

Effects of forest age and disturbance on population persistence in the understory herb, *Arisaema triphyllum* (Araceae)

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Abstract

Long-lived understory herbs experience a highly dynamic forest over space and time, yet can persist for more than a century. To understand how these populations persist, we examined effects of forest age and disturbance on potential sexual reproduction and clonal growth in the sexually labile perennial, *Arisaema triphyllum*. Potential sexual reproduction (female:male ratio) was significantly greater in the Young and Old-Gap forest states compared with Old, closed-canopy sites, where it was virtually absent. In contrast, clonal growth (estimated by cormlet production) did not differ significantly among the three forest states. Of seven environmental variables measured, only light (positively) and plant density (negatively) contributed significantly to the variation in potential sexual reproduction, while no measured variables contributed significantly to the variation in number of cormlets. The larger sexual reproductive effort (flower+stalk biomass/total biomass) for males in the undisturbed, 100 yr old forest may explain the absence of females in these sites, while the invariant vegetative reproductive effort (cormlet biomass/total biomass) may explain the similarity in average number of cormlets per individual per season across forest states. These results suggest that potential sexual reproduction is resource-limited, while clonal growth may be resource-independent. By maintaining ramet production during unfavorable periods, *A. triphyllum* populations disperse temporally, “waiting” for conditions under which sexual reproduction may resume.

Introduction

Long-lived forest understory herbs experience a highly dynamic environment over space and time, yet can persist for more than a century (Grime 1979; Hairston et al. 1996). Dispersal facilitates escape from unfavorable environments and is likely important to persistence across successional stages. Although dispersal is largely considered a spatial phenomenon, occurring between a parent site and a distinct offspring site, it is recognized that both plants and animals may disperse through time as well. Plants may disperse temporally via seed banks, while some animals disperse temporally through egg banks (Co-

hen 1966; review by Hairston et al. 1996). These forms of dormancy facilitate persistence through the inevitable unfavorable periods.

For understory herbs, the temporally and spatially dynamic forest canopy and forest floor generate highly disparate abiotic and biotic conditions over the course of forest succession. These changes often lead to the demise of some species' local populations and the rise of others (MacArthur and Wilson 1967; Gadgil and Solbrig 1972; Newell and Tramer 1978). Numerous understory herbs, however, straddle these compositional changes, particularly species with the capacity for both sexual and vegetative modes of dispersal (e.g., Holler and Abrahamson 1977; Hughes et

al. 1988; Cain and Damman 1997; Pernon et al. 1997). In understory herbs, sexual reproduction typically facilitates long distance spatial dispersal, while vegetative reproduction (clonal growth) facilitates only local spatial dispersal (Harper 1977; Bell and Tomlinson 1980). However, clonal growth can also preserve an individual genet for decades longer than the lifespan of the original, seed-derived parent (Pitelka et al. 1980; Barkham and Hance 1982), thereby conferring temporal dispersal as well (Eriksson and Kiviniemi 1999; Kudoh et al. 1999). However, only if ramets are independent of their parent (rather than integrated) can clonal growth be considered “temporal dispersal” rather than merely modular growth (Cook 1979).

When both spatial and temporal dispersal are important to persistence, both temporally and spatially dynamic abiotic and biotic factors likely drive the evolution and maintenance of life history traits essential for dispersal, such as different reproductive modes. An important body of literature describes the effects of one to several spatially variable environmental factors on reproductive modes, however these studies rarely focus on a successional (temporally variable) setting (Abrahamson 1975; Holler and Abrahamson 1977; Pitelka et al. 1980; Hartnett 1990; Nishitani and Kimura 1993; Cheplick 1995; Menges 1990; Wijesinghe and Whigham 1997; Kudoh et al. 1999; Sun et al. 2001). Another significant body of literature describes the temporally shifting conditions of old-field transitions, or old-field to closed forest transitions and their effects on reproductive variation. These studies, however, have rarely incorporated the spatial dynamics (disturbance regime) of forests within a temporal category (Newell and Tramer 1978; Pernon et al. 1997; Cain and Damman 1997; Piquot et al. 1998). These spatially-based studies have failed to incorporate the herb’s temporally changing population size, whereas these temporal studies have confounded the canopy and population size changes that occur over time. Moreover, few studies capture the natural scope of environments imposed on a given population (but see Kalisz 1986; Hughes et al. 1988)

Our study uses a forest mosaic comprised of replicated secondary forest (50-yr-old, hereafter called “Young”) sites regenerated from old field, more mature forest (100-yr-old, hereafter called “Old”) sites, and large light gaps within the mature forest (100 yr-old, hereafter called “Old-Gap”) to examine patterns of reproduction in the dramatically different environments encountered by persistent populations of the

sequentially monoecious understory herb, *Arisaema triphyllum* (L.) Schott (Araceae). By including in this examination three rather than just two different forest “states,” we capture the effects of both temporal changes (50-yr-old vs. 100-yr-old forest) and the spatial changes (100-yr-old undisturbed vs. disturbed forest) on population structure and life history traits. To examine changes in dispersal mode over the lifetime of a population, we documented the variation in both population structure and reproductive modes using replicated sites within Young (50 yrs), Old (100 yrs), and Old-Gap (100 yrs) forest states. Bierzychudek (1982) and Lovett-Doust and Cavers (1982) documented wide variation in the sex ratio and clonal reproduction of *A. triphyllum* across different sites. Neither study, however, considered these results in the context of the full spatial and temporal gradient experienced by this understory herb.

This study addressed the following questions: 1) What are the effects of forest age and disturbance state on the frequency of sexual reproduction and vegetative reproduction (clonal growth) in a perennial herb? 2) Which environmental factors are associated with sexual reproduction and clonal growth? 3) Do differences in individual biomass allocation and reproductive effort across forest states explain differences in frequency of potential sexual reproduction and clonal growth? We predicted that if *A. triphyllum* uses spatially-mediated dispersal to persist through unfavorable periods, then sexual reproduction should be the dominant dispersal mode in the closed canopy, Old forest state. Alternatively, if *A. triphyllum* employs temporal dispersal to persist, then clonal growth will be the dominant dispersal mode in the Old forest state. If the latter is true, then canopy disturbance may allow *A. triphyllum* to resume sexual reproduction between periods of only vegetative growth.

Materials and Methods

Study site and species

The study was conducted at the experimental forest of the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland during the spring and summer of 2001. We studied *A. triphyllum* in both 50-yr-old forest stands that developed on abandoned agricultural fields and in mature forest that had no signs of management for 100 years (for aging

methods see Brown and Parker 1994). The 50-yr-old forest canopy was dominated by *Acer rubrum* (L.), *Liriodendron tulipifera* (L.), and *Liquidamber styraciflua* (L.), while *Quercus alba* (L.), *Quercus rubra* (L.), *Fagus grandifolia* (Ehrh.), and *L. tulipifera*, dominated the older forest canopy.

Arisaema triphyllum is a perennial herb found in deciduous forests throughout the eastern United States and Canada (Bierzychudek 1982). Commonly known as Jack-in-the-Pulpit, this sequentially monoecious (gender labile) plant maintains the same sex through a single growing season, but can change sex from year to year, according to the size of the storage organ (corm) prior to senescence (Bierzychudek 1984). Generally, the smallest individuals are immature, intermediates are males, and the largest individuals are females. Monoecious individuals are sterile, and typically account for only 1-5% of a population (Treiber 1980; Bierzychudek 1982). Monoecious individuals were even rarer in the SERC forest, and were not included in the study. The average *A. triphyllum* ramet lifespan is unknown, though likely not more than a decade. A genet, however, may live for over a century (Hairston et al. 1996). The specialist thrips *Heterothrips arisaemae* (Heterothripidae) is the main pollinator of *A. triphyllum* (Rust 1980; Feller et al. 2003). *H. arisaemae* carries pollen only short distances; pollen transfer from male flowers to female flowers is only predictable under 1 m (Rust 1980). Consequently, populations are reproductively isolated since pollen stays within the resident population rather than traveling to distant ones. Moreover, the number of females in a population relative to the number of males will limit the amount of sexual reproduction achieved, and so sex ratio can be used to quantify potential sexual reproduction. *Arisaema triphyllum* also reproduces vegetatively via below-ground cormlets that bud off the parent corm during the growing season. The connection decomposes in the late fall. The ability to reproduce clonally appears to be independent of both size and sex (Bierzychudek 1982).

Design

Within the SERC forest mosaic, three forest states were identified and labeled: Young, Old, and Old-Gap. We chose three replicate sites in the young forest (50-yr-old, called "Young"), five replicate sites in older forest where there were no canopy disturbances

(100-yr-old, called "Old"), and four sites were in older forest in areas where there were high light conditions (100-yr-old, called "Old-Gap") due to either the presence of a canopy gap (2 sites) or proximity to the ecotone between the forest and more open habitats (2 sites). The understory communities that characterized all Old-Gap sites were similar to those in undisturbed Old forest sites. Because all three forest states had regenerated from dairy fields, we were confident that all populations included in our study were comprised only of individuals established after regeneration began. Additionally, few colonization events occurred in the Old forest state over the course of our study (M. Levine, pers. obs.). The closest two sites were located more than 300m apart.

Within each site, one 15-m transect was established through the "center" of each population—where the transect midpoint hit the highest density of individuals. We counted males, females, and immatures in 11 1×1 m quadrats randomly placed along each transect to assess variation in density and sex ratio across the three forest states.

Environmental measurements were also made along each transect to characterize the abiotic variation across these forest states. Four 0.15 m soil cores were bulk sampled at each site, one every 3.5 m along the transects. The samples from each site were combined and analyzed for pH, nitrate (NO_3^-), and phosphorus (P) by the Penn State Agricultural Laboratory (State College, PA). Soil moisture was measured in the field at four randomly chosen points along each transect with a 0.15 m probe of a "Hydrosense" soil moisture meter (Campbell Scientific, USA). The soil moisture measurements were taken in the middle of the growing season—3 d after a typical summer rainfall in late June. Light was quantified as the average global site factor (GSF) of fish-eye lens images per site at three points along each transect. GSF is the proportion of direct radiation (unimpeded light) plus diffuse radiation (scattered below plant canopy light) relative to that in the open. This index was calculated with the Hemiview software, a program that analyzes hemispherical photographic images (Hemiview, 2000).

To quantify patterns of biomass allocation, individuals were collected from two sites in each of the three forest categories. Since one of our objectives was to compare reproductive allocation among forest states, and females rarely occurred in undisturbed mature forest (see Results), only males were used in assessing the variation in sexual and vegetative allocation

and effort. At six sites (2 Young, 2 Old, 2 Old-Gap), 15 males randomly chosen along a 15-m transect parallel to the original, were harvested in early May during anthesis to obtain measures of sexual allocation (biomass of flower and flower stalk) and reproductive effort (biomass of flower and flower stalk/total biomass). Individuals were dried for 4 d until constant weight, and then flower, flowering stalk, and total biomass were weighed separately. Another set of 15 individuals per population was harvested in mid-August, immediately preceding senescence, along a parallel transect. These males were dried, after which cormlets and total biomass were measured for allocation to clonal growth and vegetative (clonal) reproductive effort (cormlet biomass/total biomass). The number of cormlets per individual per site was recorded.

Statistical analysis

A nested analysis of variance (ANOVA) model was used to detect differences in density of sex types (immature, males, females), sex ratio, and average number of cormlets per individual across forest states, with site (population) nested in forest state (Young, Old, Old-Gap). Potential differences in environmental variables among the three forest states were assessed using a multivariate analysis of variance (MANOVA), after which a univariate ANOVA for each significant variable was used to detect differences of each environmental variable among forest states. These environmental variables were then entered into a stepwise regression model, using a backwards selection process to isolate the variables that best explained sex ratio (measure of a population's potential sexual reproduction, 1:1 female:male being 100% potential) and cormlet number (measure of potential vegetative reproduction). Variation in reproductive allocation and effort among forest states was also analyzed with a nested ANOVA (mean site trait nested in forest state) model. All analyses were executed in SAS 8.1 system (SAS 1988), with the exception of the stepwise multiple regression, which was executed in Systat 9.0 (SPSS Inc. 1998).

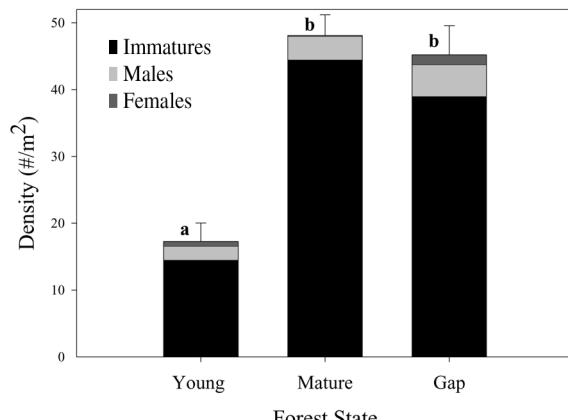


Figure 1. Density (#/m²) of all plants and of each sex-type in three forest states. Error bars are \pm SE of the mean, and refer only to total density. Bars with different letters indicate significant differences between means from a Least Square Difference test for total density.

Results

Demographics across forest states

Densities of the three sex-types (female, male, immature) differed significantly among Young, Old, and Old-Gap forests state (female: $F_{2,9} = 14.28$, $p < 0.0001$, male: $F_{2,9} = 5.50$, $p = 0.005$, immature: $F_{2,9} = 15.21$, $p < 0.0001$ Figure1). Total density of *A. triphyllum* was higher in the 100-yr-old forest sites, both in Old and Old-Gap states ($F_{2,9} = 21.22$, $p < 0.0001$, Figure1). These differences in population size validate our assumption that the forest age likely reflects the population age, i.e., older forests have larger and older *A. triphyllum* populations. We had anticipated this result because all forest states had regenerated from abandoned agricultural fields. The density of immature and male plants was lowest in the Young forest, while female density was lowest in the undisturbed Old forest (Figure 1). The proportion of sexual individuals ((females+males)/total) was significantly greater in the Young and Old-Gap forest as compared to the Old forest state ($F_{2,9}=7.52$, $p=0.0008$).

Potential sexual and vegetative reproduction across forest states

Potential sexual reproduction, quantified by the female:male sex ratio, varied significantly among forest states. (Figure 2A, $F_{2,9}=10.73$, $p < 0.0001$). The sex ratio was extremely low in Old forest (~1:100)

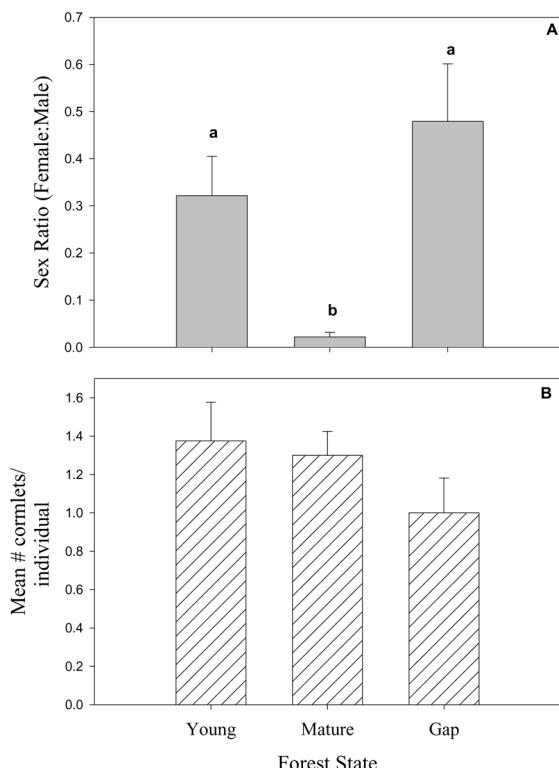


Figure 2. Variation in potential sexual and asexual reproduction. Error bars indicate \pm SE of the mean. Bars with different letters indicate significant differences between means from a Least Square Difference test. (A) Sex ratio (mean # females/m²: mean # males/m²) across three forest states. (B) Mean number of cormlets produced per individual in three forest states.

compared to the sex ratio of Young and Old-Gap forest populations (~1:3; Figure 2A). In the undisturbed Old forest, sexual reproduction was virtually zero because females were extremely rare (~2 per population), and those present had senesced ovaries prior by late anthesis. In the Young and Old-Gap forest, the dramatically higher sex ratio predicts higher potential sexual reproduction.

In contrast to sexual reproduction, clonal growth as estimated by the mean number of cormlets per individual, did not vary significantly across forest states (Figure 2B, $F_{2,5} = 0.35$, $p=0.70$).

Environmental factors among forest states and predicting variation in reproduction

The MANOVA model of all environmental variables measured—light, plant density, soil moisture, P, NO₃, and pH—in the three forest states was significant (Wilks' Lambda: $F_8=3.19$, $p=0.05$). However, only

light, density, and soil P varied significantly across forest states (Table 1). Light levels were significantly higher in the Old-Gap forest than in the Old forest state. Soil P levels were highest and plant density was lowest in the Young forest. Soil NO₃, moisture, and pH did not vary significantly across forest states.

Of the environmental factors that varied significantly across successional forest states, only light ($p=0.001$) and density ($p=0.002$) remained in the model generated by a backwards stepwise regression with sex ratio as the dependent variable ($R^2 = 0.79$, $F_{2,9}=21.99$, $p < 0.0001$). The partial regressions were highly significant. Sex ratio increased with light ($R^2 = 0.83$, $p < 0.0001$, Figure 3A) and decreased with density ($R^2 = 0.77$, $p < 0.0001$, Figure 3B), and there was no significant light x density interaction. Most Old-Gap and Young forest sites occurred in the high light, high sex ratio quadrant (Figure 3A). Young forest alone occurs consistently in the low density, high sex ratio quadrant (Figure 3B). Although soil P varied significantly across forest states, it did not contribute to variation in potential sexual reproduction.

Clonal growth (mean number of cormlets per male individual) did not correlate with any environmental factors that significantly varied across forest states.

Sexual and vegetative allocation and reproductive effort (RE)

Total male plant biomass varied significantly across forest states, lowest in Old forest ($F_{2,3}= 5.84$, $p=0.0041$) and highest in Young and Old-Gap forests (Figure 4A). However, raw allocation to sexual reproduction (flower + flower stalk biomass) and to clonal growth (dry weight of cormlets) did not vary significantly ($F_{2,3} = 0.30$, $p = 0.74$, $F_{2,3} = 1.52$, $p = 0.18$, respectively; Figure 4A). Consequently, the reproductive effort (reproductive biomass/total biomass) for sexual reproduction significantly differed across the three forest states ($F_{2,3}=10.73$, $p < 0.0001$; see Figure 4B). Male sexual reproductive effort in the Old forest sites, the most unfavorable environment (low light, high density) for *A. triphyllum*, was significantly higher compared to either Young or Old-Gap sites (Figure 4B).

To test the hypothesis that high male reproductive effort underlies the extremely low frequency of females in Old forest, we compared the sizes of randomly chosen males to the largest immature individuals (i.e., the immatures likely to become males the

Table 1. Means \pm SD and results from univariate ANOVAs of all abiotic and biotic environmental variables across three forest states. Moisture and nitrate were arcsin transformed and pH was transformed with the natural log.

Source	Young	Mature	Gap	df	F
Light	0.159(0.05)a,b	0.123(0.02)a	0.182(0.02)b	2	4.57*
Density (#/m ²)	17.27(6.2)a	52.47(11.6)b	45.22(19.2)b	2	5.17*
Moisture	0.76(0.15)	0.74(0.08)	0.65 (0.08)	2	1.09
pH	1.59(0.04)	1.68(0.12)	1.62 (0.07)	2	2.01
P (ppm)	83.67(43.1)a	37.60(4.2)b	26.75(6.2)b	2	7.02**
Nitrate (ppm)	0.17 (0.03)	0.15 (0.03)	0.14 (0.02)	2	0.65

p < .05: *; p < .01**: **

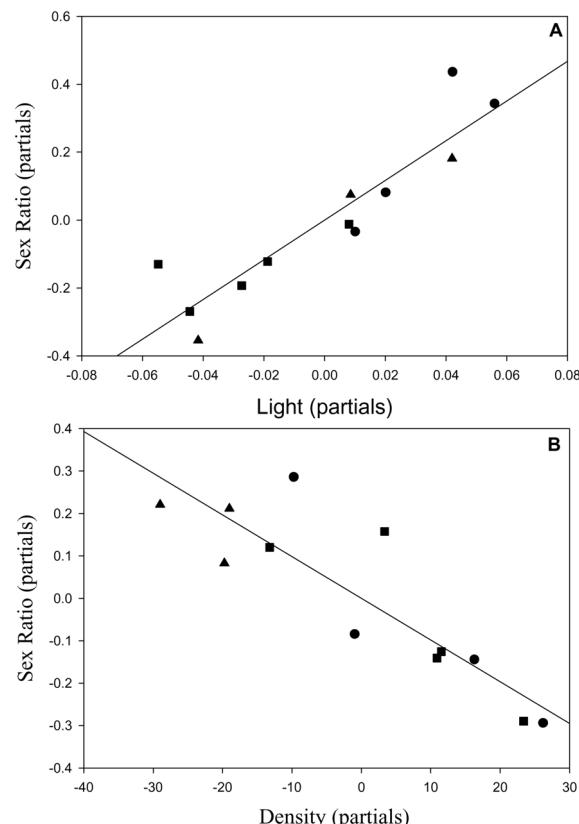


Figure 3. Partial correlations of residuals from backwards step-wise regression of sex ratio and significant environmental variables. Partial correlations show the association of a given explanatory variable and the dependent variable with all other variables held constant. ▲ = Young forest populations; ● = Gap forest populations; ■ = Mature forest populations.

following season) from sites with females (Young and Old-Gap sites) and without females (Old sites). The largest immatures were of similar size in forests with and without females, whereas the randomly chosen males significantly differed across forest states. In forests where females were present (Young and Old-

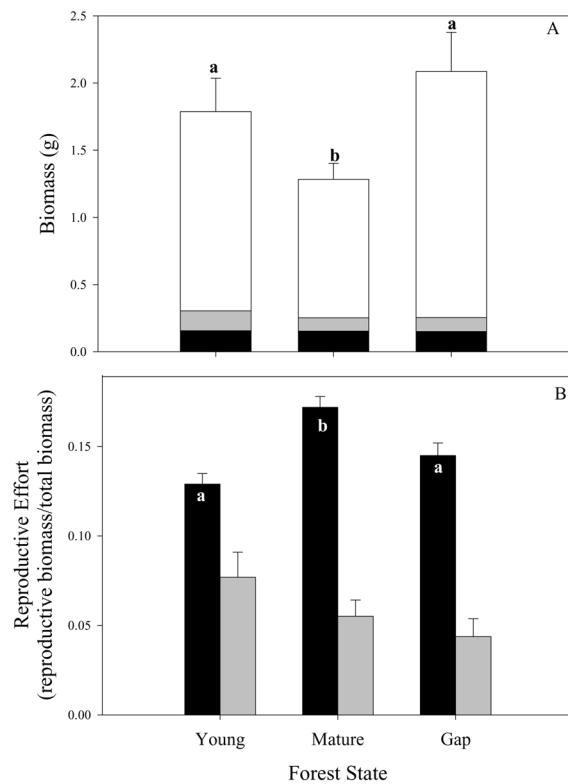


Figure 4. Variation in biomass allocation and reproductive effort. (A) Mean plant dry weight (g) across 3 forest states of total, sexual allocation (flower + flower stalk), and asexual allocation (sum of cormlet mass). □ = total, ■ = sexual, ▨ = asexual; Error bars indicate \pm SE of the total mean weight only. (B) Sexual and asexual reproductive effort (proportion of total biomass allocated to reproduction). ■ = sexual RE, ▨ = asexual RE. Error bars indicate \pm SE of the mean. Bars with different letters indicate significant differences between means from a Least Square Difference test.

Gap), males were significantly larger than immatures ($F_5=16.93$ p < 0.0001). In forest that lacked females (Old), males were of similar sized as immatures

($F_5=1.98$, $p=0.164$). The significant interaction term (forest*sex-type: $F_5=21.34$, $p=0.0007$) indicated that difference in size between these two sex-types is forest-state-dependent.

Vegetative reproductive effort (cormlet biomass/total biomass) did not vary significantly across forest states ($F_{2,5}= 2.02$, $p=0.1412$) and was significantly lower than sexual reproductive effort ($t=6.68$, $p=0.001$, Figure 4B)

Discussion

Relatively few studies of reproductive trait variation in understory herbs have incorporated both a spatial and long-term temporal component to address differences in population structure and reproductive modes. The temporal component captures the changes in both canopy thickness and population size over time, while the spatial component captures changes in canopy thickness and holds population size constant. By using a mosaic of Young, Old, and Old-Gap forest states, we captured reproductive trait variation across both components to reveal how *A. triphyllum* and other long-lived understory herbs might achieve population persistence.

Sexual reproduction

Our data indicate that *A. triphyllum* reproduced sexually only in the Young and Old-Gap forest states and not in the Old. Along the successional gradient, both light (positively) and density (negatively) predicted variation in sexual reproduction. Light was high in the Old-Gap forest while density was low in the Young forest. These data suggest that sex is limited in unfavorable environments. In past studies of *A. triphyllum*, the relatively more balanced female to male sex ratios were also correlated with higher light environments (Lovett-Doust and Cavers 1982; Bierzychudek 1984). These findings are not surprising because femaleness is not genetically determined, but rather correlates with a large corm size produced the prior year (Treiber 1980; Bierzychudek 1984), and light is typically the most important limiting resource for understory herbs (Anderson 1964; Whigham 1974; Thompson and Willson 1978).

Male plant size was significantly larger in the Young and Old-Gap states. Since biomass allocation to male sexual reproduction did not vary, the male sexual reproductive effort (biomass allocated to male

flower/total biomass) was significantly higher in the Old forest. This high reproductive effort may be responsible for the lack of females in the undisturbed, Old forest state, where plants never achieved the threshold size to become female. We subsequently examined this hypothesis and found that the largest immatures were the same size as males in the Old forest, where females were virtually absent. However in the Young and Old-Gap forests, the largest immatures were smaller than the average male. The only difference in energy expenditure between males and the immature individuals is the flower and flowering stalk of males, and this “extra” investment likely explains this difference in size. The inability to achieve a sufficiently large size in the Old forest disabled the transition to femaleness (Bierzychudek 1984). In short, sexual reproduction was constrained in unfavorable environmental conditions where male plants were smaller.

Vegetative reproduction

Vegetative reproduction, measured by mean number of cormlets produced per individual, was similar across the environmentally-variable forest states. Vegetative reproductive effort is lower than sexual reproductive effort in all forest states, suggesting that clonal growth is less expensive. Although the costs of sexual reproduction and clonal growth were not measured directly, the relatively lower biomass demands of clonal reproduction may allow for constant cormlet production regardless of forest state. Moreover, clonal growth appears to be environment-independent. Bierzychudek (1982) found that cormlet production was independent of parent corm size, a finding consistent with the lack of variation in ramet production among the three forest states in our study, despite wide variation in the mean size of parent individuals. However, because we did not follow the fate of the cormlets produced, we have to assume that cormlet mortality does not vary across forest states. It is possible, for instance, that the cormlet mortality is higher in the 100 yr old forest where population density is higher. Indeed such an investigation would strengthen our interpretation of the results.

Long-term persistence by dynamic modes of reproduction

Understory herbs typically occur in all forest successional stages (Grime 1979). The highly disparate en-

vironmental conditions experienced by understory herbs, from favorable in younger forest to unfavorable in more mature forest are known to be associated with different reproductive modes (Newell and Tramer 1978; Pornon et al. 1997; Hughes et al. 1988). In this study, sexual reproduction was associated with lower density and higher light levels; consequently, sexual reproduction occurred in Young forest (low density), ceased in undisturbed Old forests, and then resumed in Old-Gap forest (high light). In contrast, clonal growth, as measured by the number of cormlets produced per individual per yr, did not vary across forest states. Moreover, Young forest populations employed both the sexual and vegetative modes of reproduction, while Old forest populations ceased sexual reproduction but maintained vegetative reproduction (clonal growth). This Old forest population "waits" until the forest canopy is disturbed, and then resumes high levels of sexual reproduction (Kudoh et al. 1999). These findings concur with Hughes et al. (1988), who found that *Aster acuminatus* reproduced only vegetatively in an older (70-yr-old) forest, and showed no change in percent cover over a 4-yr study period; however, a 10-fold increase in frequency of *A. acuminatus* was found in an overstory removal treatment. Under these latter conditions, *A. acuminatus* reproduced both vegetatively and sexually.

Such "temporal dispersal" may also be accomplished by seed banks. To our knowledge, the only study examining this seed dormancy in *A. triphyllum* was Pickett (1913), who found that most *A. triphyllum* seeds germinated with 2-5 mo, suggesting that a seed bank may not play a major role in *A. triphyllum* population dynamics.

This "waiting stage" exhibited by *A. triphyllum* can only be considered an optimal "waiting strategy" (sensu Kudoh et al. 1999) if: 1) recruitment into the closed canopy, Old forest is limited (i.e., low source density, low dispersal, and low seedling survivorship); 2) Survivorship of females is low under the Old forest conditions, and 3) sufficient genetic diversity is maintained during the period of no sexual reproduction (i.e., when females are rare). Since *A. triphyllum* still has no known disperser and rarely any females in neighboring Old forest populations (M. Levine, pers. obs.), dispersal limitation and low source density may limit recruitment (Eriksson and Kiviniemi 1999). Additionally, since seedling establishment in mature forests is typically low for long-lived understory herbs (Tamm 1948; Whigham 1974; Hughes et al. 1988), seed production by females in the mature

(our "Old) forest likely would be futile. Secondly, Lovett-Doust and Cavers (1982) found a strong male-biased sex ratio in their unfavorable sites (similar to our Old forest state) where the probability of a female surviving from one year to the next was 82% versus a 100% probability in the more favorable site (where sex ratio was balanced). Moreover, the Old forest state populations from our study likely have higher survivorship as a result of being all male. In the prevailing environmental conditions where seedling establishment is unlikely and mortality potentially high, the more favorable population structure is possibly in the male-dominated one occurring in the Old forest. Thirdly, significant genetic diversity in a clonal population is likely maintained with even highly infrequent sexual episodes (Silander 1985; Hurst and Peck 1996). Additionally, if *A. triphyllum* maintains a long-lived seed bank, genetic variation may be "stored." This stored variation can contribute to maintaining genetic variation after long periods of only clonal growth (Tonsor et al. 1993); however, there are limits for how long a seed may remain viable while still dormant. As mentioned above, Pickett (1913) found that most *A. triphyllum* seeds germinated in 2-5 mo, while Yang et al. (1997) found in the closely related *Arisaema dracontium*, only 10% of seeds were dormant after one season. The *A. triphyllum* seed bank, if one exists at all, would not likely contribute to the maintenance of genetic variation over these long time periods. Further experimental investigation of these three assumptions is necessary to determine whether the apparent "waiting stage" is indeed an optimal "waiting strategy" for *A. triphyllum*.

The findings from our study suggest that vegetative reproduction is essential for persistence of *A. triphyllum*, and may explain its ubiquity in forests ranging in age from 30 yr to oldgrowth. The between-gap periods (100 yr, Kudoh et al. 1999) are much longer than the lifespan of an *A. triphyllum* individual (likely 10 yr, maximum), but may not be for an individual genet. Since clonal growth is possibly resource-independent (assuming constant mortality across forest states), we suggest that ramet production is critical for surviving the "wait" until the canopy reopens. Therefore, clonal growth likely enables temporal dispersal through the unfavorable periods of infrequent sexual reproduction.

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