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Organ preformation in mayapple as a mechanism for historical effects on demography

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Summary

1 The influence of past and current demographic characteristics (shoot type, reproductive condition, leaf size) on future demography were examined in mayapple (Podophyllum peltatum), a forest herb. Mayapple shoots are borne at the terminal ends of rhizome segments (one per segment), are annual, and are either vegetative or sexual. The number and type of shoots emerging next year (t + 1) are determined by developmental events that unfold in the current (t) and prior years (t − 1, etc.). Such protracted organ development is common to many other perennial species.

2 In 1990 (= year t), the growth of new rhizome segments, the success of segments in producing new shoot buds, and the types of shoots in these buds were recorded on plants for which the following data were available: the 1990 (t) shoot type and leaf area, the 1989 (t − 1) and the 1988 (t − 2) shoot types. Natural flower and experimentally induced fruit abortion in 1990 sexuals was also used to evaluate plant responses to reproduction.

3 The outcome of developmental events in year t, affecting shoots in year t + 1, was influenced by current (t) and historical (t − 1, t − 2) factors. Shoot size and reproductive condition in year t affected new rhizome size and growth and the new shoot type. Shoot type in year t − 1 influenced the number of new rhizomes that formed and whether or not branching occurred. Shoot type in year t − 2 had a weak effect on new rhizome growth and size. Thus, a complex and overlapping set of historical and current factors combined to determine future demography. The parallels between the historical influences in mayapple and other forms of carryover and maternal effects are discussed.

4 Reproduction elicited a number of demographic costs, but these were differentially expressed on the number vs. the type of new shoots. Reproduction had little effect on branching but had marked effects on shoot type. This differential sensitivity to reproduction at our site is a function of mayapple’s developmental phenology. Branch determination begins in year t − 1 and is completed by early spring of year t, and so is not affected by fruit costs incurred later in year t. Shoot type determination occurs during fruit fill and is responsive to a plant’s reproductive condition. The implications of our results for studies on the cost of reproduction are discussed.

Keywords: carryover effects, cost of reproduction, preformation


Introduction

Although plants are typically viewed as being highly plastic by virtue of rapid phenotypic adjustments to changes in their external or internal environment (e.g. resource or hormonal status), it is becoming apparent that a plant’s current phenotype and its response to environmental change often reflect historical conditions from prior generations (Roach & Wulff 1987; Bullock, Mortimer & Begon 1993, 1995). Examples
Organ preformation and demography

include maternal effects, in which the maternal environment influences the phenotype of its sexual offspring (Roach & Wulf 1987), and carryover effects, in which the parental shoot environment influences the phenotype of subsequent generations of daughter shoots within a plant (see Bullock et al. 1993). Historical effects can persist for several progeny generations, and may vary with the genotype of the parent (Alexander & Wulf 1985; Schmitt, Niles & Wulf 1992; Bullock et al. 1993, 1995). They have also been shown to condition progeny responses to environmental variation. Because of the impact of historical effects on the ecology and evolution of species (Kirkpatrick & Lande 1989; Schmitt et al. 1992; Bullock et al. 1995), there is considerable interest in the expression of these effects on progeny phenotype and plasticity and in the mechanisms that underlie their expression.

We highlight one mechanism by which historical factors can influence a plant’s future phenotype and its ability to respond to variation in present circumstances. This mechanism involves organ preformation, a phenomenon that is widespread in perennial angiosperms (Foerste 1891; Serensen 1941; Randall 1952; Geber et al., in press). In preformation, the developmental commitment to an organ precedes the organ’s elaboration by several months to several years, and environmental conditions at the time of commitment may differ from those at elaboration. The temporal separation between organ formation and elaboration raises the possibility that historical conditions may have long-term effects on demography and may constrain a plant’s response to subsequent environmental change (Watson et al. 1995).

Here, we address the effect of organ preformation on the demography of mayapple, Podophyllum peltatum (L.) (Berberidaceae), a rhizomatous forest herb. In mayapple, developmental events affecting the number and type of shoots (sexual or vegetative) that will emerge next year take place in the current and previous years. We examine the influence of a plant’s shoot history on two demographically important developmental events that affect next year’s shoot number and type. We also evaluate the ability of plants to respond to changing internal resource (or hormonal) levels brought on by current flowering and fruiting. Demographic responses to reproduction in mayapple and in other species are often manifested through trade-offs between current reproduction and subsequent growth, reproduction, or survival (Sohn & Poliansky 1977; Bell 1985). The expression of demographic costs in the short term is likely to depend on the timing of new organ formation relative to the timing of reproduction. In particular, reproduction can only affect organ production if organs are formed after or at the same time as resource investments in flowering and fruiting, but cannot affect organs that are formed prior to reproductive investments, other than to cause the abortion of these organs. Organ preformation may therefore preclude the expression of short-term demographic costs, and may explain the lack of apparent costs or the variable nature of costs in iteroparous plants. Where organs are formed prior to current reproductive investments, a plant’s short-term demographic response may reflect its prior history as much as it does its current reproductive effort.

Methods

MORPHOLOGY AND DEVELOPMENTAL PHENOLOGY OF MAYAPPLE

Mayapple morphology

Mayapple grows in the forest understory in extensive colonies of shoots consisting of one or more genets (Policansky 1983). Plants maintain long-lived rhizomes composed of a series of segments that remain interconnected for 7–10 years (Fig. 1). We refer to the interconnected segments as a rhizome system.

Each year, an aerial shoot is borne on the terminal (youngest) rhizome segment, while roots are maintained on all segments (Fig. 1). The aerial structure is annual and dimorphic, and is either vegetative or sexual. The vegetative shoot is, more accurately, a peltate leaf that emerges near the apex of the terminal segment (Foerste 1884; Holm 1899). The sexual shoot is a product of the apical meristem of the terminal segment; it is a true shoot composed of two leaves and is terminated by a flower; production of the flower consumes the apical meristem (DeMaggio & Wilson 1986). For convenience, both vegetative and sexual aerial structures are referred to as shoots. A system is considered vegetative or sexual, depending on its current shoot type. A system’s shoot type, and thus its demographic status, can change from year to year.

Above-ground phenology

At our study site, shoots emerge from overwintering buds in late March to early April and senesce by September (Lu 1996). Flowering occurs in May, and fruits mature in June–July. Typically, less than 10% of sexual shoots produce fruit, because of flower or ovary abortion. As in other spring-flowering herbs, mayapple flower buds often abort in response to cold or drought (Smith, Ronsheim & Swartz 1986). Ovary abortion is often due to pollinator limitation (Laverty & Plowright 1988; Whisler & Snow 1992).

Below-ground development of branches and shoot buds

Because events leading to new rhizome and shoot determination span several years in mayapple, we adopt the following notation in describing its developmental phenology: year $t$ refers to the current year; the years preceding and following year $t$ are denoted
as \( t - 1 \), \( t - 2 \), and \( t + 1 \). We are interested in how current \( (t) \) and historical \( (t - 1, t - 2) \) factors affect the number and types of shoots that will emerge above-ground in year \( t + 1 \).

In early May of year \( t \), following above-ground expansion of the current year's shoot from a pre-formed shoot bud, one or more new rhizome segments begin to elongate (Fig. 1). The new rhizome segments arise from axillary buds at the base of the current shoot. These axillary buds were initiated in June of year \( t - 1 \), in the axils of scale leaves that surrounded the current year's preformed shoot bud (Jones & Watson, unpublished data).

Typically, several new rhizome segments begin elongating in year \( t \) but most cease growth at an early stage, and usually only the largest (primary) segment continues to grow to form a new shoot bud (Fig. 1). Branching occurs when one or more secondary segments succeed in forming shoot buds. We refer to a 'successful' secondary rhizome as one that forms a shoot bud; an 'unsuccessful' secondary rhizome begins elongation but fails to produce a shoot bud (Fig. 1).

The determination of vegetative or sexual shoot buds on the new rhizome segments occurs in June of year \( t \). Anatomical studies of rhizome tips reveal recognizable shoots enclosed in scale leaves as early as early June, but more often by mid to late June (Jones and Watson, unpublished data). These preformed shoots then emerge in May of year \( t + 1 \).

**EXPERIMENTAL DESIGN**

The mayapple populations in this study were located in Greene Co. in southern Indiana, USA, in a beech-sugar-maple forest on north and south-west facing slopes (Landa et al. 1992). In the spring of 1990, we followed the growth and shoot determination of new rhizome segments on vegetative systems and three types of sexual systems: those with natural flower abortion, experimental fruit abortion, and fruiting sexuals.

**Shoot type and the timing of flower and fruit failure**

In early April 1990, as shoots were expanding, 6 vegetative and 6–12 sexual systems were selected at random in each of 20 colonies \( (N_{veg} = 120, N_{sex} = 168) \), with the added proviso that shoots within a colony were sufficiently far apart so as not to be connected underground through a prior branching event. Because a large proportion (38%) of the sexual systems aborted flower buds well before anthesis, we did not manipulate flower abortion experimentally, and designated these systems as having 'natural flower abortion' \( (N = 58) \). To promote fruit set in flowering sexuals, we hand-pollinated flowers three times at two-day intervals in early May with pollen from different colonies. On May 23, at a time that corresponded to the period of natural fruit abortion at our site, we manually removed fruits on a random
subset of fruiting sexuals (N = 50), and designated these as having 'experimental fruit abortion'. Experimentally aborted fruit weighed \( \approx 1/10 \) the mass of mature fruit. The remaining sexuals all matured fruit and were designated as 'fruiting sexuals' (N = 60).

**Current resource status and past history of systems:** Developmental events affecting meristem fates are likely to depend on a system's present resource status and its past history. We used the leaf area of the 1990 shoot as an estimate of a plant's current ability to acquire carbon, which is the principal limiting resource for mayapple (De Kroon et al. 1991; Lu 1996). Leaf areas were estimated from allometric functions relating linear dimensions of leaves to their predicted areas: 

\[
A = -45.8 + 0.600D_1D_2 \quad \text{for vegetative shoots (} R^2 = 0.90, \quad N = 39) \]

\[
A = -69.6 + 0.702(D_1D_2 + D_3D_4) \quad \text{for sexual shoots (} R^2 = 0.85; \quad N = 40) \]

\( A (\text{cm}^2) \) is the total leaf area of the shoot (measured on a LiCor area meter, Lincoln, NE, USA); and \( D_i \) are diameters in two perpendicular directions on the single leaf of vegetative shoots and on both leaves of sexual shoots.

Historical factors that may influence subsequent developmental events include a system's demographic status (vegetative vs. sexual, and if sexual, fruiting vs. nonfruiting) and its acquisition of resources in years past. The only way to record historical factors is to follow systems over a number of years (see Lu 1996), and even then, it is not possible to directly ascertain a system's resources without destructive harvests. Failing direct observation, it is still possible to reconstruct a system's history of shoot types from the scars left on old rhizome segments (Fig. 1). When a vegetative shoot senesces, it leaves behind a dormant apical bud at the terminal end of its rhizome segment; this bud is absent on segments that bear sexual shoots, because it is consumed in flower formation. We recorded the shoot types of systems in the two years preceding our experiment (i.e. in 1989 and 1988). This record cannot tell us whether sexual systems fruited in years past, but it does provide information about a system's past leaf area, since sexual shoots are nearly twice as large as vegetative shoots; in addition, if shoot type affects resource acquisition, the record may contain information relating to a plant's resource stores.

**New rhizome growth and new shoot type**

In order to ascertain the influence of historical and current factors on new rhizome elongation, and to understand the relationship between a rhizome's eventual fate and its growth, we measured the lengths of all new rhizome segments at approximately weekly intervals, from mid-April to late July (11 measurements on each segment). The new segments, which grow near the soil surface, were carefully uncovered, measured to the nearest mm, and immediately covered again. In mid-September, the new rhizome segments were harvested and the presence/absence of a new shoot bud, and the type of shoot bud when present, were determined by dissection.

Systems that were damaged by the stem-boring noctuid, *Papainema cerina* (Grote), and by fallen tree branches were excluded from analyses (30% of total). Damage rates did not differ between sexual and vegetative systems; stem borer damage was marginally significantly higher in flower aborted sexuals (38%) compared to other sexuals (26%) \( P < 0.15 \), and may have contributed to flower abortion. Final samples sizes for analysis were 83 vegetative systems, 36 sexuals with natural flower abortion, 34 with experimental fruit abortion and 47 fruiting sexuals.

**DATA ANALYSIS**

**Current demographic status, leaf size and past shoot history**

We use the term 'demographic status' to refer to the condition of the 1990 shoot so as to distinguish between vegetative and sexual shoots, and also among sexuals of differing reproductive condition. We examined whether systems differing in 1990 demographic status differed in leaf area by one-way ANOVA (SAS 1992; procedure GLM), and whether the 1990 demographic status was associated with past shoot types by log-linear analysis (procedure CATMOD).

**Effects of current and past demographic factors on branching and new shoot buds**

The effect of the 1990 demographic status on the likelihood of branching and of sexual shoot bud formation was examined first with log-linear analyses. The analysis of shoot bud type was limited to unbranched systems (N = 152) because there were too few branched systems to permit a formal analysis of their shoot bud fates.

We then examined the effects of a system's past shoot history and of its 1990 demographic status and leaf area on: (1) the number of new rhizome segments that began elongation; (2) on the likelihood of successful branching; and (3) on the likelihood of forming new sexual shoot buds through logistic regression analyses (procedure LOGISTIC; Trexler & Travis 1993). The number of new rhizome segments that began elongation was treated as an ordinal variable as it had only three levels (1, 2, 3); branching and new shoot bud type were treated as categorical variables. All independent variables, except for 1990 leaf area, were also categorical variables.

Because a statistical (and biological) association exists between the 1990 shoot type (S, V) and shoot types in past years (see Results), current and past demographic states of systems are not independent of one another (Philippi 1989; Shaw & Mitchell-Olids 1993). Our interest was in determining whether his-
historical factors \((t - 1, t - 2)\) could account for variation in future demography \((t + 1)\) above and beyond the effects of the current state \((t)\) of mayapple systems. We therefore performed a series of logistic regressions in which factors were added sequentially to models, beginning with current factors and proceeding on to historical factors. Thus, the first model included only the effect of mayapple colony (Table 1). This variable was included because leaf area was found to differ among colonies (see Results). Model 2 included both colony and 1990 leaf area; leaf area served to distinguish between sexual and vegetative systems and thus tested the effect of the 1990 shoot type on the dependent variables. Model 3 included colony, 1990 leaf area and demographic status, and was used to test the effect of reproductive condition in 1990 sexual shoots on the dependent variables. Subsequent models included the 1989, 1988 shoot types.

A system’s past shoot types can affect new developmental events in two ways: (1) directly through their influence on the number and growth of new rhizome segments and on the determination of new shoot types, or (2) indirectly through the influence of prior history on the 1990 shoot type, leaf area, and/or reproductive status. In our sequential analyses, any indirect influences of prior history are attributed to 1990 leaf area and demographic status. Direct effects of prior history on new developmental events are considered significant only if they account for variation in the dependent variables that is not already explained by more recent attributes of mayapple systems. We also compared the results of these sequential logistic regressions to analyses in which the effect of each independent variable was tested by adding it to a model that already contained all other independent variables. Significance tests from both sets of analyses gave similar results, indicating that the order in which variables were entered into the model did not affect the assessment of significance. We only show results of the sequential analyses.

Sample sizes were too small to test simultaneously for all two-way interactions among different years’ shoot types and for higher order interactions. We tested the effect of each two-way interaction separately by comparing the log-likelihood of a model containing the main effects but omitting the interaction, to a model that also contained the interaction. None of the pairwise interactions was statistically significant \((P > 0.3\) in all cases).

**Effects of new rhizome fate, current and past demographic factors on new rhizome growth**

We analysed the growth of new secondary and primary rhizome segments by repeated measures analysis of variance (procedure MIXED). The weekly length measurements served as the repeated measure. An autoregressive covariance structure was assumed since rhizome length measured at one time may be auto-correlated with length measured at a subsequent date. We examined the effects of current and past demographic factors on new rhizome growth. We also included the fate of a new rhizome segment (e.g. successful vs. unsuccessful secondary rhizome; sexual vs. vegetative shoot bud) as a variable in our analyses, because rhizome fate may be related to rhizome growth during the season. The effects of the independent variables on average rhizome length were tested as between-subject effects; seasonal changes in average rhizome length were tested as a within-subject effect of Time; effects of the independent variables on the seasonal pattern of rhizome length were tested as within-subject interactions between Time and main effects.

As in the logistic regressions, we were confronted with the problem of covariation among the independent variables and the effect of covariation on the attribution of effects. We adopted a sequential analysis in which the significance of a factor was assessed by the reduction in the residual Sum of Squares when the factor was added to a model that did not include it. This type of sequential analysis (type I

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**Table 1** Sequential models used to test the effects of successive yearly attributes of mayapple systems on developmental events affecting future demography. The sequence of models on the left was used in logistic regressions of the number of new rhizome segments initiated by a mayapple system (treated as an ordinal variable), on the likelihood of successful branching, and the likelihood of forming a new sexual shoot bud (unbranched systems only). Each model contains not only the factor listed but also all previously listed factors. The effect of each factor was tested by comparing the log-likelihoods of the model containing the factor to the previously listed model. For the repeated measures ANOVA of secondary and primary rhizome lengths, the order of entry of factors into the type I analyses is shown on the left.

<table>
<thead>
<tr>
<th>Model</th>
<th>Factor added to logistic regression analysis</th>
<th>Order of entry of factors in type I repeated measures analyses</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Colony</td>
<td>Colony</td>
</tr>
<tr>
<td>2.</td>
<td>1990 Leaf area</td>
<td>Presence of New Shoot Bud or New Shoot Bud type</td>
</tr>
<tr>
<td>3.</td>
<td>1990 Demographic status</td>
<td>1990 Leaf area</td>
</tr>
<tr>
<td>4.</td>
<td>1989 Shoot type</td>
<td>1990 Demographic status</td>
</tr>
<tr>
<td>5.</td>
<td>1988 Shoot type</td>
<td>1989 Shoot type</td>
</tr>
<tr>
<td>6.</td>
<td></td>
<td>1988 Shoot type</td>
</tr>
</tbody>
</table>

method) is often not advised when there is no a priori rationale for the sequential ordering of factors (Shaw & Mitchell-Olds 1993). In our case, however, there is a good rationale for the ordering of factors: the most recent factors go in first (Table 1).

We compared significance tests based on type I and type III methods of analysis. In the type III method, the effect of a factor is tested by adjusting for all other factors. Type I and type III tests will produce similar results if the covariation among independent variables is not severe. Both methods produced very similar results, and differed in only two tests. We present F-tests for both methods of analysis. F-tests were calculated from type I or type III estimable functions for each main effect (SAS 1992). In a posteriori comparisons of mean rhizome lengths, Bonferroni confidence intervals were used to control for multiple comparisons (Neter, Wasserman & Kutner 1990). We again lacked the sample size to include simultaneously all two-way interactions among years on new rhizome elongation, and could not test for higher order interactions. We examined each two-way interaction separately by including it in the repeated measures analyses. None was statistically significant when tested individually ($P > 0.6$ in all cases).

Results

Past Shoot History of Systems

Systems that were vegetative in 1990 were more likely to have been vegetative in each of the two preceding years (significantly so in 1989) compared to systems that were sexual in 1990 (Table 2). There were no significant differences in the history of shoot types among systems that were sexual but that differed in reproductive status in 1990 (Table 2). In particular, there was no apparent difference in the past history of systems that retained their flowers vs. those that naturally aborted flowers.

Leaf Area in 1990

Vegetative systems in 1990 had significantly smaller leaves than sexual systems (Table 2; 388 vs. 685 cm\(^2\)), but among sexuals, reproductive status was not significantly related to leaf size. This suggests that flower abortion was not attributable to differences in the current size of sexuals, i.e. in their ability to acquire carbon. Because mean leaf size varied significantly among colonies ($F_{1,19} = 3.73, P < 0.0001; \text{range of } 342.6-814.1 \text{ cm}^2$), we included 'Colony' as a factor in subsequent analyses.

Number of New Rhizome Segments and Branching

Branching occurs when multiple segments begin outgrowth and two or more segments form new shoot buds. Systems initiated elongation on 1–3 new segments, but only 20% of the systems branched.

Colonies did not differ significantly in rhizome outgrowth or branching (Table 3). The size of the 1990 shoot had a positive effect on the number of elongating segments, with the number increasing by 0.27 segments per 100 cm\(^2\) increase in leaf area. Branching also increased with the 1990 leaf area (Table 3). The leaf area of branched vs. unbranched vegetative systems differed by 92 cm\(^2\) (20% increase); the leaf area of branched vs. unbranched sexual systems differed by 171 cm\(^2\) (21% increase). There was no significant effect of 1990 demographic status on the number of elongating segments or on branching, above and beyond the direct effect of leaf size (Table 3). Thus, reproductive failure in 1990 sexuals had no significant effect on new rhizome production.

The number of segments that began outgrowth and the likelihood of branching was significantly affected by the 1989 shoot type (Table 3). A larger number of segments began elongating on systems that were sexual vs. vegetative in 1989 (1.63 vs. 1.36 new segments).

<table>
<thead>
<tr>
<th>Demographic status of systems in 1990</th>
<th>1990 Leaf area (cm(^2))</th>
<th>Frequency of sexual systems</th>
<th>Frequency (%) of new sexual shoot buds</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$N$</td>
<td>1989</td>
<td>1988</td>
</tr>
<tr>
<td>Vegetative</td>
<td>83</td>
<td>388 ± 11(^a)</td>
<td>11</td>
</tr>
<tr>
<td>Natural flower aborted</td>
<td>36</td>
<td>682 ± 38(^b)</td>
<td>26</td>
</tr>
<tr>
<td>Experimental fruit aborted</td>
<td>34</td>
<td>685 ± 43(^b)</td>
<td>29</td>
</tr>
<tr>
<td>Fruiting</td>
<td>47</td>
<td>692 ± 36(^b)</td>
<td>25</td>
</tr>
<tr>
<td>$G$ (all systems)(^f)</td>
<td>200</td>
<td>8.31(^f)</td>
<td>7.46(^f)</td>
</tr>
<tr>
<td>$G$ (sexual systems only)(^f)</td>
<td>200</td>
<td>0.12</td>
<td>0.44</td>
</tr>
</tbody>
</table>

\(^f\) Log-linear analyses of variation in demographic history, new branching and new sexual shoot bud formation as a function of 1990 demographic status. Analyses were first performed on all systems, and then on sexual systems separately.

\(^a\) $P < 0.05$, in one case the exact $F$-value is given.
Table 3 Logistic regression analysis of the effects of the 1990 leaf area and demographic status, and of the past history (1988, 1989 shoot type) on the number of new rhizome segments initiated by a system, on the likelihood of successful branching, and the likelihood of forming of a new sexual shoot bud (unbranched systems only) in *Podophyllum peltatum*. $G$ measures the gain in model fit that results when the independent variable of interest is added to a model that contains all previously listed independent variables (see text)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>No. of new rhizome segments</th>
<th>Likelihood of new sexual shoot buds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colony</td>
<td>19</td>
<td>29.38</td>
<td>24.65***</td>
</tr>
<tr>
<td>1990 Leaf area</td>
<td>1</td>
<td>24.90***</td>
<td>16.15***</td>
</tr>
<tr>
<td>1990 Dem. status</td>
<td>3</td>
<td>2.65</td>
<td>0.88</td>
</tr>
<tr>
<td>1989 Shoot type</td>
<td>1</td>
<td>5.09*</td>
<td>3.93*</td>
</tr>
<tr>
<td>1988 Shoot type</td>
<td>1</td>
<td>0.19</td>
<td>0.00</td>
</tr>
<tr>
<td>Full model $R^2$</td>
<td></td>
<td>0.20</td>
<td>0.25</td>
</tr>
</tbody>
</table>

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

This led to more frequent branching in systems that were sexual in 1989 (Table 3). The 1988 shoot type had no significant effect on the number of segments that began outgrowth or on branching.

**SHOOT TYPE DETERMINATION**

Our analysis of new shoot type determination was limited to unbranched systems ($N = 152$), distributed among 20 colonies. The likelihood of new sexual bud formation differed among colonies and was significantly affected by the 1990 shoot size (Table 3). Sexual systems with new sexual buds averaged 30% greater leaf area (724 vs. 550 cm$^2$) than those with vegetative buds. Vegetative systems with sexual buds had 17% greater leaf area (406 vs. 348 cm$^2$) than those with vegetative buds. Among sexuals in 1990, reproductive failure increased the likelihood of sexual shoot bud formation. Systems with natural flower abortion and experimental fruit abortion were more likely to form sexual shoot buds compared to fruiting sexuals (Table 2). Nonfruiting sexuals were also more likely to form sexual shoot buds compared to systems that were vegetative in 1990 (Table 2). The likelihood of forming a sexual bud was not significantly affected by a system’s shoot type in either 1989 or 1988 (Table 3).

**GROWTH OF NEW SECONDARY RHIZOMES**

Seventy-nine systems, in 19 colonies, began outgrowth of more than one new rhizome segment. Variation in the length of secondary segments was analysed by repeated measures analysis of variance. $F$-tests based on type I and type III analyses produced very similar results (Table 4). The main exception was a significant effect of Time (i.e. the average length of secondary rhizomes changes over time) in type I but not in type III analysis. Figure 2 shows the least squares mean lengths of secondary rhizomes as a function of the eventual fate of the rhizome segment (=1991 status; Fig. 2a), the system’s 1990 demographic status (Fig. 2b), and its past history (Figs 2c,d). Least squares means are the expected value of rhizome lengths under a balanced design with the covariate (leaf area) set to its mean value and are based on type III estimable functions (SAS 1992). Each panel illustrates the effect of a system’s shoot type in a given year on the length of new secondary rhizomes, while controlling for the effects of the 1990 leaf area and the shoot types in other years.

Colonies differed in the seasonal pattern of secondary rhizome growth (significant Time × Colony interaction), but not in average length (nonsignificant Colony effect; Table 4). The average length and seasonal pattern of growth of secondary rhizomes was related to their eventual fate (effect of ‘Presence of New Shoot Bud’ and interaction with Time; Table 4). Length differences between successful and unsuccessful secondary rhizomes were striking and emerged very early in the season (Fig. 2a). The average length and growth of secondary rhizomes increased with the leaf area of the 1990 shoot (Table 4). In late July, length increased by $\approx 5.8$ mm per 100 cm$^2$ increase in leaf area. There was some indication that the 1990 demographic status had an effect on the seasonal pattern of secondary rhizome growth (interaction between Time and 1990 Demographic status; Table 4). The effect was statistically significant in the type I but only marginally significant in the type III analysis. Comparisons of least squares mean rhizome lengths indicated that the only significant difference was in the early season growth of rhizomes. During the first
Table 4  F-tests from type I and type III repeated measures analysis of variance of new secondary rhizome lengths in *Podophyllum peltatum*. The presence of a new shoot bud on the secondary rhizome indicates successful branching, whereas the absence of a bud means that a system failed to branch.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>F-tests type I</th>
<th>F-tests type III</th>
<th>Full model $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Between-subjects effects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Colony</td>
<td>18, 53</td>
<td>1.71</td>
<td>1.41</td>
<td>0.69</td>
</tr>
<tr>
<td>Presence of new shoot bud</td>
<td>1, 53</td>
<td>49.07***</td>
<td>43.38***</td>
<td></td>
</tr>
<tr>
<td>1990 Leaf area</td>
<td>1, 53</td>
<td>13.12***</td>
<td>10.06**</td>
<td></td>
</tr>
<tr>
<td>1990 Demographic status</td>
<td>3, 53</td>
<td>0.68</td>
<td>0.74</td>
<td></td>
</tr>
<tr>
<td>1989 Shoot type</td>
<td>1, 53</td>
<td>0.00</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>1988 Shoot type</td>
<td>1, 53</td>
<td>1.06</td>
<td>1.06</td>
<td></td>
</tr>
<tr>
<td><strong>Within-subjects effects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>10, 530</td>
<td>186.20***</td>
<td>0.98</td>
<td>0.69</td>
</tr>
<tr>
<td>Time × Colony</td>
<td>180, 530</td>
<td>1.82***</td>
<td>1.62***</td>
<td></td>
</tr>
<tr>
<td>Time × Presence of new shoot bud</td>
<td>10, 530</td>
<td>47.07***</td>
<td>29.67***</td>
<td></td>
</tr>
<tr>
<td>Time × 1990 Leaf area</td>
<td>10, 530</td>
<td>7.66***</td>
<td>5.55***</td>
<td></td>
</tr>
<tr>
<td>Time × 1990 Demographic status</td>
<td>30, 530</td>
<td>1.64*</td>
<td>1.47*0.06</td>
<td></td>
</tr>
<tr>
<td>Time × 1989 Shoot type</td>
<td>10, 530</td>
<td>0.25</td>
<td>0.28</td>
<td></td>
</tr>
<tr>
<td>Time × 1988 Shoot type</td>
<td>10, 530</td>
<td>1.48</td>
<td>1.48</td>
<td></td>
</tr>
</tbody>
</table>

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

three censuses, secondary rhizomes grew faster on vegetative systems and on sexuals with flower abortion compared to other sexuals. Differences in length at the end of the season, though larger in absolute magnitude, were not statistically significant (Fig. 2b).

**GROWTH OF NEW PRIMARY RHIZOMES IN UNBRANCHED SYSTEMS**

Variation in primary rhizome length was analysed by repeated measures analysis of variance in a model that also included the new shoot bud fate (=1991 shoot type). There were no differences in significance levels between F-tests based on type I and type III analyses (Table 5). Figure 3 shows the least squares mean lengths of primary rhizomes as a function of the rhizome’s eventual fate (Fig. 3a), the system’s 1990 demographic status (Fig. 3b), and its past history (Figs 3c,d).

Colonies differed in new primary rhizome length and in seasonal growth (Table 5). The new shoot bud type and the 1990 demographic status also had

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**Fig. 2** Least squares mean lengths ($±$ SE) of new secondary rhizome segments elongating on *Podophyllum peltatum* systems from April (A) to July (J) 1990 as a function of (a) the rhizome segment’s eventual fate (○, successful secondary rhizome, $N = 42$; ●, unsuccessful secondary rhizome, $N = 37$); (b) the systems’ demographic status in 1990 (□, sexual with natural flower abortion, $N = 22$; △, sexual with experimental fruit abortion, $N = 13$; ▽, fruiting sexual, $N = 24$; ■, vegetative, $N = 20$); (c) the 1989 shoot type (○, sexual, $N = 23$; ●, vegetative, $N = 56$); and (d) the 1988 shoot type (▷, sexual, $N = 17$; ◆, vegetative, $N = 62$).

**Fig. 3** Least squares mean lengths ($±$ SE) of new primary rhizome segments elongating on unbranched systems of *Podophyllum peltatum* from April (A) to July (J) 1990 as a function of (a) the segment’s new shoot bud type (○, sexual, $N = 74$; ●, vegetative, $N = 78$); (b) the 1990 demographic status (□, sexual with natural flower abortion, $N = 24$; △, sexual with experimental fruit abortion, $N = 25$; ▽, fruiting sexual, $N = 35$; ■, vegetative, $N = 68$); (c) the 1989 shoot type (○, sexual, $N = 24$; ●, vegetative, $N = 128$); and (d) the 1988 shoot type (▷, sexual, $N = 23$; ◆, vegetative, $N = 129$).
significant effects on segment length and seasonal growth (Table 5, Figs 3a,b). Segments that formed sexual shoot buds were significantly larger and grew faster than those with vegetative buds (Table 5; Fig. 3a). Flower-abortion of sexual segments while fruiting systems had significantly smaller segments, compared to other systems (Fig. 3b).

The effects of the new shoot type and the 1990 demographic status on seasonal changes in rhizome length are best seen in comparisons of rhizome growth rates. New rhizome segments that formed sexual buds always grew faster than segments with vegetative buds (Fig. 4a). Early in the season and into mid-May, vegetative systems and sexuals with natural flower abortion had higher growth rates compared to other sexuals (Fig. 4b). Sexuals with experimental fruit abortion showed significantly elevated growth shortly after fruit removal compared to other systems (Fig. 4b).

A system's shoot history had no significant effect on the average length or seasonal growth of new segments (Table 5), although there was a marginally significant ($P < 0.05$) influence of the 1988 shoot on the seasonal pattern of new rhizome growth. New primary rhizomes tended to grow faster on systems that were sexual compared to those that were vegetative in 1988 (Fig. 3d).

**Discussion**

We wish to highlight three important messages from this study of branch and shoot determination in may-apple. First, historical attributes of plants can have far-reaching effects on subsequent demography in species that have a protracted developmental program of organ formation. The carryover of historical effects to subsequent demography most likely results both from organ preformation and resource storage, two features that are common to many perennial plants. Secondly, developmental events taking place in any given year, and the demography that unfolds from these events, are actually influenced by a complex of historical and current factors, and these may lead to complex shoot population dynamics. Lastly, a plant's developmental program affects the expression of the demographic costs of reproduction, and knowledge...
of the timing of development should guide the design of experiments aimed at studying these costs.

HISTORICAL AND CURRENT INFLUENCES ON DEVELOPMENT AND DEMOGRAPHY

Historical conditions pertaining to mayapple systems one to two years \((t - 1, t - 2)\) before organs are fully preformed influenced the outcome of developmental events in the year \(t\) in which preformation was completed. These effects were then expressed in the year \(t + 1\) when shoots expanded above ground. Historical influences were evident in the effects of the 1989 \((t - 1)\) and 1988 \((t - 2)\) shoot types on new rhizome growth and branching in 1990 \((t)\) (Tables 3 and 5; Fig. 3).

The direct effect of the 1989 shoot type was limited to the number of new rhizome segments that began outgrowth and that were successful in forming shoot buds in 1990 (Table 3). This effect makes sense in light of what we know about rhizome development (Jones & Watson, unpublished data). The rhizome segments that elongate in 1990 arise from axillary rhizome buds that were formed in 1989. The number of these buds that form in 1989 is thus likely to be influenced by the status of the 1989 aerial shoot. Thus, the carryover effect of the 1989 shoot on developmental responses in 1990 is a result of mayapple's protracted organ preformation.

The direct influence of the 1988 shoot was weak and was confined to the size and growth of new primary rhizome segments (Table 5; Figs 3d), although a similar but nonsignificant association also existed between the 1988 shoot type and secondary rhizome size (Table 4; Fig. 2d). New rhizomes tended to be larger on systems that were sexual in 1988. The most plausible explanation for this effect is that shoot history is related to a system's resource stores. Sexual systems that do not fruit (the typical condition in mayapple) accumulate larger carbon, nitrogen and phosphorous stores compared to vegetative systems (Benner & Watson 1989; de Kroon et al. 1991), and these stores contribute to new rhizome growth one or more years later (Landa et al. 1992). If differences between sexual and vegetative systems in resource stores persist for several years, they may contribute to the differential growth of new rhizomes in later years.

Our results imply that the attributes of plants in one year are carried over into the future demography of plants, through organ preformation and resource storage effects. Resource stores, which are widely recognized as important to the ecology of perennial plants (Chapin, Schulze & Mooney 1990), are likely to be a common source of carryover effects in perennial plant demography. Organ preformation, on the other hand, is a little-appreciated source of carryover effects, in spite of the fact that it appears to be common in plants. For example, in forest herbs in Wisconsin, half of the species preform their flowers (Randall 1952; Geber et al. in press). The extent of preformation can be quite extraordinary. In the genus Trillium, some asiatic species maintain 3–10 years’ worth of preformed flower buds (Samejima & Samejima 1987).

In our study we only considered historical effects of internal plant attributes (i.e. shoot type) on future demography, but it is likely that external environmental conditions can have similar long-reaching effects. Indeed carryover effects between shoot generations in perennial plants, and maternal effects between seed generations, have been observed in response to a wide range of external environmental factors, including the identity and density of competitors (Turkington 1989; Platenkamp & Shaw 1993; Bullock et al. 1995), simulated herbivory (Bullock et al. 1993, 1995), temperature and CO\(_2\) (Alexander & Wulff 1985), soil (Schmid & Dolt 1995), water, light and nutrients (Roach & Wulff 1987; Aarsen & Burton 1990; Bullock et al. 1993, 1995). The net result of carryover effects is to introduce time lags into the dynamics of plant populations (Turnchin 1993). Some striking examples of time-lags are seen in the demography of Frasera speciosa and Agave deserti (Taylor & Inouye 1985; Nobel 1987). Frasera, a montane gentian, and Agave, a desert lily, are both monocarpic perennials in which inflorescences are preformed two or more years in advance of flowering. In both species, peak flowering years for populations occur two or three years after seasons of high moisture availability.

Current attributes of mayapple systems also influenced the outcome of developmental events in year \(t\). These influences were evident in the effects of a system’s 1990 leaf area and, when sexual, in the effects of its reproductive status on many aspects of the development and shoot type determination of new rhizome segments (Tables 2–5; Figs 2b, 3b and 4b). In addition, the eventual fate of a new rhizome (e.g. successful vs. unsuccessful secondary rhizome, sexual vs. vegetative shoot bud on primary rhizome) was clearly linked to its size and growth rate, and differences in size and growth emerged very early in year \(t\) (Tables 4 and 5; Figs 2a, 3a and 4a).

At some level, current influences on development may be viewed as indirect effects of a system’s history (see Methods). For example, systems that were sexual in the past were more likely to be sexual (Table 2) and to have larger leaf areas in 1990 (effect of 1988 shoot type on 1990 leaf area: \(F_{1,188} = 4.20, P < 0.04\); effect of 1989 shoot type on 1990 leaf area: \(F_{1,188} = 15.64, P < 0.0001\)). The correlation between years in mayapple’s demographic status can make it difficult to separate statistically the effects of the current state from those of past states. However, the fact that significance tests were similar in sequential analyses and in analyses that quantified effects by controlling for other factors (e.g. type III method) suggests that the
correlation between the successive states in mayapple was not so strong as to make the attribution of effects unreliable (Philippi 1989; Shaw & Mitchell-Olds 1993). In addition, by adopting sequential analyses, we were conservative in detecting historical effects: the latter were deemed important only when they accounted for a significant amount of variation not already explained by current factors.

In mayapple, a complex and overlapping set of plant attributes spanning several years of a system's existence combined to determine the outcome of developmental events in a given year (see also Lu 1996). We see two important implications of these results. First, the multifaceted nature of historical and current effects may help explain why, in spite of the importance of a rhizome's size to its eventual fate, there is also considerable overlap in the final sizes of successful vs. unsuccessful secondary rhizomes (range of successful secondary rhizome sizes: 11–104 mm; of unsuccessful secondary rhizome sizes: 10–41 mm), and in the final size of primary segments with sexual vs. vegetative shoot buds (range of rhizome sizes with sexual shoot buds: 24–141 mm; with vegetative shoot buds: 16–100 m). This broad overlap in size between rhizomes of differing fate is a consistent feature of mayapple populations (Sohn & Policansky 1977; Benner & Watson 1989; de Kroon et al. 1991; Landa et al. 1992). Second, multigenerational influences on demography may lead to complex shoot population dynamics (see also Bullock et al. 1995). Crane & Taylor (1996) present a parallel case of maternal effects in the annual, Cardamine pensylvanica, where the environment of plants in grand-parental and parental generations may affect population size in the progeny generation and thereby lead to complex cycling dynamics.

DEVELOPMENTAL PHENOLOGY AND THE DEMOGRAPHIC COSTS OF REPRODUCTION

Reproduction in mayapple elicited a number of short-term demographic costs (Table 2; Figs. 3, 4 and 5), but these were differentially expressed on the number vs. type of new shoots that formed. Flowering and fruiting had little effect on branching (= shoot number), but they had marked effects on shoot type (Tables 2–5). The contrasting effects of reproduction on shoot vs. branch fates have been a fairly consistent result in multiyear studies of mayapple at this site (Lu 1996). The only exception has been Lu's finding (1996) of slightly higher branching in nonflowering compared to flowering males in one out of three years of a large demographic study.

The differential sensitivity of branching and shoot fate to reproduction is best explained by a difference in the timing of developmental events leading to these structures. All of our work indicates that the commitment to branch growth is completed by early spring of year t at our study site. As already indicated, the axillary buds from which new rhizome segments elongate in year t were actually initiated in year t − 1 (Jones & Watson, unpublished data), and this explains the effect of the 1989 shoot type on new rhizome initiation and branching in 1990. In addition, experimental manipulations (e.g. fertilization, severing of old rhizomes) that influence the resource status of systems only affect branching if they are performed in early spring of year t. Manipulations performed later in year t have no effect on rhizome initiation or branching (de Kroon et al. 1991; Lu 1996; Geber & Watson, unpublished data). We believe that branching is not responsive to the plant's fruiting status later in the season, and is only occasionally responsive to flowering, precisely because the commitment to branching is made so early in the season.

In contrast, because shoot buds are differentiated during the period of fruit set (Jones & Watson, unpublished data), their fates are affected by the cost of fruiting. This explains why shoot type determination was still responsive to reproduction when fruits were removed as late as May 23: the growth rate of new rhizomes increased shortly after fruit removal (Fig. 4b), and systems with fruit abortion were able to form sexual shoot buds nearly as often as systems that aborted flowers early in the season, and considerably more often than flowering males (Table 2).

Alternative explanations for the differential sensitivity of shoot vs. branch fates to fruit set in mayapple, such as a difference in the resource status of fruiting vs. nonflowering males, or a difference in the resource costs of committing to alternative rhizome fates, do not appear to have great merit. The similarity in leaf size and shoot history between between fruiting and nonfruiting males suggests that all sexuals, regardless of reproductive condition, had similar resources (Table 2). The absence of any significant interaction effect between a system's 1990 demographic status and its prior shoot history on new rhizome fate and growth also suggests that rhizome development in flower-aborted males proceeded as in other males. The cost differential between committing to branching vs. not (if measured in terms of the total length or mass of new rhizomes) was actually greater than the cost differential between committing to a sexual vs. vegetative fate (data not shown); and yet, reproduction had no effect on branching, whereas it did affect shoot fates. Thus, we would argue that reproduction does not affect branching at our site because reproductive investments cannot elicit demographic costs in developmental events (i.e. branch determination) that they follow but only in events (i.e. shoot type determination) that they precede. Thus, the early commitment to branches in mayapples at our site prevents sexual systems from adjusting branch number in response to internal changes brought on by fruiting.

There is evidence of geographical variation in the expression of demographic costs in mayapple. In a
population in central New York, where both flowering and fruiting were experimentally manipulated, costs were similar to those reported in this study: fruit and flower removal had no effect on branching but they did affect shoot fates (Geber et al., in press). By contrast, Sohn & Policansky (1977) reported that fruiting sexuals had significantly fewer new rhizome segments than nonfruiting sexuals in populations in northern Indiana and Tennessee. Population differences in the effect of reproduction on branching could arise if there is geographical variation in the relative timing of branching and fruit set (Geber et al., in press). For example, if branch growth is delayed relative to fruit fill, branching may decrease in response to fruiting, as in Sohn and Policansky’s populations. Indeed, Sohn & Policansky (1977) noted an increase in rhizome segment number in systems that lost fruit in mid-season. Variation in the expression of demographic costs via shoot number vs. shoot type have important demographic and evolutionary implications because these two demographic characteristics represent contrasting modes of propagation in clonal plants: branching affects the rate of clonal spread while shoot composition influences the potential for sexual reproduction (Geber et al., in press).

Our work on mayapple points to the need for understanding the timing of developmental events in plants with preformed organs in order to enable the proper design of experimental studies on the demographic costs of reproduction, and to understand the results of such studies. One finding that is common to many plants with preformation, including mayapple, is that experimental manipulations of reproduction or resources have little impact on plant performance—such as flowering or plant size—in the year that treatments are imposed (Sohn & Policansky 1977; Smith et al. 1986; Lubbers & Lechowicz 1989; Benner & Watson 1989; de Kroon et al. 1991; Fox & Stevens 1991; Rockwood & Lobstein 1994). This is the expected result if preformation limits plants’ abilities to respond within a season to changes in resources. Preformation may also limit plants’ abilities to respond between years to changes in resource status and may explain why, over the short-term, demographic costs to reproduction are small in some species. For example, fruiting in Pinguicula usually results in the production of smaller winter buds but has no effect on next year’s flowering (Karlsson 1986; Karlsson et al. 1990). Fruiting may not affect next year’s flowering in Pinguicula if flower buds are preformed before the current year’s seeds are filled, just as the commitment to branches is made prior to current fruit set in some mayapple populations. Thus, a closer attention to the phenoology of plant development and of resource dynamics may clarify why demographic responses to reproduction vary substantially from study to study, being present in some species but absent in others (Karlsson et al. 1990; Primack & Hall 1990); and, where present, why new vegetative growth is affected in some species (Obeso 1993), new flowering in others (Fox & Stevens 1991), or both activities in yet other species (Snow & Whigham 1989; Primack & Hall 1990; Newell 1991; Syrjänen & Lehtilä 1993).

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References


Sorensen, Th. (1941) Temperature relations and phenology of the Northeast Greenland flowering plants. *Meddelelser om Grønlund*, 125, 1–305.


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