An Ecological Life History Study of Uvularia perfoliata L.

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ABSTRACT: The ecology of the hardwood forest herb *Uvularia per-
foliata* L. (Liliaceae) was studied. Most phenological phases in the
species life history were completed or initiated during 3 weeks in March
and April, before closure of the forest canopy. Populations examined con-
sisted of seeds, seedlings, strictly vegetative plants, vegetative plants
which reproduced asexually, and sexually reproductive plants which also
reproduced asexually.

In terms of population dynamics, asexual reproduction was more
important than sexual reproduction. During one growing season, popula-
tion density increased asexually by 95%, which was 18.6 times the in-
crease due to sexual reproduction. Seventy-five per cent of all plants
were within three size classes and 67% of those reproduced asexually.
Cross-pollination was the dominant type of breeding system and a
staphylinid beetle was the pollinator. Ants dispersed the propagules.

Transplant experiments were performed to determine if the reproduc-
tive mechanisms were changed by environmental conditions. There were
significant alterations of population dynamics correlated with micro-
environmental conditions created by the experimental canopy treatments.
At the field-transplant site, where the most severe microenvironmental
conditions were measured, transplants were unable to reproduce sexual-
ly and asexual reproduction was reduced to a very low level. At the pine
site, both mechanisms were significantly altered, but the transplants were
able to successfully complete both phases of reproduction at levels signifi-
cantly below those of plants in the natural populations. At the hardwood
control site, there were no changes of either reproductive mechanism.

INTRODUCTION

Plant species with restricted distributions have been used as in-
dicators of specific conditions, because (1) they are adapted to par-
ticular environments and (2) changes in those conditions cause either
elimination of the species or life history adjustments which significantly
alter the species population dynamics (Becking, 1968; Braun-Blanquet,
1965; Sampson, 1939). As indicator plants, many species of liliaceous
spring-flowering perennials are restricted to climax stages of deciduous
forests in eastern North America. Various aspects of the ecology of
species within that group have been examined (Bazzaz and Bliss, 1971;
Björkman and Holmgren, 1963; Caldwell, 1969; Cantlon, 1953;
Castelli, 1970; Cooper, 1961; Curtis, 1959; Daxer, 1934; Holmgren,
1968; Kawano *et al.*, 1968; Lieth and Ashton, 1961; Rabotnov, 1969;
Rackham, 1966; Randall, 1952 and 1953; Sparling, 1967; Struik,
1965; Struik and Curtis, 1962; Whitford, 1949), but there is still little
information concerning the relationship between life history and pop-

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ulation biology for any one species. This paper reports an investigation of the ecology of *Uvularia perfoliata* L., a liliaceous, perennial indicator species. The objectives of the study were to examine the species life history and population dynamics, determine and quantify mechanisms which enable populations to persist and proliferate in the natural habitat, and to determine how those mechanisms were affected by environmental change.

BACKGROUND INFORMATION

The research sites were part of the Blackwood Division of the Duke Forest which is located in the Piedmont region of North Carolina approximately 7 miles N of Chapel Hill in Orange Co.

The regional climate is classified as warm-temperate, humid (Walter and Lieth, 1967), and, for the last 38 years, the mean temperature was 15.6 C with a mean annual maximum of 21.2 C and a mean annual minimum of 10.0 C. Precipitation during the same period was evenly distributed throughout the year and averaged 1150 mm per year. Peak precipitation months were normally July and August and the least precipitation normally occurred during October and November. Snow or hail occurred almost every year between December and March but accumulations over long periods were rare (U.S. Department of Commerce, 1969-70).

Vanatta (1921) originally described the soils of the study site as Iredell loam, but a more recent survey by the Soils Department of North Carolina State University showed that eight soil types are present. Iredell loam and Enon fine sandy loam are the most widely distributed types, and they are both characterized by very high amounts of clay in the B horizon (Kaster, 1960; Whigham, 1971). As a result of the clay soil horizons and flat topography of the area, surface runoff of water is slight and subsurface drainage is very slow over much of the site. Consequently, a distinct moisture gradient exists and portions of the area are under water for 5-6 months of each year. Plant responses to the moisture gradient have resulted in the segregation of three recognizable climax vegetation types.

A hydric-hardwood oak forest is restricted to the wet end of the gradient and characteristic herb species are: *Ligustrum sinense, Agrostis stolonifera, Arisaema triphyllum, Ilex montana, Ruellia caroliniensis, Aster lateriflorus* and *Leersia virginica. Quercus phellos* is the dominant canopy constituent. Nomenclature follows Radford *et al.*, 1968. The area circumscribed by that vegetation type is non-alluvial even though it is floristically equated with secondary lowland vegetation types as described for the Piedmont of North Carolina by Oosting (1942). A mesic-hardwood oak forest is restricted to intermediate moisture conditions and is characterized by the following species: *Uvularia perfoliata, Thalictrum thalictroides, Chrysogonum virginianum, Obolaria virginica, Monotropa hypopithys, Scleria triglomerata, Hypoxis hirsuta* and *Galium triflorum.* Several species of oaks dominate the canopy and there are distinct shrub and understory tree strata dominated by *Vaccinium* sp., *Cornus florida* and *Acer*

rubrum. On the few upland areas a third vegetation type occurs which is floristically similar to the white oak association described by Oosting (1942). Much of the Blackwood Division is occupied by pine stands in various stages of secondary succession and species characteristic of those stands are common to abandoned fields and pine stands in the southeastern Piedmont region (Keever, 1950; Oosting, 1942; Wells, 1928; and Whigham, 1971). The dominant species is *Pinus taeda,* but there are a few stands where *P. echinata* and *P. virginiana* are important canopy constituents.

Wilbur (1963) reported that *Uvularia perfoliata* occurs "in open to densely forested deciduous slopes or well-drained uplands but occasionally in floodplain or swampy forests and more rarely growing in piney woods or even in meadows or along road or railroad embankments." At the Blackwood Division the species was almost exclusively restricted to the late seral stages of the mesic-hardwood oak forest. A few populations were found in pine stands, but in every case the stands represented late stages in succession and each had a well-developed hardwood understory (Whigham, 1971). Also, those populations were only short distances from populations in the mesic-hardwood oak forest and, in many cases, individuals were distributed continuously between the two areas.

U. perfoliata L. is one of five species in a genus which is endemic to eastern North America (Wilbur, 1963). All species are perennial herbs whose aerial parts die each autumn. *U. perfoliata* has a very short underground stem with prominent, thickened, fleshy storage roots. One aerial stem is produced annually. For convenience, the entire underground portion of the plant will be referred to as a rhizome in this paper.

METHODS

Life history of Uvularia perfoliata.—Three 1m² quadrats were placed in the mesic-hardwood oak forest within each of four naturally occurring populations, and observations of the following phenophases were made during the growing season:

1. (Elongation of terminal bud) when the apical bud began to elongate beneath the litter but before emergence above the litter surface.

2. (Vegetative phase) photosynthetic period of the aerial shoots marked by their emergence above the litter in the spring and death in the autumn.

3. (Leaf expansion) when the first leaf blade became fully expanded.

4. (Anthesis) from the time that the tepals first appeared yellow until they withered and fell from the floral axis.

5. (Fruit maturation) time between the loss of floral parts and capsule dehiscence.

6. (Seed shed) time during which capsules dehisced.

7. (Shoot elongation) the period during which the aerial shoots were growing.

8. (Asexual reproduction) time between the initiation of stolon growth and death of the aerial shoots.

Population structure.—Measurements were made within the 12 quadrats to quantitatively determine the composition of *Uvularia* populations, to measure the species reproductive potential, and to determine characteristics of individual plants. The density of aerial stems, number of sexually reproducing individuals, number of plants which produced mature seeds, number of seeds and number of seedlings were determined. The number of plants which reproduced asexually was also determined for eight of the 12 quadrats and for 23 quadrats (10cm x 10cm) which were also sampled for biomass determinations. Heights of 20 randomly selected plants from each quadrat were measured on five dates during the growing season. Individual plants within 100cm² quadrats were harvested for biomass determinations of aerial stems, parent rhizomes and asexually reproduced rhizomes. Three of the 12 m² quadrats were harvested at the end of the growing season when aerial stem biomass and total underground biomass were determined. Samples were weighed after oven drying at 105 C for 24 hr. To determine the rate at which populations spread, measurements were made of the length of stolons connecting parent plants and the asexually reproduced offspring.

The breeding system was examined by covering plants with nylon mesh before anthesis. This was done to exclude pollinators. Other flowers were emasculated before the stigmas had matured and plants were also self-pollinated. These experiments were performed in the field and repeated in the greenhouse. During the period of anthesis, daily trips were made to the populations to collect pollinators. Seed distribution was studied by observing what happened to the seeds after dehiscence of the capsules and also by performing an experiment to determine if the seeds were transported by animals. In the latter, seeds were dropped through a template either directly onto the litter surface or onto the soil surface after the litter had been removed. The litter was then replaced.

Transplant experiment.—Because the species was restricted to the climax stage of the mesic-hardwood oak forest, a 2x2 factorial experiment was designed to determine what effects different canopy and litter types would have upon the species life history. Three levels of the canopy factor and four levels of the litter factor were used: hardwood, pine and open field (none) canopies; hardwood, pine, field and no litter. All combinations of the two factors were used and there were twelve replications of each experimental treatment. Corresponding to the three canopy types, transplant sites were established in a field, pine forest and mesic-hardwood oak forest. At each site the 20m x 20m plots were subdivided into 400 1m² quadrats and, from the latter, randomly selected quadrats were cleared of all material to the soil surface. The four types of litter were collected and transported to the experimental quadrats where the humus layer was placed on the bare soil surface and then the undecomposed litter was placed on top. An

attempt was made to remove and replace all materials with as little disturbance as possible. *Uvularia* plants, in the overwintering condition, were collected from natural populations and transplanted into the experimental quadrats. Except for density measurements, the same qualitative and quantitative observations and measurements were made on the transplants as described for plants in natural populations. At the end of the growing season the transplants were harvested and analyzed for dry matter production in the manner previously described.

Micrometeorological stations were established to measure daily and seasonal variations in microclimatic conditions at the transplant sites. At each station the following parameters were measured (Whigham, 1971): maximum and minimum air temperatures at 10, 50 and 100cm above the soil surface; soil temperatures at 0-5 and 5-10cm intervals in the soil; solar radiation at the ground surface; soil moisture at 0-5, 5-10 and 10-15cm depth intervals; weekly evaporation, and precipitation.

RESULTS

Life history and phenology.—Seeds were shed in August and the mean number was 4.1 per capsule (range: 1-13). The seeds fell to the ground directly beneath the capsule and most were immediately removed by ants. Ninety-eight per cent of the seeds dropped upon the litter, and 56% of the seeds placed beneath the litter were removed by ants within 3 days. The ants removed the seeds by grasping the aril and then carrying the seeds to their nests. It was apparent that the ants were utilizing the fleshy parts of the seeds, because the arils of those seeds not carried away but wedged into the litter were removed by the ants. Some seeds did not fall from the capsule immediately after dehiscence, and the arils of those seeds dried out within a few days. Then, when the seeds did fall from the capsule, the arils remained in place and were not removed by ants. No other animals were observed removing the seeds.

In the field, seed germination occurred in the spring and the species exhibited a double dormancy mechanism. During the 1st year seedlings produced a root system consisting of one or two main branches. No photosynthetic tissue was produced during the 1st year and at the end of the first growing season the seedlings remained attached to the seeds and consisted of the root system and an apical bud. In the second spring, epicotyl dormancy was broken and an aerial shoot was produced. After the 2nd year of growth none of the seedlings were yet capable of either sexual or asexual reproduction.

Vegetative growth was first observed when the apical buds began to elongate beneath the litter as early as the 3rd week in February. Leaves appeared during the 1st week of April and almost all plants had completed aerial stem growth within 20 days (Fig. 1). Asexual reproduction, indicated by the growth of stolon initials, began at the same time that the apical buds were expanding. The stolons grew centrifugally from the parent rhizomes for approximately 1 month.

After completion of stolon growth, preexisting embryonic buds, formed during the preceding growing season, began to develop at the tip of each stolon. The propagules were established at a mean distance of 20cm from the parent plants. Growth continued until the aerial stems died in late September and early October (Fig. 1), and by the end of the growing season the asexually reproduced rhizomes were as large (.11 ± .01g) as the parent plants (.10 ± .04g). The stolons decomposed during December and January and the mean number of asexually reproduced propagules was 1.5 per plant (maximum was two).

Phenologically, sexually reproductive plants became active at the same time as other individuals in the populations (Fig. 1). Floral primordia had been formed during the previous growing season and, by the time that the apical buds appeared above the litter, the flowers were mature and the yellow tepals appeared at the same time that the first vegetative leaf unfolded. The flowering period lasted for ap-
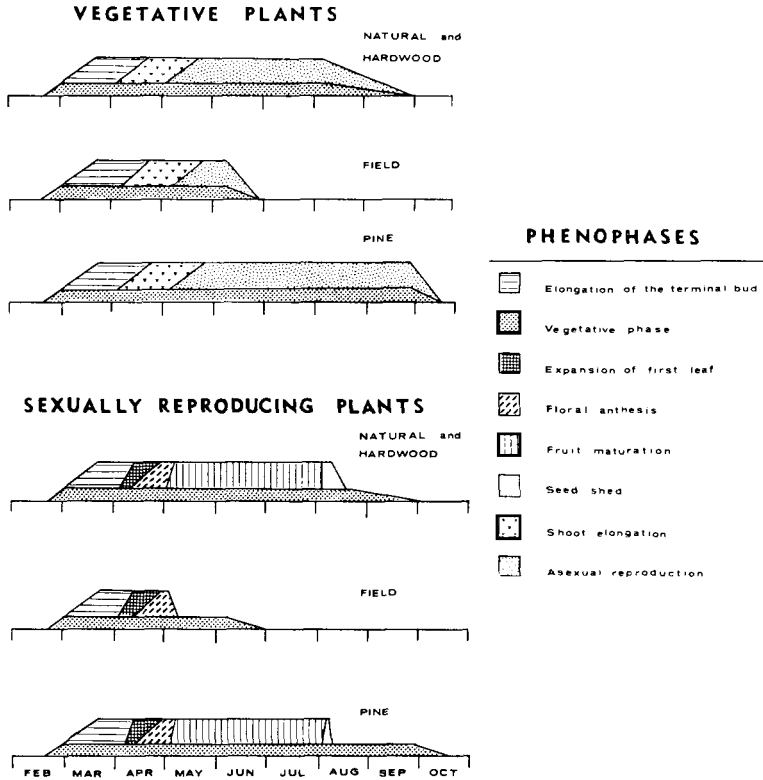

Fig. 1.—Comparative phenological spectra of vegetative and sexually reproductive plants at the three transplant sites and under natural conditions

proximately 2 weeks, and pollination occurred before the flowers were fully expanded.

Outcrossing was the dominant type of breeding system. In field experiments the frequency of self-fertilization was very low (4.8%), and only 3.3% of the bagged plants produced seeds while 90% of the emasculated plants produced seed. In addition, each of the plants which were cross-fertilized in the greenhouse produced seeds while none were produced by self-pollinated plants under similar conditions. Two days after anthesis first began in the populations, flightless insects belonging to the Coleopteran suborder Staphylinidae were collected inside the flowers and on the main stems of sexually reproductive plants. Fruit maturation began immediately, and destruction of developing fruits, by herbivores or natural causes, was extensive, with only 40% surviving to shed seeds. At the end of the growing season the sexually reproductive plants were lost to the populations, with not only the aerial stems but also the underground rhizomes dying.

Population structure.—Mean density within the four populations studied varied from a high of 407 plants/m² to a low of 75/m², with a mean density for all populations of 241/m² (Table 1). Of all individuals examined, 35% did not reproduce either sexually or asexually and the number of plants which reproduced sexually was small in all populations. The number of sexually reproducing individuals varied from 0-20/m² ($\bar{X}$ = 8.3/m²), which represented between 0 and 6.8% of the populations ($\bar{X}$ = 4.6%) (Table 1). The number of asexually reproducing plants was much greater ($\bar{X}$ = 67%) and quite constant (range: 60-70%) (Table 1). Seedling (arbitrarily defined as plants which had no more than three roots) density averaged 11/m². A mean of 12 seeds/m² was produced within the populations studied

TABLE 1.—Population parameters. All values are means for 3 1m2 quadrats sampled within each of four *Uvularia perfoliata* populations

	Plants/m²	% of population with flowers	Flowers/m²	% of population with fruits	Fruits/m²	Seeds produced/m²	Seeds not removed/m²	Seedlings/m²	Percentage of plants reproducing asexually	Number of plants/m² added to population by asexual reproduction	% increase in population size via sexual reproduction	% increase in population size via sexual reproduction A = based on no seed loss	B = based on seed loss
												A	B
Population 1	75	6.7	5	6.7	5	18	4	16	63	71	95	24.0	5.3
Population 2	243	4.5	11	1.2	3	11	4	10	70	255	105	4.5	1.6
Population 3	407	0.2	1	0.2	1	5	0	5	60	366	90	1.2	0.0
Population 4	237	6.8	16	1.7	4	15	5	13	63	224	95	6.3	2.1
Means for all populations	241	4.6	8.3	1.4	3.3	12.3	3.3	11	67*	229	95	5.1	1.4

* Included in calculation of that value was the percentage of plants harvested for biomass analysis

but only three seeds/m² remained after ants had removed those seeds not wedged into the litter.

Individuals were divided into size classes based upon the number of leaves per plant, and the number of plants, height and biomass was determined for each class. Of the plants not reproducing sexually, the greatest number of individuals (32%) had six leaves/plant and the number of plants with five (25%) and seven (22%) leaves/plant was approximately equal. As the number of leaves/plant increased, the height and biomass increased (Figs. 2 and 3). Biomass of plants which reproduced sexually was greater than that of vegetative plants (Fig. 3). Within the five, six and seven leaves per plant classes, 67% of all individuals reproduced asexually. All individuals within the larger size classes also reproduced asexually but they only contained 3.5% of the total number of plants.

Dry weight biomass of individuals was distributed as follows: aerial stems: .08 ± .01g; asexually reproduced rhizomes: .11 ± .01g; parent rhizomes: .09 ± .01g. As indicated by Figure 3, sexually reproductive individuals were much larger (.44 ± .02g) than other plants in the populations (.18 ± .01g). For the populations examined, most of the biomass was underground: aerial stem biomass: 19.4 ± 7.0g/m²; underground biomass: 44.5 ± 12.6g/m².

Transplant study.—Figure 1 shows comparative phenological spectra for plants at the three transplant sites. All of the transplants at the pine and hardwood sites emerged at the same time as plants in natural populations, but the first plants at the field site did not emerge until 5 days later. However, the length of time from the appearance of the first plants until all had emerged was approximately 20 days for all
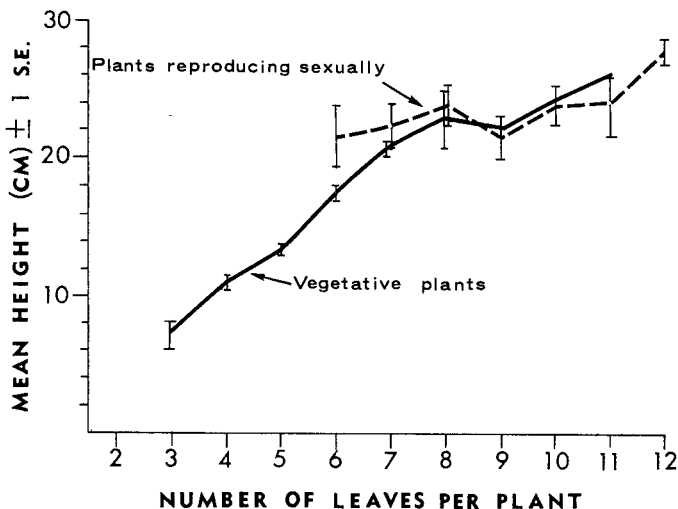

Fig. 2.—Analysis of the composition of sample populations which shows the relationship between plant height and the number of leaves per plant

sites. The length of the vegetation growing season was approximately 7 months for plants in natural populations and at the hardwood site, while the growing season at the field site was reduced by 3 months (Fig. 1). Plants at the pine site persisted longer than any others. Aerial stems of plants at the latter transplant site were green until the 4th week in October, which was almost 1 month longer than plants at the hardwood site and in natural populations (Fig. 1). As stated, the length of the asexual reproduction phenophase was concomitant with that of the vegetative phase (Fig. 1).

Figure 1 also shows comparative phenological spectra for sexually reproductive plants. Elongation of terminal buds, expansion of leaves and anthesis were all the same at the sites except for the slightly later appearance of plants at the field site. Fruits were not produced at the
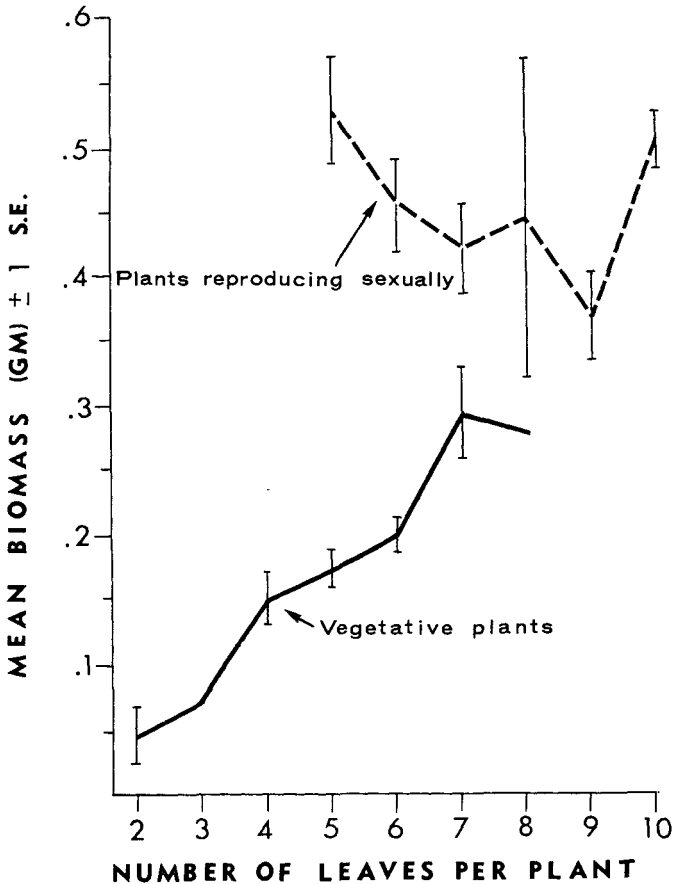

Fig. 3.—Analysis of the composition of the sample populations which shows the relationship between plant biomass and the number of leaves per plant

field site. Asexual reproduction of those plants is not shown on that particular portion of the figure but was similar to that described for vegetative plants.

To determine if there was any correlation between the proportion of plants which emerged (Table 2) and the canopy and litter treatments, data were analyzed using a computer program for categorical data by linear models (Forthofer *et al.*, 1969). There was no canopy-litter interaction but there was a significant correlation between canopy treatment and the number of plants which emerged in the spring (P = .05).

Transplant survival was also significantly (P = .01) affected by the litter treatments. To determine which canopy and litter treatments were causing the observed effects, further comparisons were made and it was found that, at all three transplant sites, significantly fewer transplants emerged from those quadrats where the litter had been removed (hardwood site: P = .01; pine site: P = .01; field site: P = .01) (Table 3). Again, the litter-canopy interaction was negligible (P = .30) but there was a significant effect due to canopy treatments (P = .01) and the response due to litter treatments (P = .35) was not significant. Among the canopy treatments, significantly more plants reproduced asexually under the hardwood canopy than at the field (P = .01) and pine (P = .01) sites (Table 3).

In relation to sexual reproduction, it was difficult to interpret data collected at the transplant sites because of the high variability in numbers of sexually reproducing plants in natural populations. Based upon a preliminary study which showed that 85% of all rhizomes which had terminal buds 1-1.5cm high and 0.5-1cm wide contained floral primordia, one rhizome with an apical bud in that size range was transplanted into each experimental quadrat and each transplant site received equal numbers of rhizomes in which floral primordia

TABLE 2.—The percentages of transplants which emerged for all litter and canopy combinations

Litter treatment	Canopy treatments		
	Field	Hardwood	Pine
Hardwood	96	91	88
Pine	91	98	91
Field	73	86	96
None	38	55	79

TABLE 3.—The percentages of transplants which reproduced asexually

Litter treatment	Canopy treatments		
	Field	Hardwood	Pine
Hardwood	46	66	55
Pine	28	58	53
Field	44	75	34
None	44	50	26

were present. Twenty plants (22%) flowered at the hardwood site while five plants (13.9%) flowered at the pine and field sites. Seeds were produced at the hardwood and pine sites, but none of the transplants at the field site produced seeds. The Staphylinid beetle pollinator was observed at the two forested sites but not in the field.

When aerial stems died back, entire plants were collected from the experimental quadrats. A multivariate analysis (Grizzle and Starmer, 1968) was performed on the three plant-weight components: aerial stems, parent rhizomes and asexually reproduced rhizomes (Fig. 4). For none of the categories was the canopy-litter interaction highly significant, but it was sufficiently close (P = .07) that further analyses were performed. Those investigations failed to aid in the interpretation of the interaction because the multivariate variable differed so much over the course of the experiment. The test for litter treatment
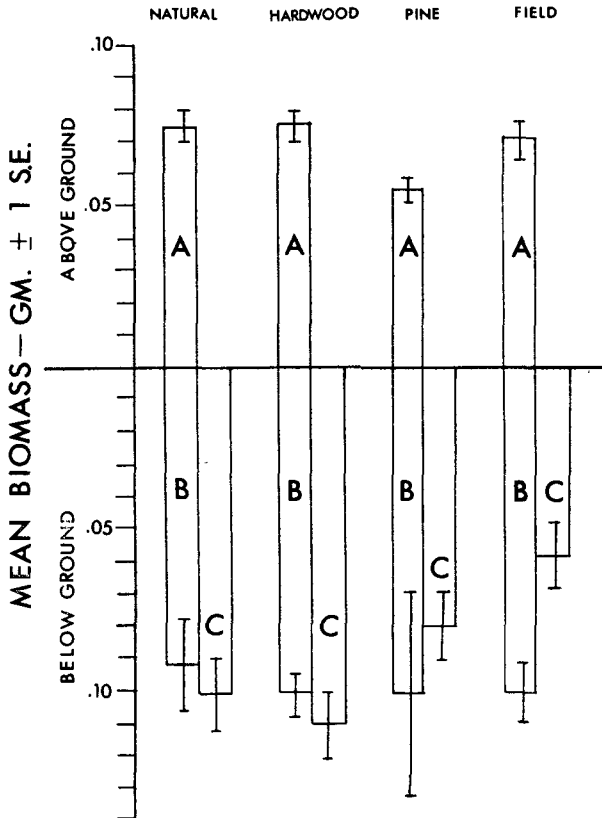

Fig. 4.—Results of the transplant experiment. Biomass, divided into above- and belowground components, is in grams (± 1 Standard Error) for aerial stems (A), parent rhizomes (B) and asexually reproduced rhizomes (C)

showed no significant correlation using the multivariate test (P = .95), and, in addition, there was no correlation for any of the three biomass categories when univariate tests were made (aerial stems: P = .85; parent rhizomes: P = .85; asexually reproduced rhizomes: P = .55). The multivariate test for correlations of canopy treatment and biomass was highly significant (P = .01). Biomass of the aerial stems (P = .05) and asexually reproduced rhizomes (P = .05) was significantly affected by the different canopies while the weight of the transplanted rhizomes was not affected (P = .65). Aerial stems at the hardwood site weighed significantly more than those at the pine site (P = .01) and, although not highly significant, aerial stems of transplants at the field site also weighed more than those at the pine site (P = .10) (Fig. 4). Aerial stems of plants at the field site were not different from those at the hardwood site (P = .55). Mean weight of asexually reproduced growth at the field site was significantly less than that at the hardwood site (P = .05) and pine site (P = .05), while mean weight of that component at the hardwood site was not different from that at the pine site (P = .60) (Fig. 4).

DISCUSSION

As in the case of other species (Curtis, 1959; Daxer, 1934; Morgan, 1971; Randall, 1952), growth and reproduction of *Uvularia* occurred over the very short period of time between the onset of favorable growing conditions and closure of the overhead canopy. Aerial stem growth of most plants was completed within 2 weeks and all. other phenophases, except seed shed, were completed before canopy closure had occurred (Fig. 5). Not only was the species life history closely geared to life history events of other floral components of the community but reproductive success was dependent upon faunal activities. Sexual reproduction, in this part of the species range, was primarily dependent upon successful outcrossing, and a Staphylinid beetle was the only animal observed transferring pollen. When insect activity first began, the *Uvularia* flowers were still half-enclosed in immature vegetative leaves so that the tepals were compressed against the anthers. This caused the beetles to come into contact with the anthers when they moved toward the nectar pouches at the base of the flowers. The pollen adhered to their bodies and was then transferred when the insects visited other flowers in the populations. Randall (1952) has also reported that many spring-flowering herbs are insect-pollinated. Ants were responsible for seed dispersion, and this could explain why individual plants were frequently encountered some distance away from populations. This type of seed dispersion has been observed for other spring-flowering species and many have their seeds dispersed by specialized means, including a conspicuous relationship with ants (Brezinsky, 1963; Curtis, 1959; Randall, 1952; Struik, 1965; Uphoff, 1942). In most cases the animals actively seek the seeds because they are attracted to substances present in the external fleshy parts. In *Uvularia* it was apparent that the ants were attracted to the fleshy

outgrowth on the seeds, for they removed the arils from those seeds which they could not carry away.

Another objective of the study was to determine what mechanisms enabled *Uvularia* populations to persist and proliferate in their natural habitat. Population growth was primarily controlled by asexually reproductive plants in very definite size classes. Seventy-five per cent of all plants in the populations examined had five, six and seven leaves per plant, and 67% of all individuals within those classes reproduced asexually (Table 1). During one growing season, as a result of asexual reproduction, the number of individuals within the populations would be increased by as much as 95%. In comparison, population size would be increased by 5.1% if total seed production was considered and 1.4% if seed losses were considered (Table 1). In most perennial herbaceous plants, because of predation and failure of seedlings to survive competition, there is a high mortality rate for any year's seed crop (Rabotnov, 1969). There are, however, some forest herbs which have a high percentage of seed survival, for Morgan (1917) found that a greater proportion of the seeds of *Hydrophyllum appendicula-tum* survived. Another indication that sexual reproduction is not employed as a means of adding many individuals to the population was the low density of seedlings (Table 1). Asexual reproduction was much more important than sexual reproduction to the success of *Uvularia* populations. First, aerial extension of the populations was primarily due to the growth of asexually reproduced plants at the tips of stolons which grew centrifugally away from the parent plants. Second, whereas it would take several years before a seedling would be
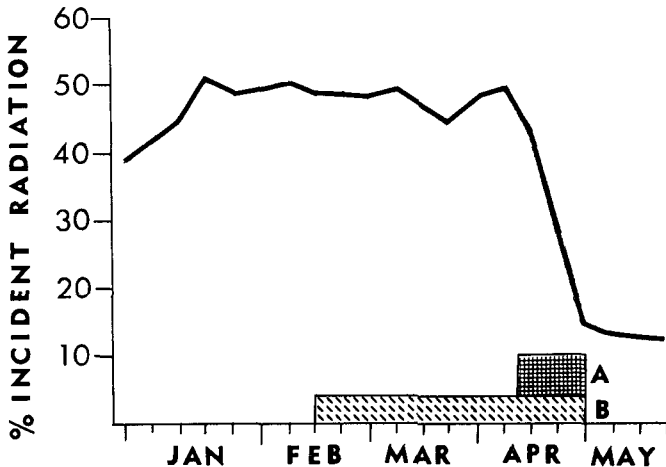

Fig. 5.—Per cent incident solar radiation recorded at the hardwood trans-plant site. The length of time during which the following events occurred is also shown: A — period of canopy leaf development; B — period of *Uvularia perfoliata* growth and reproduction. Refer to Figure 1 for details of which phenophases occurred during that time period

reproductively mature, asexually reproduced plants were as large as parent plants and were themselves capable of reproduction during the following growing season. Many other perennial herbaceous plants develop slowly and several years of vegetative growth occur before the plants are mature enough to reproduce sexually or asexually (Rabotnov, 1969).

Another objective of the study was to determine how the reproductive mechanisms were affected by environmental alteration. Reproduction was affected and the responses were correlated with both experimental canopy and litter treatments. Of the life history alterations observed, three would have significant effects upon the success of the populations.

Successful completion of sexual reproduction was completely suppressed at the field transplant site. Significantly fewer plants produced flowers in the spring and all flowers had withered within less than 1 week after anthesis. Also, no pollinators were observed at the field site, and expansion of the ovary wall of unfertilized flowers, a normal occurrence with unfertilized flowers in natural populations, did not occur at the field site. Those responses were correlated with conditions created by the lack of an overhead canopy. At the pine site, too, fewer plants reproduced sexually, but, unlike the field site, most of the plants which produced flowers produced seeds. The Staphylinid beetles pollinated flowers at the pine site. Significantly fewer plants reproduced asexually at the pine and field transplant sites and those responses were also correlated with conditions created by the pine canopy and lack of canopy at the field site. Biomass production of asexually reproduced rhizomes was also significantly decreased at the pine and field sites.

It is obvious that the life cycle of individual plants could be altered by changes in the microenvironment and that, as a consequence, the mechanisms responsible for maintenance of the species populations would also be changed. The results of this study explain why *Uvularia* populations at the Blackwood Division were not present in earlier successional stages of the mesic oak forest. Under conditions associated with the mesic oak forest, populations would increase and spread centrifugally at the rate of approximately 20cm per year. If the overhead canopy was completely removed, it is doubtful that any population would survive for more than a few years. In 1 year density of a population would be reduced by approximately 50%, sexual reproduction would be completely eliminated and gene recombination, a most important phenomenon if plants are to successfully adapt to new and changing environments, would not occur. Asexual reproduction would also be significantly reduced, and biomass of the asexually reproduced rhizomes produced during the 1st year following disturbance would be smaller and the surviving individuals from that group would not be as successful in reproducing asexually as the original plants were. A population would maintain itself in a mature pine forest, but at a level of reproduction significantly less than the norm. Fewer popula-

tions were found in the pine forests at the Blackwood Division because the populations, if ever present, would have been completely eliminated when the original forest was cut. Also, reinvasion of pine stands from existing populations would be very slow because of the dispersion means exhibited by the species. The species was only infrequently found in the hydric hardwood oak forest. The most salient difference between the latter and the mesic oak forest was that standing water was present in the hydric oak forest for approximately half the year. In a preliminary experiment to determine what effect waterlogging conditions would have upon *Uvularia*, individuals were transplanted into the hydric hardwood oak forest and into greenhouse pots which were maintained under several centimeters of water. None of the plants survived under either of those situations. There may be other factors which would eliminate the species from the hydric oak forest, but conditions associated with the standing water are obviously important.

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