

THE IMPORTANCE OF PREDATION AND SMALL SCALE DISTURBANCE TO TWO WOODLAND HERB SPECIES

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Abstract

The ecology of woodland herbaceous species is reviewed. Many factors affect woodland herbs but there have been few studies of their impacts on long-term patterns. Results from a 10-year study of two species in a deciduous forest in Maryland are presented. Populations of *Cynoglossum virginianum* were influenced by their proximity to tree gap disturbances. Populations of *Tipularia discolor* were primarily influenced by the activities of leaf and corm predators.

Introduction

Information and concepts about the population and community ecology of plants has expanded greatly in recent years (Dirzo and Sarukhan 1984; Givnish 1986; Grime 1979; Harper 1977; Solbrig 1980; Solbrig *et al.* 1979; White 1985). A number of investigations have focused on herbaceous and woody species in forests and various aspects of their ecology have been studied (Brewer 1980; Cook 1985; Davison and Forman 1982; Good and Good 1972; Hough 1965; Kawano 1985; Kawano *et al.* 1982; Nakagoshi 1985; Nakashizuka and Numata 1982; Newell *et al.* 1981; Pitelka and Ashmun 1986; Shorina and Smirnova 1985; Solbrig *et al.* 1980; Tamm 1972; Traczyk and Traczyk 1977; Werger and Van Laar 1985). A brief summary of our current understanding of the ecology of woodland species follows:

Life history strategies

Kawano and his colleagues have published a series of articles and provide a thorough analysis of life history strategies and biomass allocation patterns of herbs in temperate forests. Kawano (1985) has recently summarized his work and suggests that life history characteristics of the groups that he has identified are primarily influenced by variations in yearly environmental factors associated with temperate forests. Others (Bratton 1976; Shorina and Smirnova 1985) have also recognized temporally distinct life history patterns and Bratton suggested that woodland herbs form guilds along microtopographic gradients. Distinct patterns of convergence and a biomechanical basis for the formation of guilds has been described by Givnish (1982, 1986).

Distribution

The distribution of herbs and seedlings of woody species is influenced by many

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factors. The most important appear to be microtopographic gradients (Bratton 1976), the distribution of safe sites (Thompson 1980), and animals which act as seed predators, seed dispersal agents, and herbivores (Culver and Beattie 1978; Hough 1965; Kawano *et al.* 1982; Newell *et al.* 1981; Sork 1984).

Tree gaps

Tree gaps have been shown to be important in many ecosystems (Pickett and White 1985) and it has been proposed that they play an important role in controlling the diversity of understory herbs and seedlings of woody species (Ehrenfeld 1980; Maguire and Forman 1983; Runkle 1984). Recent work, however, has demonstrated that their role is complex and contradictory results have been obtained. Brewer (1980) found that long-term fire disturbance had a greater impact on herb diversity than tree gap disturbances in a Michigan forest. Collins and Pickett (1987) also found that the experimental creation of gaps had little effect on herb cover or species richness. They concluded that the lack of understory response was due to the relatively small size of their gaps (< 150 m²) and/or that plant responses may take a longer time than the period of their study. Davison and Forman (1982) provide some support for this conclusion. Over a 30-year period, the Hutcheson Memorial Forest in New Jersey had undergone a significant change due to an increase in the frequency of gap creation (*i.e.*, more area of the forest was disturbed) caused by drought and gypsy moth defoliation. We will demonstrate in this paper, however, that the population structure of an understory herb species can change dramatically soon after a tree gap is created.

Primary production

Biomass production of understory herbs varies spatially (Kawano 1985) and temporally. Reasons for spatial variations are not clear although microtopographic and resource heterogeneity are undoubtedly important (Bratton 1976). Yearly differences in aboveground biomass have been shown to vary with weather conditions (Rogers 1983) but the long-term impacts of those variations are unknown.

Age and size class distribution

Most populations of understory species are relatively stable over long periods of time (Falinski 1986; Inghe and Tamm 1985) even though annual mortality and natality rates can be high (Newell *et al.* 1981). Most species have Type I and II Deevey survivorship curves with high mortality of seedlings and decreasing mortality with increasing age or size (Kawano *et al.* 1982). Development from seedling to reproductive (sexual or asexual) stages is usually a slow process (Shorina and Smirnova 1985).

Competition

There is little evidence for inter- or intraspecific competition (Bazzaz and Bliss 1971; Rogers 1985) even though many species are clonal and can form dense

stands (Cook 1985; Pitelka and Ashmun 1985; Sobey and Barkhouse 1977; Whitford 1949). It has been suggested that understory plants can avoid competition by asexually spreading over the forest floor or by increasing rates of ramet mortality and natality in order to maintain optimum population density for given levels of environmental resources (Pitelka and Ashmun 1985). Herbs do, however, appear to influence reproduction of tree seedlings (Maguire and Forman 1983).

Reproduction

The majority of woodland species are perennial or pseudo-annual (Kawano 1985; Salisbury 1942) and reproduce by asexual propagation. Only a few species have been shown to rely completely on sexual reproduction (Kawano *et al.* 1982; Muller 1980). Sexual reproduction often has a high energy cost and many individuals often die or decrease in size following flowering (Inghe and Tamm 1985; Kawano 1985).

Physiology

Woodland species have evolved a variety of adaptations to the range of microclimatic conditions that occur in the forest. Most physiological characteristics seem to be related to phenological patterns of the overstory vegetation (Kawano *et al.* 1978) and leaf geometry and morphology has been shown to be important (Givnish 1986). Many clonal species also show a range in physiological integration between ramets (Pitelka and Ashmun 1985).

This introduction is intended to demonstrate that woodland species have evolved many life history characteristics and that we are beginning to compile enough information to draw broad generalities about their ecological implications. It is also clear that the establishment, growth, and maintenance of forest understory plants are influenced by many biotic and abiotic variables and that those variables act over a wide range of spatial and temporal scales. Given all of this complexity, can we predict the long-term fate of any woodland population or community and do the long-term changes in population structure alter ecosystem function? We don't believe that an answer to this question is possible without much more information on the degree of and cause of changes that occur in populations of woodland species. We will use two examples to demonstrate that populations of long-lived woodland species can change significantly in response to herbivory and to small scale disturbance (tree gaps). Our objective is to use these two examples to suggest that we need much more information on factors that are responsible for seedling recruitment and factors that control the rate at which individuals initiate and maintain successful sexual or asexual reproduction.

Methods

The data that we present were compiled as part of a long-term study of plants in a deciduous forest on the Inner Coastal Plain of Maryland. The forest is located

on the property of the Smithsonian Environmental Research Center which is near Annapolis, Maryland. The forest is dominated by a variety of hardwood species and the herb and shrub strata are well-developed (Whigham 1984). Only selected results from the research are presented here as other detailed papers are in preparation.

In 1976 we identified 34 distinct groups (hereafter referred to as populations) of *Tipularia discolor* L. (*Orchidaceae*). It is a winter-green perennial that only rarely reproduces asexually. The annual pattern of biomass and nutrient allocation and pollination ecology have been described (Whigham 1984; Whigham and McWethy 1980) for plants in this forest. For purposes of this paper, it is important to note that each plant normally produces only one leaf and one underground corm per year. The locations of the populations are permanently marked with wire flags. The locations of all individuals within each population are marked with aluminum tags. The number of each plant is written on the tag which is placed on the ground within a few centimeters of the plant. The tags are held in place with aluminum nails that are pushed into the ground. All individuals were monitored yearly and the leaf area measured. When appropriate, we also estimated the percent of the leaf area removed by predators and counted the number of flowers and fruits of sexually reproductive plants. When leaves were not present at the time of the annual census, we determined whether or not the underground corms were present and characterized their status. When the plants were missing completely, we attempted to identify the source of mortality.

Cynoglossum virginianum L. (*Boraginaceae*) is a long-lived summer-green perennial that does not reproduce asexually. Each plant produces a basal rosette of leaves each year and the belowground stem can be quite large. In 1978, we located three populations of *Cynoglossum* and have monitored all individuals yearly. Procedures for marking the plants were similar to those described for *Tipularia*. The number of leaves was counted and percent leaf predation estimated. The number of flowers and fruits produced by sexually reproductive plants were determined and we also counted the number of leaves on each inflorescence. In this paper, we will present data from two populations: one in an area where there have not been any canopy disturbances since the start of the study; the other population is located within an area of disturbance created by the death of a canopy tree in 1980.

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Results

Tipularia discolor

Percent leaf predation is variable from year to year (Fig. 1) but is so high that few plants go for more than two or three years without having their leaves eaten. White-tailed deer are the primary predators and they almost always remove 100% of the leaf tissue. The main impact of leaf predation is to inhibit the plant from increasing in size and we have demonstrated experimentally that either 50% or 100% annual leaf predation results in a significant decrease in plant size and a delay in the frequency of flowering (Whigham unpublished).

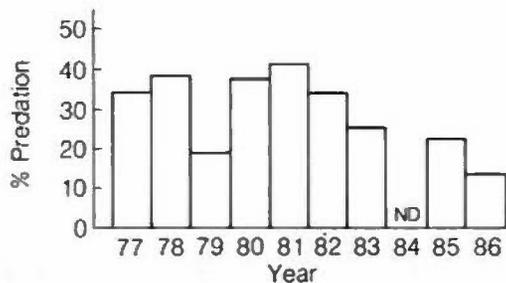


Fig. 1. Percent of all marked plants in populations of *Tipularia discolor* that suffered some amount of leaf predation on an annual basis for a 10-year period. ND indicates that data were not taken.

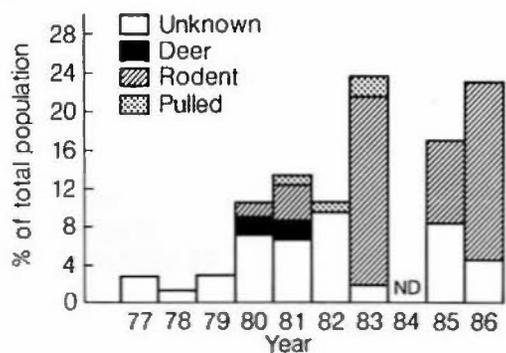


Fig. 2. Mortality of *Tipularia* plants. Sources of mortality are identified by the legend. Deer kill plants by stepping on them or by pulling them out of the ground. Small mammals (rodents) completely eat underground corms of the plants.

Complete predation of plants also occurs and over the 10 years of this study, 12 of the 34 populations have been completely eaten. We have identified two types of mortality associated with deer (stepping on plants and pulling small plants from the soil) and small mammals consume underground corms. Small mammals have accounted for most of the mortality since 1982 (Fig. 2). Mortality due to small mammals has been high in the 1980's, 1982 was a mast year for nut bearing trees in the forest and there was a resultant increase in the density of small mammals (James Lynch, unpublished data). This suggests that the dynamics of *Tipularia* populations may be indirectly controlled by mast cycles of forest trees.

The impact of both types of predation has been to reduce the number of plants being monitored from 159 to 55 over the 10-year period. The size distribution of the populations has also changed over that time as the larger populations have been destroyed or converted into smaller groupings (Table 1).

Cynoglossum virginianum

This species relies completely on sexual reproduction for propagation and suffers very little leaf predation. Only a small number of established plants in the popula-

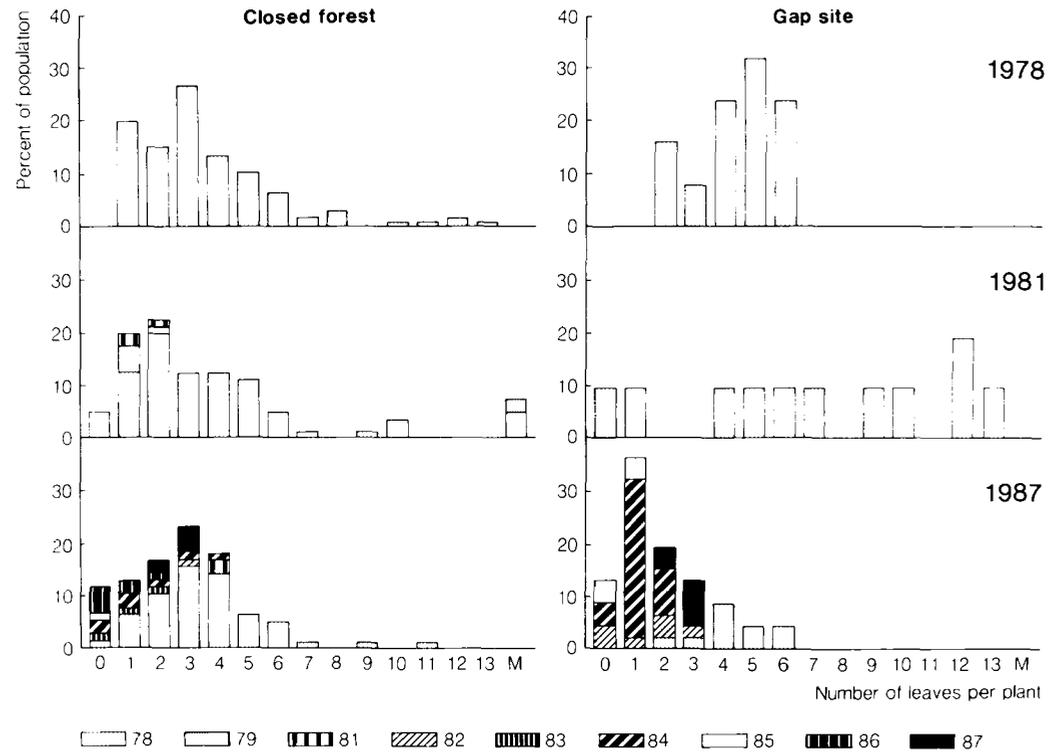


Fig. 3. Changes in the size class distribution of plants in two populations of *Cynoglossum virginianum* in an area where the canopy has remained intact (Closed) and in an area where a tree gap (Gap) was formed in 1980. Years when individuals were recruited into the population are indicated on the legend. M indicates mortality and 0 represents plants that did not produce any aboveground tissue but which were still alive. The horizontal axis is the number of leaves per plant. Data are given for the first year of the study (1978), the first year after the canopy disturbance (1981), and the most recent census year (1987).

Table 1. Eleven year changes in the number of individuals in monitored populations of *Tipularia discolor*. Values across the top of the table are numbers of plants per population. Values in the Table are numbers of populations. Data are only given for the first and most recent years of the study.

Number of plants per population	1	2	3	4	5	6	7	8	9	10	11	...	16
1976	9	5	5	2	2	2	4	3	0	1	0	...	1
1987	9	4	3	3	0	1	0	1	1	0	0	...	0

tions have died since 1978 (Fig. 3). There have been few changes in the size class distribution of the population in the area where the canopy has remained intact but plants in the tree gap area have undergone large changes. Most individuals increased in size after the creation of the tree gap (Fig. 3) and many flowered for approximately three years after which time the 'window-of-opportunity' had passed. The size-class structure of the population then returned to pre-gap form with the exception that the number of seedlings and juveniles had increased. The overall impact of this disturbance had been a three-fold increase in the size of that population, from 14 plants in 1978 to 46 in 1987. During the same time period, the population in the undisturbed area declined from 108 to 77 individuals.

Discussion

Rogers (1985) and Inghe and Tamm (1985) have demonstrated that climatological variables can affect species of woodland plants in forests. Others (Falinski 1986; Kawano *et al.* 1982) have demonstrated the degree of spatial variation that can occur within forests. In this study, we have focused on changes that can occur in established populations of two long-lived species. Leaf and corm predation were the most important factors that affected *Tipularia*. Frequent removal of leaf tissue results in a decrease in plant size and a decrease in the frequency of flowering (Whigham unpublished). Unfortunately, we still know little about the factors that are required for successful establishment of juveniles and there has not been any successful recruitment of juveniles into the populations that we have been monitoring. In contrast, *Cynoglossum* was not affected by predation. It appears to be a species which can persist in the understory for long periods of time without any reproductive activity. When a canopy disturbance occurs near an established plant, it is able to increase size rapidly and begin to reproduce sexually. The period of sexual activity lasted for only a few years in the one population that we have been studying but the size of the disturbance is probably the factor that determines how long that period lasts. Recruitment of juveniles into populations occurs primarily during disturbance events.

The impact of disturbances can be large. In the case of *Tipularia*, entire populations were lost due to corm predation and the total number of plants being studied has decreased by more than 65%. There has not been any seedlings recruitment and reproduction by asexual branching is very slow. In *Cynoglossum*, one population increased in size by a factor of three while the other had a net loss of several individuals even though recruitment of seedlings had occurred. These results

demonstrate the importance of understanding the factors that are responsible for the establishment of new individuals in populations and for the increase in size that enables individuals to either reproduce sexually or asexually. For *Tipularia*, the size of individual plants appears to be primarily controlled by the frequency of leaf predation which tends to cause plants to be smaller. Reproduction in *Cynoglossum* is clearly limited by light and it takes advantage of short-term increases in light availability associated with tree gaps. Similar results have been shown for *Ranunculus repens* L. in a floodplain forest in Poland (Falinski 1986).

These results also demonstrate the importance of knowing more about the establishment requirements of species in the understory (Cook 1979) as seedling recruitment may only occur infrequently in ecosystems with well-established vegetation (Tamm 1972). Similar problems can be identified for herbaceous species in other types of ecosystems (Wells 1981; Willems 1982; Zhang 1983) and especially for rare and endangered species (Harvey 1985). As indicated, over the 11 years of the *Tipularia* research, no new individuals have successfully become established from seed. For *Cynoglossum*, we know that seedlings can become established in both the intact forest and in disturbed areas. Populations are, however, only likely to expand in disturbed areas as mortality has been greater than seedling recruitment in the population in the intact forest.

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