proposed for translocation of carbohydrate in rhizomatous plants appear to be important in mayapple: storage, maintenance of old roots and reserve meristems and response to localized stress. The high levels of physiological integration may be involved in allowing mayapples to respond to spatial and temporal variability in environmental conditions.

For physiological integration to be useful in buffering spatial variation in resource availability, the scale over which integration occurs must be at least as large as the scale of resource patchiness (e.g., Alpert and Mooney 1986, Evans 1988, 1991). Because of their clonal architecture, with single terminal shoots and extensive root systems, mayapples are able to integrate mineral nutrients and water over larger scales than for light. Soil nutrient and water levels can vary spatially at our study site on scales smaller than the size of the interconnected rhizome system. For example, our mayapples often grow over rocky terrain, with portions of their rhizome systems exposed aboveground and presumably in nutrient-poor, dry zones. Maintenance of active roots in old segments could allow mayapple rhizome systems to average out such fine scale heterogeneity, with forward transport of mineral nutrients and water from old roots to support the growth of the terminal shoot. This potential for distributed collection of water and mineral nutrients may be unimportant to the demography of mayapples, however, because the limited responses we have seen to nutrient augmentation and root pruning so far suggest that mayapples at our study site are usually not limited by water and nutrients.

Physiological integration in mayapples is probably more important in responding to temporal variation in environmental conditions, both predictable and unpredictable. Growing conditions change in a fairly predictable manner over the course of the growing season, leading to distinct phenologies of assimilation and growth. Although mayapples maintain a positive net photosynthetic rate throughout the summer (Taylor and Peircey 1976), most photosynthetically active radiation is available to mayapple plants early in the spring before closure of the forest canopy. New rhizome growth and development, however, do not begin until early summer and continue into the autumn. Within-season storage of carbohydrate (Chiarello and Roughgarden 1984, Chappin et al. 1990), followed by remobilization during the summer and fall, is essential to support the virtually non-overlapping processes of assimilation and growth.

Finally, although mayapples contain podophyllin, they are fed upon by a number of herbivores, including deer (Whigham, pers. comm.) and several species of insects (pers. obs.). Herbivore damage can be quite unpredictable in both time and space. For example, many colonies in our study site had high levels of stem borer infestation in 1990 (a noctuid moth, Papaiemapera cerina), causing extensive damage to underground rhizomes, while other colonies were untouched. Such high levels of stem borer damage, although not specifically looked for, were not apparent in any of the prior years of study at this site. The maintenance of, and the high levels of carbohydrate storage in, old segments of the rhizome system may be a bet-hedging strategy for recovery of the plant from damage to young portions of the rhizome system.

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23* OIKOS 63:3 (1992) 355


