Propagule Type and Planting Time Affect Subsequent Mayapple Growth

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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 planting area). In 2004, spring-planted Nt+N1 produced colonies 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 Deswick, 1985; Lernald 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 dominant apical bud and many dormant lateral buds and leaf scars (Holm, 1899). Nodes of lily-of-the-valley are sometimes referred to as pisps 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 other 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.](image-url)
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).

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 dry mass was not recorded in 2001.

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 time (T) | Propagule type (P) | Leaf dry mass (g m⁻²) | 2001 | 2002 | 2003 | 2004 |
|------------------|-------------------|-----------------------|------|------|------|------|
| Fall 2000        | Nt+N1             | ---                   | 10.4 b | 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 x P            | T x P            |
|------------------|------------------|
| <0.0001          | 0.0005           |
| 0.0001           | 0.0003           |
| 0.0015           | 0.0045           |

| 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. |
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) | Total leaf area (cm²·m⁻²) | 2001¹ | 2002 | 2003 | 2004 |
|------------------|------------------|---------------------------|-------|------|------|------|
| Fall 2000        | Nt+N1            | 880 be¹                    | ---   | 6,930 b | 12,900 bc |
|                  | Nt               | 600 cd                     | ---   | 5,320 bc | 10,600 bc |
|                  | Nt+N1            | 1,920 a                    | 13,700 a | 27,000 a |
|                  | Nt               | 370 d                      | 5,000 bc | 11,500 bc |
|                  | Nt+N1            | 1,090 b                    | 6,390 bc | 13,500 bc |
| Summer 2001      | Nt+N1            | ---                        | 4,410 bc | 10,100 bc |
|                  | Nt               | ---                        | 7,160 b | 17,100 b |
|                  | Nt               | ---                        | 700 d   | 1,590 d   |

Significance

| T     | P     | T × P |
|-------|-------|-------|
| 0.0002 | <0.0001 | <0.0001 |

¹Two-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).
²Leaf area was not recorded in 2002.
³Means of four replications. Values in columns followed by the same letter are not significantly different at P ≤ 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) | Shoot emergence (shoots/m²) | 2001² | 2002 | 2003 | 2004 |
|------------------|------------------|-----------------------------|-------|------|------|------|
| Fall 2000        | Nt+N1            | 19.6 b                      | ---   | 28.3 a | 54.2 bc | 108.7 a |
|                  | Nt               | 31.0 a                      | ---   | 23.4  | 40.1 b–d | 78.3 b–d |
|                  | Nt+N1            | 27.4 b                      | 24.5  | 34.4 b–e | 50.1 c–e |
|                  | Nt               | 17.5 c                      | 16.7  | 25.3 d–e | 42.5 d–f |
|                  | Nt+N1            | 24.5 b                      | 17.5  | 21.3 ef | 34.2 ef |
| Summer 2001      | Nt+N1            | ---                        | 28.3 a | 40.1 bc | 78.3 bc |
|                  | Nt               | ---                        | 59.9 d | 43.1 bc | 84.0 bc |
|                  | Nt+N1            | ---                        | 28.5 ab | 41.0 b–d | 78.3 b–d |
|                  | Nt               | ---                        | 32.1 a | 41.7 | 68.7 a |
|                  | Nt               | ---                        | 41.7  | 89.1 a | 168.7 a |
|                  | Nt+N1            | ---                        | 28.0  | 51.9 b | 114.6 b |
|                  | Nt               | ---                        | 41.5  | 7.0 f  | 10.2 f  |

Significance

| T     | P     | T × P |
|-------|-------|-------|
| 0.5081 | <0.0001 | <0.0001 |

²Leaf area was not recorded in 2002.
³Means of four replications. Values in columns followed by the same letter are not significantly different at P ≤ 0.05. Each experimental unit consisted of 30 propagules.
⁴Means of four replications.

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 significantly greater leaf dry mass (g·m⁻²) and leaf area (cm²·m⁻²) 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 dry mass (g·m⁻²) 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 (cm²·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 (cm²/shoot) and leaf dry mass (g/shoot) in 2003 and 2004 than spring- or summer-planted propagules (Tables 1 and 2). 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 other treatment combinations except fall-planted Nt+N1. Leaf dry mass was not recorded in 2001. Nt+N1 produced significantly greater leaf area (cm²/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.
segments consisting of a single terminal node (Nt).

\[ T \times P \ 0.8602 \ --- \ 0.1607 \ 0.1139 \]
\[ P \ 0.0098 \ --- \ 0.0147 \ 0.0191 \]
\[ T \ 0.0003 \ --- \ 0.0002 <0.0001 \]

clearly show the interacting in
to Nx. This was an unexpected result for the
Nt+N1 propagules transplanted during sum-
Nt+N1 propagules produced more shoots
junction of plant-
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 sum-
er 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 plant-
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-transplanted 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 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. 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 propa-
gules were allowed four years of growth and
establishment (2001 to 2004) whereas sum-
mer-planted propagules were allowed 3 years
(2002 to 2004). This confounded analyses of
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 per-
formance 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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tion of the antiviral activity of Podophyllum

| Planting time (T) | Propagule type (P) | Leaf dry mass (g/shoot) |
|------------------|-------------------|------------------------|
| Fall 2000        | ---               | 0.363 0.810 a\*        |
| Summer 2001      | Nt+N1             | 0.375 0.707 a           |
|                  | Nx                | 0.341 0.674 a           |
|                  | Nt                | 0.198 0.553 b           |
| Fall 2000        | Nt+N1             | 0.423 ab**              |
|                  | 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 ed                |
|                  | Nx                | 0.296 bc                |
|                  | Nt                | 0.057 d                 |

**Significance**

\[ T \times P \]

| T     | P          |
|-------|------------|
|       | <0.0001    |
| <0.0001 |

*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 (Nt), or one-node segments consisting of a single terminal node (Nt).*  
*Leaf dry mass was not recorded in 2001.*

*Values in columns followed by the same letter are not significantly different at \( P \leq 0.05 \). Each experimental unit consisted of 30 propagules.*

*Means of four replications and averaged across three levels of the other factor.*

*Means of four replications.*

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 time (T) | Propagule type (P) | Leaf area (cm²/shoot) |
|------------------|-------------------|-----------------------|
| Fall 2000        | ---               | 26.9 b                 |
| Summer 2001      | Nt+N1             | 45.3 a                 |
|                  | Nx                | 49.7 a                 |
|                  | Nt                | 25.9 b                 |
| Spring 2001      | Nt+N1             | 53.7 a                 |
|                  | Nx                | 50.7 a                 |
|                  | Nt                | 25.2 b                 |

**Significance**

\[ T \times P \]

| T    | P           |
|------|-------------|
| 0.0003 | ---         |
| 0.0098 | 0.0147      |
| 0.8602 | 0.1007      |

*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 (Nt), or one-node segments consisting of a single terminal node (Nt).*

*Leaf area was not recorded in 2002.*

*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.*

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.

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.
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