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Developmental ecology of mayapple: effects of rhizome severing, fertilization and timing of shoot senescence

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Abstract. Mayapple (*Podophyllum peltatum* (L.)) is a perennial herb that forms rhizome systems, each terminated by a vegetative or sexual shoot. Such systems consist of previously formed annual segments, that are kept alive for many years. By severing rhizomes and fertilizing shoots, we have investigated whether new rhizome growth depends on nutrients acquired by roots of older segments. The treatments were imposed in spring and the effects evaluated in the following autumn, when formation of new rhizomes was complete.

Neither severing alone, nor the combination of severing and fertilization significantly affected rhizome branching, determination of the new rhizome bud type, rhizome length or dry weight. Fertilization and even severing alone increased the accumulation of nutrients in new rhizomes. Timing of shoot senescence had a major impact, with later senescing shoots producing longer and heavier new rhizomes. Later senescence also increased the biomass increment of the penultimate rhizomes, i.e. those immediately preceding the current year's shoot.

We conclude that in mayapple nutrient uptake by older roots does not contribute, at least immediately, to new rhizome growth. The lack of fertilization effects and the presence of strong effects of the timing of shoot senescence upon new rhizome growth indicate that light rather than nutrients was the limiting factor in this growth phase. The increased nutrient accumulation in response to fertilization suggests, however, that growth of the rhizome system may be affected by nutrient availability over a longer period of time. Data are presented that suggest that rhizome segments store nutrients that are needed to support the growth of developing shoots in subsequent years. Given the capability of dormant buds on old rhizome segments to form new shoots after damage, an important function of rhizome longevity in mayapple may be to maintain the potential to regenerate.

Key-words: Clonal plants, dormant bud bank, fertilization, mayapple, nutrient translocation, phenology, physiological integration, *Podophyllum peltatum*, rhizome severing, senescence

Introduction

Mayapple (*Podophyllum peltatum* (L.)) is a common rhizomatous understorey herb of deciduous forests in the eastern United States. Unbranched rhizome systems produce only a single annual shoot each year, which may be either sexual or vegetative. The larger double-leaved sexual shoots are morphologically and developmentally distinct from the smaller single-leaved vegetative shoots (Sohn & Policansky, 1977; Benner & Watson, 1989; Watson, 1990). Usually a rhizome system produces one new rhizome segment per year, but occasionally two or three are produced and form overwintering buds by the end of the growing season. Typically rhizome systems consist of branched or unbranched chains of as many as 7 years of interconnected segments (Sohn & Policansky, 1977; K. Landa, personal communication), each branch terminated by a shoot. Roots are found on even the oldest node of the system.

In clonal species with such long-lived rhizome systems, older segments, nodes and roots have been shown to receive significant amounts of carbon assimilated by the shoots at the forward (distal) end of the system (Allessio & Tieszen, 1975; Ashmun, Thomas & Pitelka, 1982; Jónsdóttir & Callaghan, 1988). This is also the case in mayapple. Approximately 50% of the carbon assimilated by the shoot in spring is translocated

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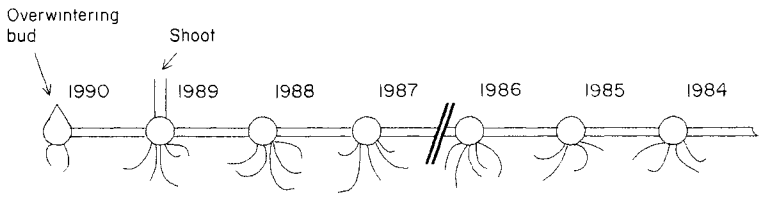

Fig. 1. Diagrammatic presentation of a linear mayapple rhizome system in 1989, consisting of interconnected rhizome segments and nodes. A system produces only one shoot generation per year. Consecutive segments are designated by the year in which they bear a shoot. Roots remain attached up to the oldest node. The point at which the 1987 rhizome was severed is indicated with bold parallel lines (see text).

to rhizome segments that are 2 years old or older (K. Landa, personal communication). It would seem that these costs of maintaining older rhizome segments must be outweighed by benefits manifested in increased growth and survival of the clone. One such benefit may be that roots on older nodes are necessary to meet the demands of growing sinks for inorganic nutrients (Jónsdóttir & Callaghan, 1990; de Kroon & Schieving, 1990; Marshall, 1990). For several clonal species it has been shown that nitrogen and phosphorus absorbed by older (proximal) roots are indeed transported acropetally to the growing tips (Noble & Marshall, 1983; Headley, Callaghan & Lee, 1988; Jónsdóttir & Callaghan, 1990).

In a field experiment, we tested the proposition that new rhizome growth in mayapple depends on nutrients acquired by older parts of the rhizome system. Two different treatments were imposed in the spring. We hypothesized that the first treatment, in which rhizome connections were severed, should cause a reduction in growth compared to unmanipulated controls. The growth reduction would be manifested in reduced branching frequency, in a lower probability of sexual shoot formation, and/or in shorter new rhizomes with smaller weights and nutrient contents. We expected that the effects of severing would be less dramatic in the second treatment, in which, following severing, nutrients were applied to the base of the current year's shoot.

Material and methods

The developmental phenology of mayapple

Mayapple shoots in Maryland emerge in late March to early April, and sexual shoots start flowering by the end of April. At about the time of flowering, one or more new rhizome segments are initiated at the base of the shoot. Most of the new rhizome growth is accomplished when the shoot is green but new growth may continue after leaf senescence in early to mid-summer. One or more of the new rhizomes forms a terminal overwintering bud that differentiates before the summer's end into either a nascent vegetative or sexual shoot (Y. Lu, personal communication; see Watson, 1990). This overwintering bud gives rise to next year's shoot (Fig. 1).

Experimental procedure

The experiment was carried out in a mixed deciduous hardwood forest at the Smithsonian Environmental Research Center (SERC) near Annapolis, Maryland. Site descriptions can be found in Whigham (1984). In mid-April 1989, at the time of leaf expansion, three vegetative and three sexual shoots were selected at random within each of 29 colonies. The shoots were randomly assigned to one of the following three treatments:

1 Severing (SC). The 1987 rhizome segment was cut at its backward end with a sharp knife (Fig. 1). As a result, older nodes and all their attached roots were separated from the growing tip of the rhizome system.

2 Severing and fertilization (SF). In addition to severing performed as above, the current year's shoot also was fertilized with 50 ml of 9·09 g l^{-1} ammonium phosphate solution (100 mg N in total), applied at the base of the shoot with a syringe. This amount of fertilizer was applied twice, on 11 April and 28 June.

3 Unmanipulated controls (CC) that were neither severed nor fertilized.

Shoots that senesce early in the season may form shorter new rhizomes than shoots that senesce later (Sohn & Policansky, 1977). In order to account for any effects of timing of senescence, the phenological status of all experimental shoots was determined on 12 June. Shoots were assigned to one of the following categories: (1) completely

senesced ('early' senescing shoots), (2) partly senesced, (3) completely green ('late' senescing shoots), and (4) damaged (mostly eaten by white-tailed deer). Only the early and late senescing categories (88% of the total sample) were used to evaluate the effects of the timing of senescence on new rhizome size and overwintering bud type.

Rhizome systems were harvested in mid-September 1989. For the severed systems (SC and SF treatments) the forward part of the system was excavated from the point of severing; the backward, older part was left intact for later examination. Unmanipulated control systems were completely harvested. All material was washed clean of soil particles and roots were cut off. In addition to new rhizome segments, the older segments of the forward part of the systems (1989 and 1988; see Fig. 1) were also analysed for effects of treatment because these segments may actually accumulate resources during the course of the growing season (Benner & Watson, 1989). The following characteristics were recorded:

1 Rhizome segment length.
2 Type of shoot produced by a node. The type of shoot produced at old nodes can be determined by the form of the scar left at the node; vegetative shoots leave a dormant bud at the top of the node while sexuals do not (see Sohn & Policansky, 1977). The type of shoot contained in the overwintering bud of new rhizome segments was determined macroscopically after dissection.
3 Number of rhizome branches produced by a node and their fate, i.e. whether or not their apices formed an overwintering bud. Rhizome segments that did not form a bud were recorded only if their length exceeded 4 mm.

Segments and nodes were separated and dried to constant weight. Total (Kjeldahl) nitrogen and phosphorus concentrations of rhizome segments were calorimetrically determined with a continuous-flow auto-analyser (Skalar, The Netherlands) after wet digestion.

In order to reduce sources of variability, three types of rhizome system were excluded from the analyses: (1) systems with 1990, 1989 or 1988 rhizome segments or nodes that were damaged either by injury or herbivory; (2) those few systems with fruiting sexual shoots in 1989; (3) systems in which the 1989 or 1988 segment grew from a dormant bud left behind at an older vegetative node (see Sohn & Policansky, 1977). Such rhizome segments grow vertically out of the node instead of horizontally, and are usually much shorter and thicker than segments that are formed by lateral meristems. 1988 rhizomes produced by dormant buds at 1987 vegetative nodes were excluded only in the analysis of the 1988 rhizomes. In total, 44% of the rhizome systems were discarded.

χ^2 analyses of branching frequency and new bud type were carried out within the groups of the vegetative and sexual 1989 shoots. Differences in length, dry weight and nutrient concentrations of rhizome segments and nodes were tested with analyses of variance. The effects of shoot type and new bud type on segment size and nutrient content can be profound (Sohn & Policansky, 1977; Benner & Watson, 1989) and were included in the analyses. Where necessary, data were transformed in order to improve normality.

In May 1990, the older parts of the experimental rhizome systems that had been left in the ground were harvested in order to assess the response of older nodes to severing. The following characteristics were recorded: (1) the number of older nodes; (2) the presence, location and type of new shoots formed; (3) the presence of lateral rhizome branches that were already present at the time of severing and that were terminated by a shoot.

Results

Rhizome branching and new bud type

There were no significant effects of treatment on the number of new rhizome segments produced by 1989 shoots or on the type of shoot contained in the overwintering bud terminating these new segments (Table 1). In all rhizome systems, whether they bore vegetative or sexual shoots in 1989, the total number of new rhizome segments formed tended to increase from the CC to the SC to the SF treatment but these trends were not significant. For those systems that bore a sexual shoot, and gave rise to only one new segment in 1989, the proportion of new overwintering buds containing sexual shoots tended to be smaller in the severed (22%), and larger in the severed + fertilized treatment (67%), than in the control treatment (45%), but again the effects were not significant. Across all treatments, sexual shoots produced significantly more new rhizome segments than vegetative shoots (Table 1). The type of shoot found in the overwintering bud did not vary as a function of the current year's shoot type.

Late senescing sexual shoots produced significantly more total new rhizome segments than early senescing sexual shoots ($P = 0{\cdot}010$; Table 1). A similar effect on the number of new segments that

Table 1. Contingency tables of the effects of treatment and timing of senescence on branching and new bud type, for the 1989 vegetative (V) and sexual (S) shoots separately. Treatments are unmanipulated controls (CC), severing (SC) and severing + fertilization (SF). Timing of shoot senescence is early (E) or late (L). Overwintering bud type is vegetative (v) or sexual (s). Effects on overwintering bud type are analysed separately for shoots that produced only one new rhizome segment (unbranched) and those that produced multiple segments (branched).

		Total number of new rhizome segments (>4 mm)				Number of rhizome segments with overwinter buds			Overwintering bud type			
									Unbranched		Branched	
	n	1	2	3	4	1	2	3	v	s	v	s
Effects of treatment												
V-CC	18	12	6	0	0	15	3	0	11	4	5	1
V-SC	13	8	4	1	0	11	2	0	5	6	4	3
V-SF	18	8	9	1	0	12	6	0	6	6	10	3
V-SUM	49	28	19	2	0	38	11	0	22	16	19	7
S-CC	17	3	11	3	0	11	6	0	6	5	8	4
S-SC	16	4	9	3	0	9	6	1	7	2	11	6
S-SF	14	4	7	2	1	6	7	1	2	4	17	8
S-SUM	47	11	27	8	1	26	19	2	15	11	36	18
Effects of timing of senescence												
V-E	34	18	15	1	0	25	9	0	14	11	14	5
V-L	14	9	4	1	0	12	2	0	7	5	3	2
S-E	15	8	5	2	0	11	4	0	6	5	9	3
S-L	21	1	15	4	1	10	9	2	5	5	16	6

None of the differences in branching and overwintering bud type between treatments or senescence categories were statistically significant at the 5% level, except one: the total number of new rhizomes was significantly larger in late than in early senescing sexual shoots ($\chi^2 = 11{\cdot}43$, d.f. = 3, $P = 0{\cdot}010$).

formed overwintering buds was not significant. Timing of senescence did not affect rhizome branching in vegetative shoots. The type of shoot found in the overwintering bud was unaffected by date of senescence for both of the current year's shoot types.

Sizes of new rhizome segments and nodes

Treatments had no effect on new rhizome segment lengths and dry weights (Table 2). Nutrient concentrations were higher in the SF than in the CC treatment, while the SC treatment was intermediate (nitrogen) or similar to the control (phosphorus). These effects were stronger in segments formed by vegetative than by sexual shoots. In the absence of treatment effects on rhizome dry weight, differences in nutrient contents between treatments were similar to those in nutrient concentrations but, due to the larger variation in contents, they were not significant.

Late senesced shoots produced longer and heavier new rhizome segments than early senesced shoots, but the dry weight of the overwintering bud was not affected (Table 2). Nutrient concentrations in new rhizomes of early senesced shoots were significantly higher than those of late senesced shoots, but, due to opposite effects on rhizome dry weight, there were no such effects on total nutrient contents.

New rhizome segments produced by sexual shoots were longer and had higher dry weight and nutrient content, and heavier overwintering buds, than those produced by vegetative shoots (Table 2). Overwintering bud type affected biomass and nutrient content in a similar way, but had no effect on rhizome length. The near absence of interactions in Table 2 indicates that the timing of senescence, the 1989 shoot type and the type of the overwintering bud affected new rhizome growth independently.

Sizes of old rhizome segments and nodes

There were no effects of treatment on the size of the penultimate (1989) rhizome segments (data not shown). The only observable trend was that 1989 segments in the SF treatment had higher phosphorus concentrations than in the other two treatments (main treatment effect $P < 0{\cdot}05$; analysis as in Table 2), but a posteriori tests showed that these differences were not significant. Treatment effects

Table 2. The effects of treatment and timing of senescence (E/L) and overwintering bud type (v/s) on the length, dry weight, nutrient concentrations and nutrient contents of the new rhizome segment, and the dry weight of the overwintering bud. Treatments are unmanipulated controls (CC), severing (SC) and severing + fertilization (SF). For 1989 shoots that produced multiple new segments only the primary (longest) segment was included in this analysis. The data presented are means (± SE).

n	Rhizome segment length (mm)	Rhizome segment dry weight (mg)†	Rhizome segment N concentration (mg g^{-1})‡	Rhizome segment P concentration (mg g^{-1})‡	Rhizome segment N content (mg)‡	Rhizome segment P content (mg)‡	Overwintering bud dry weight (mg)†
Effects of treatment							
V-CC 18/18§	111 (10)	463 (55)	24·6 (1·7)^{a}	4·43 (0·23)^{a}	10·9 (1·3)	1·93 (0·17)	53 (6)
V-SC 14/13	111 (10)	548 (86)	26·7 (2·1)^{ab}	4·48 (0·25)^{ab}	12·8 (1·7)	2·11 (0·24)	59 (7)
V-SF 19/18	114 (6)	510 (80)	32·4 (2·3)^{b}	5·27 (0·23)^{b}	13·3 (1·1)	2·39 (0·33)	58 (7)
S-CC 17/17	139 (9)	713 (74)	21·5 (1·5)^{a}	4·47 (0·28)^{a}	14·1 (1·5)	3·07 (0·39)	68 (7)
S-SC 16/16	130 (11)	678 (90)	24·8 (2·2)^{a}	4·39 (0·26)^{a}	15·2 (1·9)	2·84 (0·34)	64 (5)
S-SF 14/14	131 (9)	686 (86)	26·9 (2·3)^{a}	5·03 (0·33)^{a}	16·8 (1·6)	3·30 (0·38)	61 (4)
Shoot type	**	**	*	NS	*	***	*
Treatment	NS	NS	**	*	NS	NS	NS
Interaction	NS	NS	NS	NS	NS	NS	NS
Effects of timing of senescence							
V-vE 19/10§	109 (7)	361 (33)	26·7 (2·1)	4·66 (0·29)	9·2 (1·2)	1·63 (0·21)	43 (4)
V-vL 8/7	128 (17)	659 (155)	20·6 (3·2)	3·92 (0·31)	10·9 (2·6)	2·00 (0·34)	46 (11)
V-sE 16/8	104 (9)	490 (68)	27·0 (2·1)	5·02 (0·27)	11·8 (2·0)	2·14 (0·29)	70 (6)
V-sL 7/5	123 (10)	762 (122)	26·4 (3·6)	3·89 (0·40)	17·6 (2·7)	2·59 (0·30)	71 (11)
S-vE 8/5	129 (13)	486 (60)	28·4 (1·2)	4·86 (0·68)	16·3 (2·6)	2·82 (0·69)	54 (5)
S-vL 12/8	143 (10)	687 (74)	18·4 (1·7)	4·31 (0·25)	11·0 (0·7)	2·66 (0·24)	57 (3)
S-sE 6/3	118 (13)	613 (86)	23·2 (4·6)	4·69 (0·65)	15·1 (3·5)	3·00 (0·25)	76 (9)
S-sL 8/7	146 (17)	1063 (143)	21·0 (3·5)	4·35 (0·47)	19·4 (2·7)	4·47 (0·74)	91 (7)
Shoot type (Sh)	*	*	NS	NS	NS	***	**
Bud type (Bud)	NS	*	NS	NS	*	*	***
Senescence (Sen)	*	***	*	*	NS	NS	NS
Sh × New	NS	NS	NS	NS	NS	NS	NS
Sh × Sen	NS	NS	NS	NS	NS	NS	NS
Bud × Sen	NS	NS	NS	NS	*	NS	NS
Sh × Bud × Sen	NS	NS	NS	NS	NS	NS	NS

† Statistical tests on log-transformed data.

‡ For the effects of timing senescence, only rhizome systems of CC and SC (unfertilized) treatments analysed.

§ *n* length, dry weight data/*n* nutrient data.

Significance levels are * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. A posteriori analyses were carried out separately for the vegetative (V) and sexual (S) shoots; means with different letters are significantly different at $P < 0.05$.

Table 3. Effects of timing of senescence (E/L) and type of the 1989 shoot (V/S) on segment lengths, dry weights, nutrient concentrations and nutrient contents of penultimate (1989) and antepenultimate (1988) rhizomes.

	n	Rhizome segment length (mm)	Rhizome segment dry weight (mg)	Rhizome segment spec.weight (mg mm^{-1})	Rhizome segment N concentration (mg g^{-1})	Rhizome segment P concentration (mg g^{-1})	Rhizome segment N content (mg)	Rhizome segment P content (mg)	Node dry weight (mg)
1989 rhizomes									
V-E	31	96 (6)	651 (43)	6·97 (0·29)	18·2 (0·9)	3·88 (0·14)	11·3 (0·7)	2·41 (0·12)	156 (8)
V-L	14	94 (11)	750 (102)	7·97 (0·46)	16·6 (1·7)	3·19 (0·23)	11·0 (1·4)	2·18 (0·25)	192 (18)
S-E	14	118 (8)	988 (109)	8·37 (0·62)	18·2 (1·4)	3·78 (0·26)	16·5 (1·2)	3·49 (0·28)	196 (16)
S-L	20	122 (8)	1140 (91)	9·34 (0·37)	14·6 (0·9)	3·29 (0·16)	15·8 (1·0)	3·64 (0·27)	240 (11)
Shoot type		**	***	**	NS	NS	***	***	***
Senescence		NS	NS	*	*	**	NS	NS	**
Interaction		NS	NS	NS	NS	NS	NS	NS	NS
1988 rhizomes†									
V-E	27	88 (4)	540 (37)	6·17 (0·30)	15·7 (0·9)	2·98 (0·12)	8·1 (0·5)	1·58 (0·11)	179 (9)
V-L	13	90 (6)	600 (54)	6·66 (0·43)	12·2 (1·1)	2·47 (0·20)	7·3 (1·0)	1·45 (0·16)	193 (20)
S-E	9	82 (9)	524 (79)	6·24 (0·39)	18·4 (1·9)	3·27 (0·28)	8·7 (0·7)	1·57 (0·15)	193 (15)
S-L	14	131 (6)	982 (94)	7·37 (0·52)	12·5 (1·0)	2·70 (0·25)	11·5 (0·8)	2·49 (0·18)	242 (11)
Shoot type		*	***	**	NS	NS	***	***	***
Senescence		**	**	NS	**	*	NS	NS	NS
Interaction		**	*	NS	NS	NS	*	**	NS

† Only 1988 rhizomes with vegetative 1988 nodes included in this analysis.
Significance levels are * $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.

were subsequently ignored in the analysis of effects of timing of senescence and 1989 shoot type.

Late shoot senescence resulted in higher dry weight for 1989 rhizome segments and nodes compared to those that senesced early (Table 3). This effect was significant only for rhizome specific dry weight (i.e. dry weight per unit of length) and not for total rhizome dry weight, because specific weight was less variable. Nutrient concentrations in 1989 segments were significantly higher in early than in late senescing shoots, but nutrient content was similar because of the opposite effects on rhizome dry weight. All effects of the timing of senescence on 1989 rhizome segments were similar for vegetative and sexual shoot types. Rhizomes preceding 1989 sexual shoots were longer and heavier, and had higher nutrient contents, than rhizomes preceding 1989 vegetative shoots.

There were also no effects of treatment on the size of antepenultimate (1988) rhizome segments (data not shown), and treatment effects were subsequently ignored. Table 3 shows that 1988 segments preceding late senescing sexual shoots were longer and heavier and had higher nutrient contents than 1988 segments preceding early senescing sexual shoots. The interaction between 1989 shoot type and senescence reflects the fact that most of the effects of senescence date were nearly absent in vegetative shoots. Early senescing sexual shoots had 1988 rhizome segments that were comparable to those of vegetative shoots (Table 3).

Shoot formation by severed rhizome systems

More than 1 year after severing, only five out of 76 rhizome systems left in the ground had completely decayed. Of the 71 intact systems, 69% had successfully produced a shoot from at least one old node. Regeneration was significantly affected ($P < 0{\cdot}001$) by the presence of a lateral branch at one of the older nodes: 83% of the unbranched, but only 24% of the branched systems formed new shoots (Table 4). Linear systems that successfully regenerated had significantly more older rhizome segments than those that failed. All newly formed shoots were vegetative. In 82% of all regenerating systems the shoots were formed by the 1986 node, which was just behind the point of severing, and in 16% by the next older (1985) node. Only one out of the 49 regenerating systems formed two new shoots.

Discussion

Even in the absence of fertilization, the nutrient content of new rhizome segments, particularly of nitrogen, increased rather than decreased in response to separating the two to four oldest segments from the growing tip of the mayapple rhizome system (Table 2). We conclude that roots of these older nodes do not contribute significantly to nutrient accumulation in new rhizomes. Rather, the higher nitrogen concentration in the severed new rhizome segments suggests the opposite situation: nitrogen acquired by roots at younger nodes near the growing tips may be transported basipetally and, if severing prevents this transport, nutrients may actually accumulate in the new rhizomes. This pattern of strong basipetal transport has been observed only rarely (Jónsdóttir & Callaghan, 1990; Marshall, 1990), whereas acropetal transport over long distances appears to be more common. But the actual amounts of nutrients that growing points receive from older roots is reported to be very small (Headley *et al.*, 1988;

Table 4. Regeneration by severed rhizome systems in 1990, 1 year after severing. 'Yes' means that at least one of the backward nodes had produced a shoot; 'no' means that no shoot was formed. Unbranched systems are linear; in branched systems a lateral branch, terminated by a shoot, is connected to one or more of the backward nodes. The number of backward rhizome segments (mean ± SE) refers to the primary branch only.

	Regeneration		
	Yes	No	
Number of rhizome systems			
Unbranched	45	9	$\chi^2 = 21{\cdot}6$
Branched	4	13	$P < 0{\cdot}001$
Total	49	22	
Number of backward segments per system			
Unbranched	3·33 (0·22)	2·11 (0·39)	$P < 0{\cdot}05$
Branched	4·25 (0·49)	4·15 (0·39)	NS

Jónsdóttir & Callaghan, 1990) and the impact of this acropetal transport on new growth is also likely to be small, but this aspect has rarely been investigated. Only the study by Jónsdóttir & Callaghan (1988) with *Carex bigelowii* shows that severing older rhizome segments significantly decreases shoot survival and new growth at the forward part of the rhizome system.

The timing of shoot senescence had no effect on the type of the shoot found in the overwintering bud (Table 1). The reason for this may be that determination of the overwintering bud of the developing rhizome segment may have already taken place prior to senescence (Y. Lu, personal communication; Watson, 1990). Timing of shoot senescence did affect the extent of new rhizome branching, length and dry weight (Tables 1 and 2), indicating that the growth of new rhizome segments was carbon, rather than nutrient limited. Mayapple maintains positive net CO_2 uptake rates after canopy closure (Taylor & Pearcy, 1976), and, apparently, the carbon assimilated late in the season supports significantly new rhizome growth. While biomass accumulation was significantly affected by the timing of senescence, nutrient accumulation was not, as shown by the fact that the nutrient content of new rhizome segments was similar for early and late senescing shoots (Table 2). It is interesting to point out that while timing of senescence affected biomass accumulation patterns only, current year's shoot type or overwintering bud type affected the accumulation patterns of both biomass and nutrients.

While nutrient availability apparently did not limit growth of new rhizome segments, the additional nutrients that accumulated in new rhizomes in response to severing and especially fertilization (Table 2) may become important over longer periods of time. Benner & Watson (1989) showed that the nutrient content of the rhizome segment immediately preceding the current year's shoot decreases during the period of leaf expansion. Similar seasonal changes in nutrient storage and translocation have been reported for many other species (e.g. Whigham, 1984; Bobbink, den Dubbelden & Willems, 1989; Zimmerman, 1990). Most nutrients required for shoot growth in mayapple must be obtained through translocation because nutrient uptake from the soil in spring is nearly absent (Blank, Olson & Vitousek, 1980). An increase in the accumulation of nutrients in new rhizome segments may thus significantly stimulate shoot growth in the following growing season. Future studies are required to elucidate the longer-term effects of nutrient acquisition, storage and translocation in mayapple.

The penultimate rhizome segment, immediately preceding the shoot, has been shown to increase in weight from May to August (Benner & Watson, 1989). Our results show that this increase is significantly smaller when shoots senesce early than when they senesce late (Table 3). Antepenultimate (1988) segments of systems with late senescing sexual shoots were significantly longer and heavier, and had higher nutrient content, than those with early senescing sexual shoots (Table 3). As the length of this segment was already determined 2 years before the current shoot senesced, this result suggests that the size of the 1988 rhizome segment exerts an effect on the timing of sexual shoot senescence, rather than the reverse. The much smaller weight, nutrient concentration, and nutrient content of 1988 segments than of 1989 segments (Table 3) indicates that 1988 segments had exported significant amounts of resources over the past year. Possibly, antepenultimate rhizome segments export nutrients to the developing shoot in spring, in a way similar to penultimate rhizomes (Benner & Watson, 1989). If translocation is limited due to small rhizome size, the shoot is more likely to senesce early. Sexual shoots may be similarly supported by resources from the 1986 or older rhizome segments because severing the 1987 segment, preventing transport from it, significantly stimulated early senescence of sexual shoots ($\chi^2 = 3{\cdot}974$, $P = 0{\cdot}046$). In contrast, the size of the 1988 rhizome segment did not influence the timing of vegetative shoot senescence (Table 3). This may be due to the fact that vegetative shoots are only half the size of sexuals, and may require less support. Early senescence in vegetative shoots may be caused by factors other than a limited supply of resources from the rhizome system. The effects of 1988 rhizome segment size on 1989 shoot senescence reinforces the argument that nutrient accumulation in rhizomes may have profound long-term effects on mayapple shoot demography.

We conclude that it does not appear that nutrient uptake by roots on older nodes of the rhizome system supports the growth of the rhizome apex, at least in the short term. It seems more likely that these older nodes are kept alive in order to enable the rhizome system to recover from damage occurring in its forward parts. The regeneration capacity of old nodes is very good: after severing, five out of every six linear rhizome systems successfully produced a new shoot from a dormant bud (Table 4). Each of these buds was at

least 4 years old. As the viability of dormant buds is likely to decline with increasing age, it is probable that shoot formation by younger nodes will occur even more readily. Most of the branched systems did not regenerate, suggesting that older buds are able to develop only after the release of apical dominance. A similar release of bud dormancy in response to severing has been demonstrated in *C. bigelowii* (Jónsdóttir & Callaghan, 1988). Damage of mayapple rhizomes by herbivores (probably mice or voles) is not uncommon: 14% of the 170 shoots that were monitored in the experiment had one or more aborted new rhizome segments as a result of damage. Keeping dormant buds alive in order to maintain the capacity to regenerate may increase genet survival, and hence be an important function of rhizome longevity in mayapple (cf. Cook, 1985). Nutrient acquisition by roots on old nodes may satisfy local nutrient requirements only.

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References

Allessio, M.L. & Tieszen, L.L. (1975) Patterns of carbon allocation in an arctic tundra grass, *Dupontia fisheri* (Gramineae) at Barrow, Alaska. *American Journal of Botany*, **62**, 797–807.

Ashmun, J.W., Thomas, R.J. & Pitelka, L.F. (1982) Translocation of photoassimilates between sister ramets in two rhizomatous forest herbs. *Annals of Botany*, **49**, 403–415.

Benner, B.L. & Watson, M.A. (1989) Developmental ecology of mayapple: seasonal patterns of resource distribution in sexual and vegetative rhizome systems. *Functional Ecology*, **3**, 539–547.

Blank, J.L., Olson, R.K. & Vitousek, P.M. (1980) Nutrient uptake by a diverse spring ephemeral community. *Oecologia*, **47**, 96–98.

Bobbink, R., den Dubbelden, K. & Willems, J.H. (1989) Seasonal dynamics of phytomass and nutrients in chalk grassland. *Oikos*, **55**, 216–224.

Cook, R.E. (1985) Growth and development in clonal plant populations. In *Population Biology and Evolution of Clonal Organisms* (eds. J.B.C. Jackson, L.W. Buss & R.E. Cook), pp. 259–296. Yale University Press, New Haven.

de Kroon, H. & Schieving, F. (1990) Resource partitioning in relation to clonal growth strategy. In *Clonal Growth in Plants: Regulation and Function* (eds. J. van Groenendael & H. de Kroon), pp. 113–130. SPB Academic Publishing, The Hague.

Headley, A.D., Callaghan, T.V. & Lee, J.A. (1988) Phosphate and nitrate movement in the clonal plants *Lycopodium annotinum* L. and *Diphasiastrum complanatum* (L.) Holub. *New Phytologist*, **110**, 487–495.

Jónsdóttir, I.S. & Callaghan, T.V. (1988) Interrelationships between different generations of interconnected tillers of *Carex bigelowii*. *Oikos*, **52**, 120–128.

Jónsdóttir, I.S. & Callaghan, T.V. (1990) Intraclonal translocation of ammonium and nitrate nitrogen in *Carex bigelowii* Torr. ex Schwein. using ^{15}N and nitrate reductase assays. *New Phytologist*, **114**, 419–428.

Marshall, C. (1990) Source-sink relations of interconnected ramets. In *Clonal Growth in Plants: Regulation and Function* (eds. J. van Groenendael & H. de Kroon), pp. 23–41. SPB Academic Publishing, The Hague.

Noble, J.C. & Marshall, C. (1983) The population biology of plants with clonal growth. II. The nutrient strategy and modular physiology of *Carex arenaria*. *Journal of Ecology*, **71**, 865–877.

Sohn, J.J. & Policansky, D. (1977) The costs of reproduction in the mayapple *Podophyllum peltatum* (Berberidaceae). *Ecology*, **58**, 1366–1374.

Taylor, R.J. & Pearcy, R.W. (1976) Seasonal patterns of the CO_2 exchange characteristics of forest understory plants from a deciduous forest. *Canadian Journal of Botany*, **54**, 1094–1103.

Watson, M.A. (1990) Phenological effects on clone development and demography. In *Clonal Growth in Plants: Regulation and Function* (eds. J. van Groenendael & H. de Kroon), pp. 43–55. SPB Academic Publishing, The Hague.

Whigham, D.F. (1984) Biomass and nutrient allocation of *Tipularia discolor* (Orchidaceae). *Oikos*, **42**, 303–313.

Zimmerman, J.K. (1990) Role of pseudobulbs in growth and flowering of *Catasetum viridiflavum* (Orchidaceae). *American Journal of Botany*, **77**, 533–542.

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