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Propagule Type and Planting Time Affect Subsequent Mayapple Growth

Kent E. Cushman[1] and Muhammad Maqbool
North Mississippi Resaerch and Extension Center, 5421 Highway 145 South, Verona, MS 38879

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***Abstract.* Leaves of american mayapple (*Podophyllum peltatum* L.) contain podophyllotoxin, a compound of interest to the pharmaceutical industry. Cultural practices for establishment of mayapple in field plantings for commercial harvest have not been investigated. A factorial arrangement of three planting dates (Fall 2000, Spring 2001, or Summer 2001) and three propagule types (Nt+N1, Nt, or Nx; as described by Maqbool et al., 2004) were used to investigate strategies for establishing mayapple plantings. Rhizome segments were harvested from the wild and transplanted into plant beds in full sun in northern Mississippi. Plant emergence was recorded during March and April of each year from 2001 to 2004. Leaves within each plot were harvested as soon as they began to yellow, from the third week of April to the first week of June each year. Propagule type and planting time interacted to affect subsequent plant growth when measured on an area basis (per square meter of growing area). In 2004, spring-planted Nt+N1 produced more shoots with greater total leaf area and dry mass than spring-planted Nx or Nt. In contrast, Nt+N1 transplanted during fall or summer was equal in performance to that of Nx or Nt. Performance of summer-planted Nt was poor, producing far less leaf area and dry mass than any of the other treatment combinations. On a per plant basis, fall-planted propagules produced greater leaf area and dry mass in 2004 than spring- or summer-planted propagules, and Nt+N1 produced greater leaf area than Nx or Nt. The effect of year was not analyzed in this study due to complications of the experimental design. In conclusion, overall plant growth and performance of spring-planted Nt+N1 can be recommended as excellent and that of fall-planted Nt as poor. All other treatment combinations can be recommended as good. These results will assist growers of specialty crops in establishing mayapple plantings under field conditions in full sun.**

Podophyllotoxin is a botanical compound of interest to the pharmaceutical industry because it is used as a precursor in the manufacture of several types of drugs. Drugs that contain podophyllotoxin-based compounds are either used in, or being tested for, the treatment of particular forms of cancer, arthritis, and skin ailments (Bedows and Hatfield, 1982; Canel et al., 2000; Jackson and Dewick, 1985; Lerndal and Svensson, 2000). Currently, the commercial source of podophyllotoxin is obtained from Indian mayapple (*Podophyllum emodi* Wall.; syn. *P. hexandrum* Royale), and the compound is extracted from its roots and rhizomes. Due to overexploitation and destructive harvest, Indian mayapple was reported to be an endangered species (Foster, 1993; Rai et al., 2000). The american mayapple (*P. peltatum* L.) also contains podophyllotoxin and it was reported that leaves contain high levels of the compound (Canel et al., 2000, 2001). The species grows throughout eastern North America, and the herbaceous shoots emerge from underground rhizomes in early spring. Colonies of plants are most often located in wooded areas, though colonies can also be found in full sun.

Rhizome structure of american mayapple is similar to that of lily-of-the-valley (*Convallaria majalis* L.). Rhizomes are indeterminate and branching and are described by Hartmann et al. (1990) as leptomorphic. Internodal segments are long and slender, and nodes are thickened, complicated structures consisting most often of a single dominate apical bud and many dormant lateral buds and leaf scars (Holm, 1899). Nodes of lily-of-the-valley are sometimes referred to as pips and are used as propagules to force flowering out of season (Hartmann et al., 1990). Roots of mayapple and lily-of-the-valley arise mostly from the base of each node but may also be present along the length of the internode.

As with lily-of-the-valley, mayapple rhizome segments appear to be useful propagules for establishing greenhouse and field plantings. Maqbool et al. (2004) harvested two types of mayapple rhizome segments from the wild, chilled them for 30, 45, 60, 75, or 90 d at 4 °C, and planted them in pots in the greenhouse. Two-node segments performed better than one-node propagules, and segments chilled 60 days or longer performed far better than those chilled for a shorter duration. Two-node segments harvested from the wild were also used successfully to establish field studies, one exploring increasing levels of shade (Cushman et al., 2005a) and the another exploring the use of organic mulches in combination with different rhizome planting depths (Cushman et al., 2005b).

The purpose of this research was to explore strategies for establishing field plantings of mayapple in full sun. This research is part of a larger effort to domesticate american mayapple for use as a renewable source of podophyllotoxin. In perennial plantings, rhizomes would remain intact while leaves would be harvested annually. This research is also directed to growers of specialty crops interested in the possibility of supplying mayapple leaf material to the pharmaceutical industry (Meijer, 1974; Moraes et al., 2000).

Materials and Methods

Mayapple rhizome segments were harvested from the wild near Oxford, Miss. (34.372° N, 89.541° W, elevation 100 m), on 12 Oct. 2000, 22 Feb. 2001, or 26 July 2001. This was a shaded location and the habitat was mixed mesophytic. Rhizome segments were transplanted to raised beds at the Horticulture Research and Education Unit in Verona, Miss., the day after each harvest. At the time of each planting, rhizome segments were separated into three types of propagules as shown in Fig. 1. Briefly, types were 1) two-node rhizome segments with a terminal node and its adjacent 1-year-old node, referred to as Nt+N1 (see Maqbool et al., 2004), 2) one-node rhizome segments with a single node, other than Nt, of

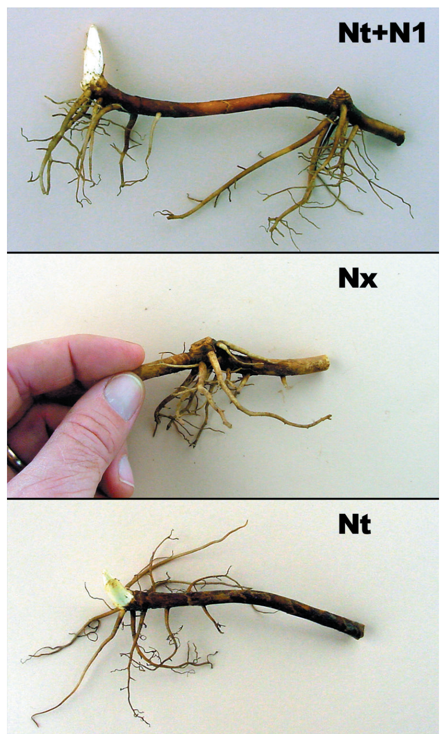

Fig. 1. Three types of rhizome segments of american mayapple were used as propagules in this study. Two-node segment with a terminal node and its adjacent 1-year-old node, referred to as Nt+N1. One-node segment with a single node, other than Nt, of unknown age, referred to as Nx. One-node segment with a single terminal node, referred to as Nt.

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[1]Current address: Southwest Florida Research and Education Center, 2686 SR 29 North, Immokalee, FL 34142; e-mail kecushman@ifas.ufl.edu.

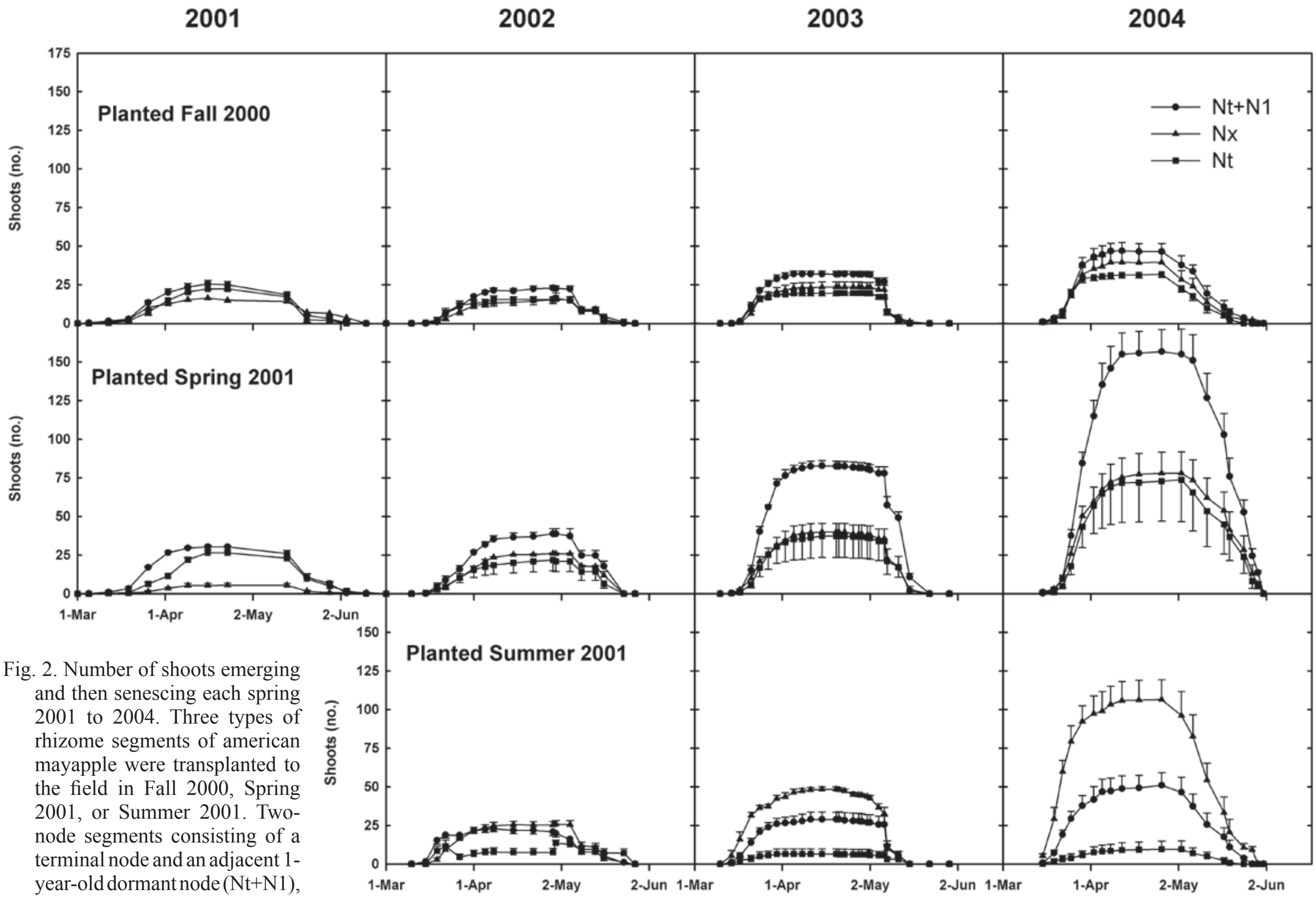

Fig. 2. Number of shoots emerging and then senescing each spring 2001 to 2004. Three types of rhizome segments of american mayapple were transplanted to the field in Fall 2000, Spring 2001, or Summer 2001. Two-node segments consisting of a terminal node and an adjacent 1-year-old dormant node (Nt+N1), one-node segments consisting of a single node, other than a terminal node, of unknown age (Nx), or one-node segments consisting of a single terminal node (Nt). Values are means of four replications ±SE.

unknown age, referred to as Nx, or 3) one-node rhizome segments with a single terminal node, referred to as Nt. Each propagule consisted of the above-mentioned nodes and 4 to 6 cm of adjacent rhizome tissue. All rhizome segments were harvested and planted with roots intact. The experimental design was a 3 × 3 factorial arrangement of three planting dates and three propagule types in a randomized complete block design with four blocks. Regardless of propagule type, the largest rhizome segments were planted to block one, the second largest to block two, and so on. Raised beds were prepared with a press-pan-type bed shaper and spaced 1.8 m apart, center to center. Beds were formed 15 cm high and 75 cm wide across the top and drip irrigation tubing was installed in the middle of the bed. Each experimental unit (plot) consisted of 30 rhizome segments arranged in two parallel rows. Rows were spaced 30 cm apart on top of each plant bed and were 1.5 m in length. Propagules were spaced 10 cm apart within each row and planted 3.8 cm below the soil surface. Plots were watered by hand immediately after transplant. A 13-cm layer of wheat straw was maintained on all plots the first year. The wheat straw settled and degraded after 1 year so a 10 cm layer of coarse pine bark mulch was added in Summer 2001 to all plots (particle size 1.0 to 2.5 cm). The bark mulch layer was maintained throughout the remainder of the experiment. The soil at Verona is a Quitman fine sandy loam (fine-loamy, siliceous, thermic, Aquic Paleudult).

Table 1. Leaf dry mass of shoots arising from propagules of the american mayapple. Propagules were one of three types of rhizome segments and were planted in Fall 2000, Spring 2001, or Summer 2001 in northern Mississippi. Observations were made during spring of each year.

Planting	Propagule	Leaf dry mass (g·m^{-2})			
time (T)	type (P)[z]	2001[y]	2002	2003	2004
Fall 2000	Nt+N1	---	10.4 b[x]	30.3 b	55.0 bc
	Nx	---	7.3 b	23.2 bc	44.3 bc
	Nt	---	4.1 cd	13.8 cd	29.9 c
Spring 2001	Nt+N1	---	21.8 a	57.2 a	103.3 a
	Nx	---	8.3 b	23.2 bc	46.9 bc
	Nt	---	9.1 bc	28.5 bc	55.9 bc
Summer 2001	Nt+N1	---	4.6 cd	19.4 bc	42.0 bc
	Nx	---	8.4 b	30.0 b	63.7 b
	Nt	---	0.9 d	3.0 d	7.1 d
Significance					
T		---	<0.0001	0.0005	0.0024
P		---	<0.0001	0.0003	0.0011
T × P		---	0.0015	0.0045	0.0086

[z]Two-node segments consisting of a terminal node and an adjacent 1-year-old dormant node (Nt+N1), one-node segments consisting of a single node, other than a terminal node, of unknown age (Nx), or one-node segments consisting of a single terminal node (Nt).
[y]Leaf dry mass was not recorded in 2001.
[x]Means of four replications. Values in columns followed by the same letter are not significantly different at $P \leq 0.05$. Each experimental unit consisted of 30 propagules.

Weed control, pest control, fertilization, and irrigation were identical to that described in Cushman et al. (2005a). Construction fabric made of 0.9-m-wide woven plastic material and supported by wooden stakes was installed alongside plots in 2003 and 2004 to reduce wind damage to mayapple shoots and leaves. Plant emergence data were recorded two or three times per week during March and April of each year from 2001 to 2004. Individual leaves within each plot were harvested as soon as leaves began to yellow, from the third week of April to the first week of June until all leaves from all plots were harvested. Leaf area of harvested leaves was measured using an area meter (LI-3100; LI-COR, Lincoln, Nebr.). Leaves were then dried in a forced-air, constant-temperature oven (model 1380FM; VWR Scientific Products, Cornelius, Ore.) at 60 °C and dry mass recorded. Planting time

Table 2. Total leaf area of shoots arising from propagules of the american mayapple. Propagules were one of three types of rhizome segments and were planted in Fall 2000, Spring 2001, or Summer 2001 in northern Mississippi. Observations were made during spring of each year.

Planting time (T)	Propagule type (P)[z]	Total leaf area ($cm^2·m^{-2}$) 2001[y]	2002	2003	2004
Fall 2000	Nt+N1	880 bc[x]	---	6,930 b	12,900 bc
	Nx	600 cd	---	5,320 bc	10,600 bc
	Nt	360 d	---	3,040 cd	6,710 cd
Spring 2001	Nt+N1	1,920 a	--	13,700 a	27,000 a
	Nx	370 d	---	5,000 bc	11,500 bc
	Nt	1,090 b	---	6,390 bc	13,500 bc
Summer 2001	Nt+N1	---	---	4,410 bc	10,100 bc
	Nx	---	---	7,160 b	17,100 b
	Nt	---	---	700 d	1,590 d
Significance					
T		0.0002	--	0.0005	0.0016
P		<0.0001	--	0.0001	0.0006
T × P		0.0004	--	0.0014	0.0024

[z]Two-node segments consisting of a terminal node and an adjacent 1-year-old dormant node (Nt+N1), one-node segments consisting of a single node, other than a terminal node, of unknown age (Nx), or one-node segments consisting of a single terminal node (Nt).

[y]Leaf area was not recorded in 2002.

[x]Means of four replications. Values in columns followed by the same letter are not significantly different at $P \leq 0.05$. Each experimental unit consisted of 30 propagules.

Table 3. Shoot emergence from propagules of the american mayapple. Propagules were one of three types of rhizome segments and were planted in Fall 2000, Spring 2001, or Summer 2001 in northern Mississippi. Observations were made during spring of each year.

Planting time (T)	Propagule type (P)[z]	Shoot emergence (shoots/m^2) 2001[y]	2002	2003	2004
Fall 2000			19.6 b[x,w]		
Spring 2001			31.0 a		
Summer 2001			22.4 b		
	Nt+N1		30.3 a		
	Nx		24.2 b		
	Nt		18.5 c		
Fall 2000	Nt+N1	27.4 b[x,v]	24.5	34.4 b–e	50.1 c–e
	Nx	17.5 c	16.7	25.3 de	42.5 d–f
	Nt	24.5 b	17.5	21.3 ef	34.2 ef
Spring 2001	Nt+N1	32.6 a	41.7	89.1 a	168.7 a
	Nx	5.9 d	28.0	43.1 bc	84.0 bc
	Nt	28.5 ab	23.4	40.1 b–d	78.3 b–d
Summer 2001	Nt+N1	---	24.8	31.2 c–e	54.9 c–e
	Nx	---	28.0	51.9 b	114.6 b
	Nt	---	14.5	7.0 f	10.2 f
Significance					
T		0.5081	0.0006	<0.0001	<0.0001
P		<0.0001	0.0007	<0.0001	0.0002
T × P		<0.0001	0.0711	<0.0001	<0.0001

[z]Two-node segments consisting of a terminal node and an adjacent 1-year-old dormant node (Nt+N1), one-node segments consisting of a single node, other than a terminal node, of unknown age (Nx), or one-node segments consisting of a single terminal node (Nt).

[y]First year of growth for fall- and spring-planted propagules was Spring 2001 and for summer-planted propagules Spring 2002.

[x]Values in columns followed by the same letter are not significantly different at $P \leq 0.05$. Each experimental unit consisted of 30 propagules.

[w]Means of four replications and averaged across three levels of the other factor.

[v]Means of four replications.

and propagule type were arranged factorially in a randomized complete block design. Year was not included as a repeated measure factor for two reasons. First, treatment combinations could not be arranged in a complete factorial arrangement because of differences in how each propagule type commenced first-year growth. Fall- and spring-planted propagules commenced first-year growth in Spring 2001 whereas summer-planted propagules commenced first-year growth in Spring 2002 (Fig 2). This precluded analyses of year, planting time, and propagule type in a complete factorial arrangement. Second, when 2001 data were excluded and only 2002, 2003, and 2004 data were analyzed, there were significant three-way interactions that unduly complicated interpretation. Significant three-way interactions also occurred when summer-planted propagules were excluded and only fall- and spring-planted propagules were analyzed. The Mixed procedure of SAS v. 8.2 was used for all analyses (SAS Institute Inc., Cary, N.C.).

Results

Mayapple shoots emerged from the ground each year in northern Mississippi during the last two weeks of March. For the entire month of April leaves were mostly green, healthy, and fully expanded. Leaves began to yellow and senesce throughout the month of May, and all shoots had completely senesced by the first week of June (Fig. 2).

Regardless of year, spring-planted Nt+N1 produced significantly greater leaf dry mass ($g·m^{-2}$) and leaf area ($cm^2·m^{-2}$) than any of the other treatment combinations (Tables 1 and 2). Spring-planted Nt+N1 also produced significantly greater numbers of shoots during 2003 and 2004 than any of the other treatment combinations (Table 3, Fig. 2). In contrast, summer-planted Nt produced significantly less leaf dry mass ($g·m^{-2}$) than any of the other treatment combinations in 2004 (Table 1). Summer-planted Nt also produced significantly less leaf dry mass than any of the other treatment combinations except fall-planted Nt in 2003 and significantly less than any of the other treatment combinations except fall-planted Nt and summer-planted Nt+N1 in 2002 (Table 1). Summer-planted Nt also produced significantly less leaf area ($cm^2·m^{-2}$) than any of the other treatment combinations except fall-planted Nt in 2003 and 2004 (Table 2). Leaf area of summer-planted Nt could not be determined in 2001 and was not measured in 2002. Summer-planted Nt produced fewer numbers of shoots than most of the other treatment combinations in 2003 and 2004 (Table 3).

Results were slightly different from that described above when leaf dry mass and leaf area data were analyzed on a per shoot basis rather than on a per area basis. Fall-planted propagules produced significantly greater leaf area (cm^2/shoot) and leaf dry mass (g/shoot) in 2003 and 2004 than spring- or summer-planted propagules (Tables 4 and 5). Propagule type did not affect leaf dry mass (g/shoot) in 2004, but Nt+N1 and Nx propagules produced significantly greater leaf dry mass in 2003 than Nt propagules (Table 4). In 2002, spring-planted Nt+N1 and fall-planted Nx produced significantly greater leaf dry mass than any other treatment combination except fall-planted Nt+N1. Leaf dry mass was not recorded in 2001. Nt+N1 produced significantly greater leaf area (cm^2/shoot) than Nx or Nt in 2004 and significantly greater leaf area than Nt in 2001 and 2003 (Table 5). Leaf area was not recorded in 2002.

Discussion

Propagule type and planting time interacted to affect subsequent plant growth when measured on an area basis (per square meter of growing area). In 2004, after 3 to 4 years of growth and establishment, spring-planted Nt+N1 produced more shoots with greater total leaf area and dry mass than spring-planted Nx and Nt. The superior growth of Nt+N1 was expected due to its greater mass compared to Nx and Nt. In addition, Nt+N1 consisted of two nodes whereas Nx and Nt each consisted of one node. Maqbool et al. (2004) reported superior growth of Nt+N1 compared to Nx after dormant rhizome segments were exposed to increasing durations of low temperature and

Table 4. Leaf dry mass of shoots arising from propagules of the american mayapple. Propagules were one of three types of rhizome segments and were planted in Fall 2000, Spring 2001, or Summer 2001 in northern Mississippi. Observations were made during spring of each year.

Planting	Propagule	Leaf dry mass (g/shoot)			
time (T)	type (P)[z]	2001[y]	2002	2003	2004
Fall 2000		---	0.363	0.810 a[x,w]	1.001 a
Spring 2001		---	0.372	0.588 b	0.606 b
Summer 2001		---	0.178	0.536 b	0.660 b
	Nt+N1	---	0.375	0.707 a	0.816
	Nx	---	0.341	0.674 a	0.718
	Nt	---	0.198	0.553 b	0.732
Fall 2000	Nt+N1	---	0.423 ab[x,v]	---	---
	Nx	---	0.427 a	---	---
	Nt	---	0.240 c	---	---
Spring 2001	Nt+N1	---	0.521 a	---	---
	Nx	---	0.298 bc	---	---
	Nt	---	0.298 bc	---	---
Summer 2001	Nt+N1	---	0.182 cd	---	---
	Nx	---	0.296 bc	---	---
	Nt	---	0.057 d	---	---
Significance					
T		---	<0.0001	<0.0001	<0.0001
P		---	<0.0001	0.0241	0.1108
T × P		---	0.0101	0.2600	0.0890

[z]Two-node segments consisting of a terminal node and an adjacent one-year-old dormant node (Nt+N1), one-node segments consisting of a single node, other than a terminal node, of unknown age (Nx), or one-node segments consisting of a single terminal node (Nt).

[y]Leaf dry mass was not recorded in 2001.

[x]Values in columns followed by the same letter are not significantly different at $P \leq 0.05$. Each experimental unit consisted of 30 propagules.

[w]Means of four replications and averaged across three levels of the other factor.

[v]Means of four replications.

Table 5. Leaf area of shoots arising from propagules of the american mayapple. Propagules were one of three types of rhizome segments and were planted in Fall 2000, Spring 2001, or Summer 2001 in northern Mississippi. Observations were made during spring of each year.

Planting	Propagule	Leaf area (cm^2/shoot)			
time (T)	type (P)[z]	2001	2002[y]	2003	2004
Fall 2000		26.9 b[x]	---	184 a	233 a
Spring 2001		53.7 a	---	133 b	149 b
Summer 2001		---	---	123 b	160 b
	Nt+N1	45.3 a[x]	---	164 a	198 a
	Nx	49.7 a	---	154 a	177 b
	Nt	25.9 b	---	124 b	167 b
Significance					
T		0.0003	---	0.0002	<0.0001
P		0.0098	---	0.0147	0.0191
T × P		0.8602	---	0.1607	0.1139

[z]Two-node segments consisting of a terminal node and an adjacent 1-year-old dormant node (Nt+N1), one-node segments consisting of a single node, other than a terminal node, of unknown age (Nx), or one-node segments consisting of a single terminal node (Nt).

[y]Leaf area was not recorded in 2002.

[x]Means computed from four replications and averaged across three levels of the other factor. Values in columns followed by the same letter are not significantly different at $P \leq 0.05$. Each experimental unit consisted of 30 propagules.

then transplanted to pots in the greenhouse.

In contrast to spring transplant, Nt+N1 transplanted during fall did not exhibit greater growth compared to Nx and Nt. In addition, Nt+N1 propagules transplanted during summer did not exhibit greater growth compared to Nx. This was an unexpected result for the reasons mentioned above, but these results clearly show the interacting influence of planting time and propagule type on subsequent growth and establishment. Results with Nt also exhibited these interacting effects. When initially transplanted during fall or spring, Nt performed as well as any of the other treatment combinations except spring-planted Nt+N1. Growth of summer-planted Nt, however, was poor, producing far less leaf area and dry mass than any of the other treatment combinations. This was expected because Nt propagules harvested during the summer were small and undeveloped. Mayapple rhizome systems in the wild produce new rhizomes during the summer by extending new growth out from the terminal node (Geber et al., 1997). This occurs after shoot senescence in late spring or early summer but before rhizomes become dormant during winter. As a result, terminal nodes harvested in fall and spring were fully developed but when harvested in summer they were small and undeveloped. This may account for the poor performance of summer-planted Nt in this study.

Nt+N1 propagules produced more shoots with greater total leaf area and dry mass when initially transplanted during spring than the same propagule type transplanted during fall or summer. Landa et al. (1992) reported that mayapple rhizomes translocate resources from distal locations within the rhizome system to more proximal locations during spring. The most dominant nodes or buds of the rhizome system then use these resources to support spring growth. As a result, Nt+N1 propagules transplanted during spring may have greater resources for growth and establishment compared to those transplanted during fall or summer.

The effects of planting time and propagule type described above on an area basis did not interact to the same extent when growth was measured on a per plant basis. In 2004, fall-planted propagules produced greater leaf area and dry mass than spring- or summer-planted propagules, and Nt+N1 propagules produced greater leaf area than Nx or Nt propagules. These results appear to indicate that fall-planted Nt+N1 were the most productive treatment combination, but it has already been presented above that spring-planted Nt+N1 produced significantly greater leaf area and dry mass than that of fall-planted Nt+N1. Clearly, larger-sized shoots produced by fall-planted propagules were not sufficient to compensate for their fewer numbers. The reason fall-planted Nt+N1 produced larger plants and spring-planted Nt+N1 produced more shoots is not known. In a somewhat similar manner, spring- and summer-planted Nx produced significantly more shoots than fall-planted Nx (Table 3), though leaf dry mass and leaf area of Nx were not affected by planting time.

Year was not included as a factor in this study, but it is clear that number of shoots, leaf area, and leaf dry mass roughly doubled for almost all treatment combinations from 2003 to 2004 (Tables 1 and 2). This indicates that rhizome segments had established successfully and were producing increasing numbers of growing points and larger shoots.

Comparisons of treatment combinations in this report were arranged by year. Figure 2 shows that fall- and spring-planted propagules were allowed four years of growth and establishment (2001 to 2004) whereas summer-planted propagules were allowed 3 years (2002 to 2004). This confounded analyses of these data by penalizing summer-planted propagules with less time to grow and establish than fall- or spring-planted propagules. These data could have been arranged by growth cycle (growth cycle 1 to 4) instead of year (2001 to 2004). Analysis by growth cycle, however, was equally confounding. Fall- and spring-planted propagules were allowed four growth cycles (1 to 4) whereas summer-planted propagules were allowed three (1 to 3). Therefore, we decided to present these data by year despite the limitations of this approach.

In conclusion, overall plant growth and performance of spring-planted Nt+N1 propagules can be considered excellent and that of fall-planted Nt propagules poor. All other treatment combinations can be considered good.

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