

The Role of Tree Gaps in Maintaining the Population Structure of a Woodland Herb: *Cynoglossum virginianum* L.

DENNIS F. WHIGHAM¹⁾, JAY O'NEILL and MARTIN CIPOLLINI²⁾

Smithsonian Environmental Research Center, Box 28, Edgewater, MD 21037, U.S.A.

Abstract Tree gaps may be important habitats for the establishment and spread of understory herbs in eastern (US) deciduous forests. Data from past studies, however, have not shown any clear patterns for either species diversity or increased percent cover. The lack of clear patterns of response to gaps by herbs may be due to evolutionary differences among species or, in part, due to the fact that most studies have been short-term and long-term patterns have, therefore, not been observed. In addition, few studies have considered the responses of individual genets and/or ramets. We have been conducting a long-term study of *Cynoglossum virginianum*, now in its 16th year, to determine subpopulation and individuals' responses in gap and non-gap habitats. A larger percentage of individuals flowered in the gap subpopulation shortly after it was created. Seed production rates were also higher in the gap subpopulation. The long-term benefits gained by the short-term flowering response have, however, been few as all but two of the seedlings produced within a few years of gap formation have died. In addition, all of individuals that flowered and produced seeds decreased in size and most have remained in the smaller size classes. In addition, only one of the individuals in the gap subpopulation has flowered since the initial flowering response while plants in non-gap subpopulations have flowered and produced seeds throughout the study period. Gaps may only be beneficial to *C. virginianum* if seeds are dispersed into non-gap areas or if seeds can remain dormant in the soil until conditions are more suitable for seedling survival.

Key words: *Cynoglossum virginianum*, deciduous forest, Maryland, tree gaps, woodland herb.

The creation of canopy gaps is an important component of almost all forests (Pickett and White, 1985; Runkle, 1982, 1984, 1985; McCune et al., 1988) and it has been proposed that gaps are "essential for new genotypes and new species to enter plant communities" (Silvertown and Smith, 1988). Canopy gaps clearly allow enhanced light conditions in the understory of most types of forests (Canham, 1988; Canham et al., 1990) and Endler (1993) has shown that gap environments represent two of four distinct types of light habitats in forests (forest shade, woodland shade, small gaps, large gaps). The increase in light quantity beneath gaps has been shown to have a positive effect on photosynthesis (Taylor and Percy, 1976; Wallace and Dunn, 1980) and to increase the reproductive output of woody and herbaceous understory species (Dahlem and Boerner, 1987; McCall and Primack, 1987; Niesenbaum, 1993). There appear, however, to be few paradigms that explain how species will respond to canopy gaps in a particular type of forest.

Most studies have focused on the invasion of woody species into gaps and the wide variety of responses that have been noted range from almost no invasion in small gaps (Hibbs, 1982; Ehrenfeld, 1980) to the maintenance of species richness and evenness by the establishment of shade tolerant and intolerant species in small and/or large gaps (Barden, 1980; Runkle, 1982). Fewer authors have considered the role of gaps in maintaining the diversity of understory herbaceous species in forests but, in general, they appear to be relatively unimportant even though it has been shown that reproduction (Pitelka et al., 1980; Thompson, 1980; Ashmun and Pitelka, 1984; Moore and Vankat, 1986; Dahlem and Boerner, 1987; McCall and Primack, 1987) and cover (Davison and Forman, 1982; Ashmun and Pitelka, 1984; Hook, 1984) of herbaceous species are likely to increase in gaps. Collins and Pickett (1987, 1988a, 1988b) and Collins et al. (1985) found little evidence that gaps had a positive influence on understory herbs in a deciduous forest in Pennsylvania (USA) and Moore and Vankat (1986) found that only two of five species responded positively to small gaps in a southern Ontario (Canada) deciduous forest. Reader and Bricker (1992a, 1992b) also found variable species responses of understory herbs to canopy removal in an Ontario forest and concluded that gap size was relatively unimportant.

Most of the conclusions that have been reached concerning the importance of gaps to understory her-

¹⁾ Author for correspondence.

²⁾ Present address: Department of Zoology, 223 Bartram Hall, University of Florida, Gainesville, FL 32611, U.S.A

baceous species have been based on short-term studies of phenomena (i.e. changes in cover and/or density, sexual reproduction, clonal spread) that can potentially change in their magnitude and/or direction over longer periods of time (Tamm, 1991). The few long-term studies of woodland herbs that have been conducted have shown that population changes can be dramatic (Inghe and Tamm, 1985, 1988; Tamm, 1991) and/or that factors other than gaps can have an important impact (Brewer, 1980) on understory herbs. What are the long-term influences of gaps on processes that are responsible for the maintenance and/or spread of understory species? In this paper, we expand on our earlier publication on this subject (Whigham and O'Neill, 1988) and report results after 15 years of studying gap and non-gap patches (hereafter called subpopulations) of the woodland herb, *Cynoglossum virginianum* L. (Boraginaceae).

Materials and Methods

1. Species Description and Study Site

Cynoglossum virginianum (Wild Comfrey) is a long-lived non-clonal summer green perennial that occurs throughout the deciduous forest region of eastern North America. Plants emerge from a very large rootstock (D.F. Whigham, pers. com.) in the early spring and produce between one and seven basal leaves; reproductive plants also produce cauline leaves that decrease in size acropetally on the single inflorescence. Flowering occurs in May-June at our study site. Seeds (mericarps) mature in August and they appear to be adapted for animal dispersal as they have long recurved glochidiate trichomes and readily attach to fabric. Most seeds, however, remain attached to the inflorescence and fall to the ground very close to the parent.

We have studied three subpopulations of *C. virginianum* that occur in an approximately 125 year old deciduous forest on the property of the Smithsonian Environmental Research Center (SERC). SERC is located (38°51'N, 76°32'W) approximately 45 miles east of Washington (DC) on the Inner Coastal Plain of Maryland. The forest is part of the 'tulip poplar association' (Brush et al., 1980) and the canopy is dominated by a variety of species (e.g. *Fagus grandifolia*, *Liriodendron tulipifera*, *Quercus alba*, *Quercus falcata*, *Carya glabra*, *Carya tomentosa*). *Cornus florida* and *Carpinus caroliniana* are the dominant understory woody species and there is a well-developed herbaceous layer that includes spring ephemerals (e.g. *Claytonia virginiana*, *Dentaria laciniata*) and summer-green species such as *Arisaema triphyllum*, *Podophyllum peltatum*, *Smilacina racemosa*, *Geranium maculatum*, *Sanguinaria canadensis*, *Desmodium nudiflorum*, etc.

2. Methods

All individuals in three subpopulations of *C. virginianum* were marked in 1978 and the areas have been censused annually thereafter. The subpopulations were chosen by walking through the forest and locating distinct patches of plants that were at least 50 meters from other patches. The locations of plants were marked with numbered aluminum tags held in the ground with aluminum nails and with numbered plastic 'swizzle sticks'. The annual census of each plant included counting the number of rosette leaves on asexual plants and the number of rosette and cauline leaves on flowering individuals. The number of flowers and mature mericarps (each flower can potentially produce four mericarps) were counted on sexual plants. Inflorescence heights were measured on all flowering plants in 1991 and 1993. The annual census also included searching each subpopulation and the immediate areas for seedlings. When seedlings were encountered, their locations were marked and the number of leaves recorded. In 1993, we measured the distances between plants marked in 1978 and the probable seedlings that they had produced. Subpopulations 1 and 2 have not experienced any canopy disturbances since the inception of the study while Subpopulation 3 occurred beneath a canopy gap that was created in 1980 by the blow-down of a large *Quercus alba* which created a gap of approximately 1,100 m².

Results

1. Changes in Subpopulation Size and Size Class Distribution

Subpopulations 1 and 2 gradually decreased in size for the first 10–12 years of the study but then began to increase dramatically and are now larger than they were initially (Fig. 1). The decline of Subpopulations 1 and 2 for the first decade were due to significantly ($P \leq 0.0001$; Peto and Peto's Logrank Test) higher rates of mortality, compared to the gap subpopulation, of the plants that were initially marked (Fig. 2) and little seedling recruitment (Fig. 3). After 1988, seed production and seedling recruitment increased in Subpopulations 1 and 2 (Fig. 3) and subpopulation size has sharply increased (Fig. 1).

Subpopulation 3 has had a very different history during the 15 years (Fig. 1). The size of the subpopulation was initially smaller ($n=14$) than the other two ($n=108$ for Subpopulation 1 and 83 for Subpopulation 2), the mortality of the plants initially marked has been less (Fig. 2), and there was no seedling recruitment during the first three years (Fig. 3). Seed production and seedling recruitment increased dramatically between 1982 and 1985 (Fig. 3). Figure 3 also demonstrates that some of the seeds may have entered into a dormant

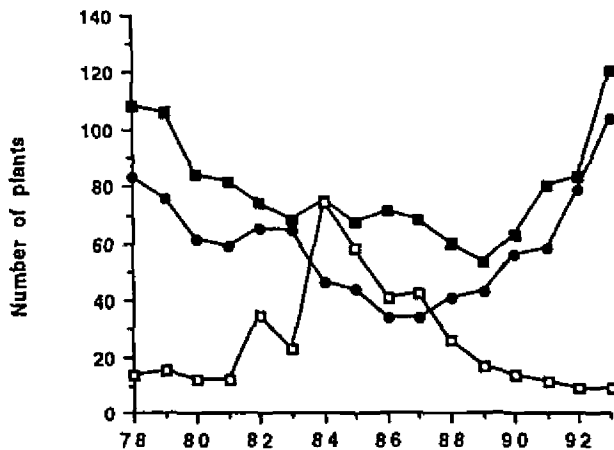


Fig. 1. Changes in the sizes of three subpopulations of *Cynoglossum virginianum* from 1978 until 1993. Subpopulations 1 (solid squares) and 2 (solid circles) are in non-gap areas while Subpopulation 3 (open squares) occurs in a gap of @ 1,100 m² that formed in 1980.

seed pool as there was no seedling recruitment in 1983 even though more than 100 seeds were produced in 1982. Continued low mortality of plants that had been initially marked and successful seedling recruitment resulted in an almost 4X increase in the size of Subpopulation 3 by 1985 (Fig. 1). After 1985, there has only been one year (1991) in which any plants in Subpopulation 3 flowered and all but two of the seedlings recruited between 1982 and 1987 have died.

The combined effects of mortality and recruitment on the size structure of the three subpopulations are shown in Fig. 4. The relationship between large (four or

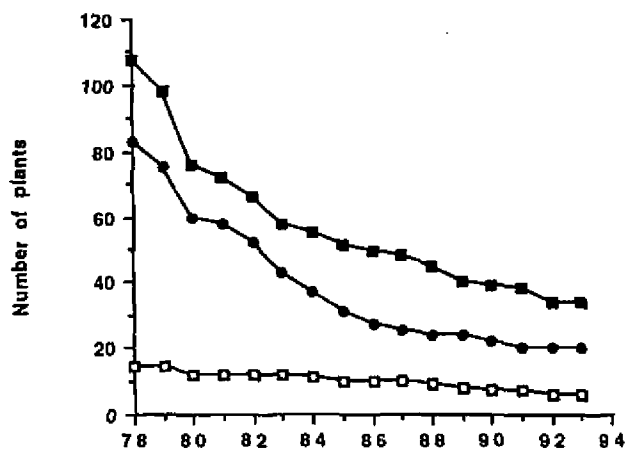


Fig. 2. Mortality of plants marked in 1978 for three subpopulations of *Cynoglossum virginianum*. Subpopulations 1 (solid squares) and 2 (solid circles) are in non-gap areas while Subpopulation 3 (open squares) occurs in a gap of @ 1,100 m² that formed in 1980.

more leaves) and small (less than four leaves) plants has remained fairly constant for Subpopulations 1 and 2 compared to Subpopulation 3 which has shifted from domination by large plants to domination by smaller plants, mostly due a decrease in the size of most individuals following the active period of flowering between 1981 and 1985. The size structures of Subpopulations 1 and 2 have, however, changed in the last four years to include a larger percentage of seedlings (Fig. 4) because of higher rates of seedling recruitment (Fig. 3).

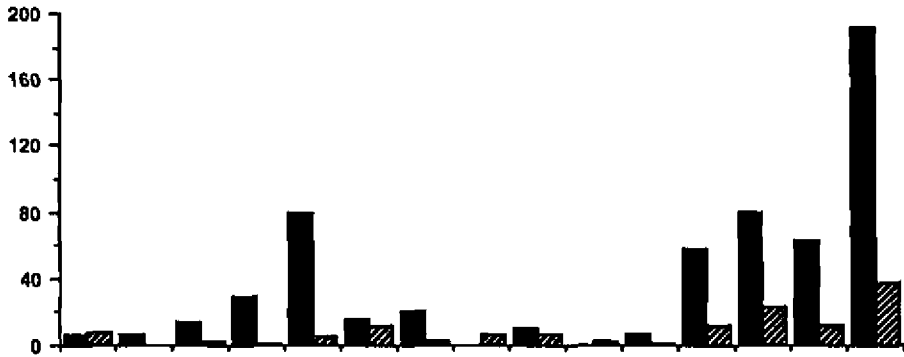
Changes in sizes of individuals that were marked in 1978 have been most pronounced in Subpopulation 3 (Fig. 5). Plants had between two and six leaves in 1978. The range of size classes increased from 3 to 12 by 1982 and most individuals were in large size classes (7–12 leaves). By 1985, size class distribution had shifted downward and by 1988 individuals ranged in size from 1–4 leaves. In 1993 (data not shown) size classes ranged from 2–6 leaves per plant; exactly the same range of plants in the populations in 1978 (Fig. 5).

2. Sexual Reproduction

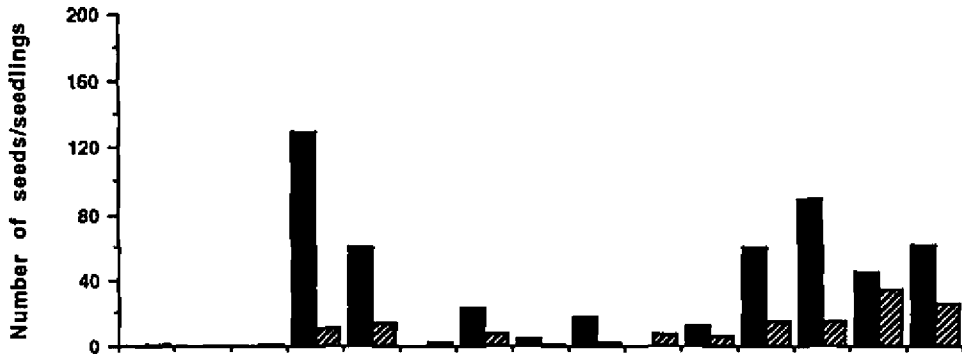
Recruitment into *C. virginianum* subpopulations only occurs as a result of sexual reproduction and seedling establishment. None of the seedlings that we have marked during the study have reached sexual maturity, so that all seedling recruitment has resulted from flowering of individuals marked in 1978 or from seeds imported into the subpopulations from other areas. The flowering histories of the three subpopulations are shown in Table 1. Increased flowering occurred in all subpopulations between 1980 and 1984 but the percentage of plants that flowered was greater in the gap subpopulation (Fig. 4). The percentage of initially tagged plants that have flowered in Subpopulation 3 (57.1%) is significantly higher ($P \leq 0.005$; Chi-square test) than the flowering percentages of plants in Subpopulations 1 and 2 (32.4 and 30.1% respectively). Subpopulations 1 and 2 had a second increase in flowering activity beginning in 1989. Most of the flowering that has occurred in Subpopulation 3 was, with the exception of 1991, restricted to the six year period following gap formation.

Flowering frequency has also differed between gap and non-gap subpopulations (Table 2). Most individuals in Subpopulations 1 and 2 that have flowered have done so only once or twice and the average number of years between flowering events has been different for the two subpopulations. Individuals in Subpopulation 1 have flowered on an average of every 6.1 years (range 0–12 years) compared to an average flowering interval of 2.6 years (range 0–8 years) for Subpopulation 2. In contrast, most reproductive plants in Subpopulation 3 have flowered three or four times (Table 2) and the average number of years between flowering was 0.9

Subpopulation 1



Subpopulation 2



Subpopulation 3

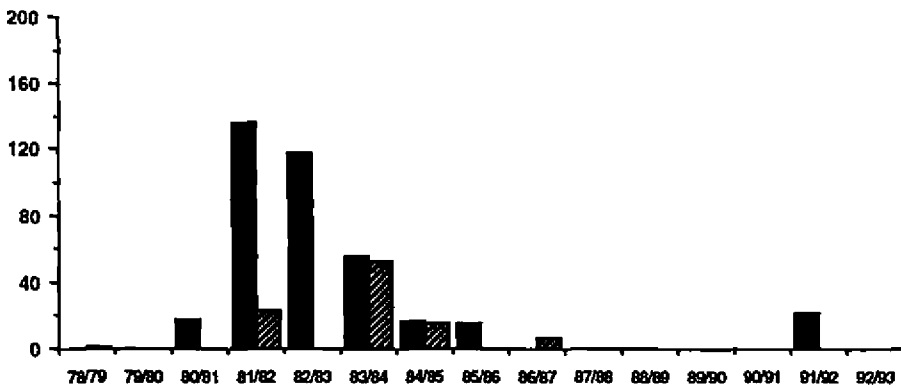


Fig. 3. Numbers of seeds (solid bars) and seedlings (diagonally lined bars) in three subpopulations of *Cynoglossum virginianum* between 1978 and 1993. Subpopulations 1 and 2 occur in non-gap areas while Subpopulation 3 occurs in an area where an approximately 1,100 m² gap formed in 1980. The couplets of numbers on the horizontal axis refer to the year in which seeds were produced and the number of seedlings found the following year.

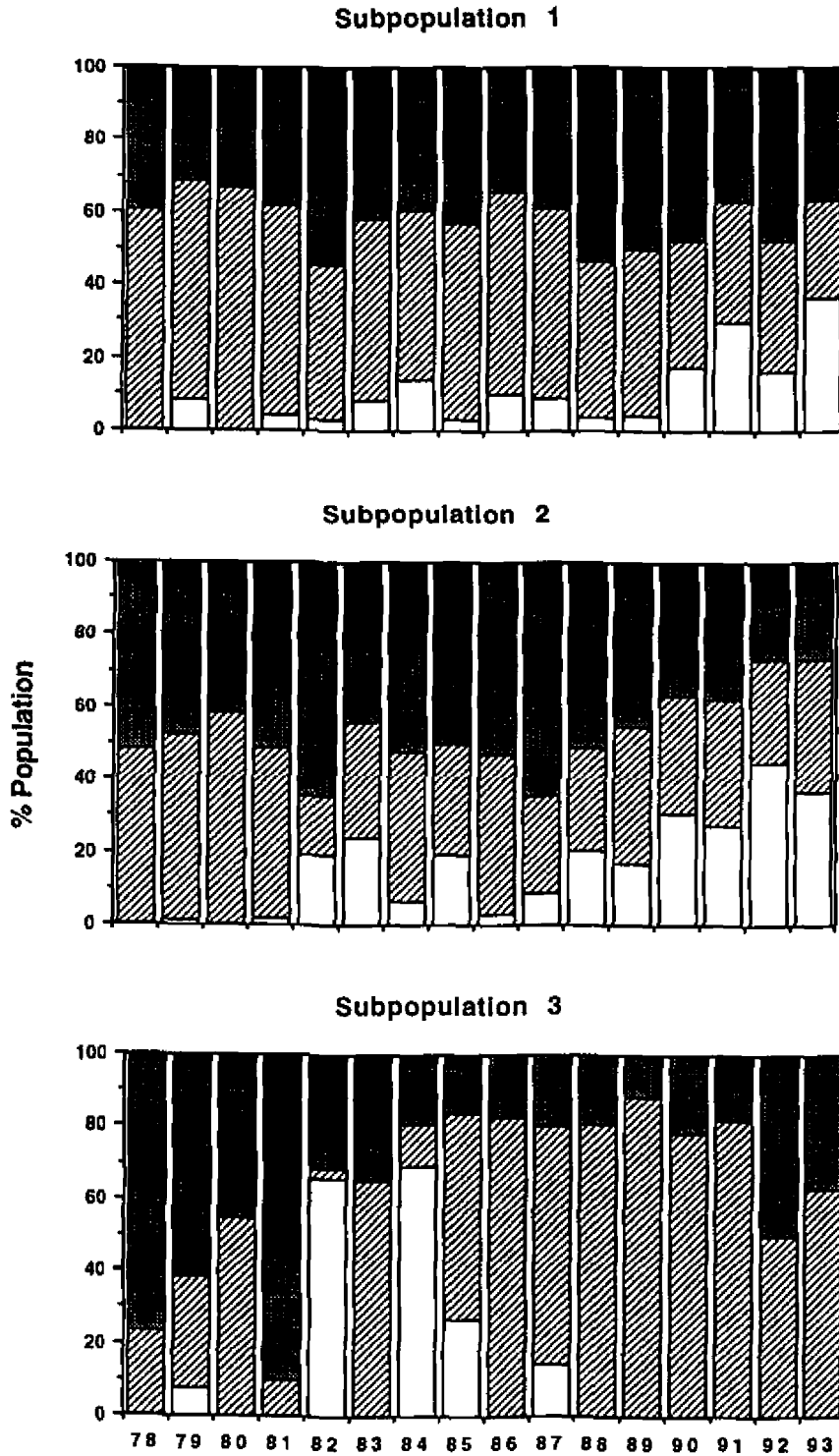


Fig. 4. Yearly changes in the percent of all individuals that were in three life history stages in three subpopulations of *Cynoglossum virginianum*. Subpopulations 1 and 2 occur in non-gap areas while Subpopulation 3 occurs in an area where an approximately 1,100 m² gap formed in 1980. Life history stages are: flowering individuals (solid black bars), plants with four or more leaves (shaded bars), plants with less than four leaves (diagonally lined bars), seedlings (white bars).

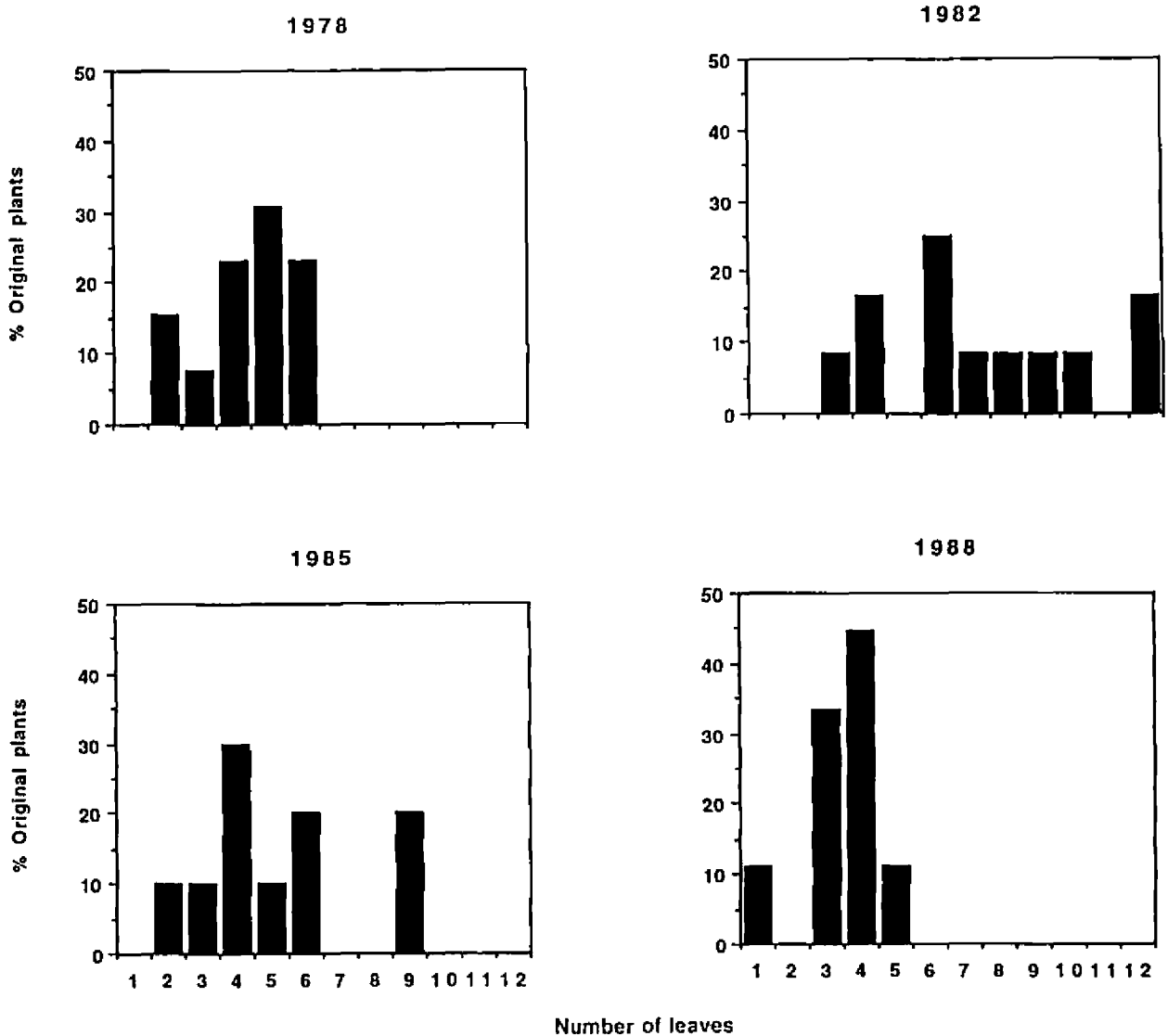


Fig. 5. Changes in the size distribution of individuals of *Cynoglossum virginianum* in Subpopulation 3 during four years of the 16 year study. Subpopulation 3 occurs in an area where an approximately 1,100 m² gap formed in 1980. The number of leaves per plant is used to express plant size and the data are given as the percentage of all individuals in the subpopulation.

(range 0-7).

There were significant ($P \leq 0.02$, ANOVA) year to year differences in the number of flowers per inflorescence (data not shown) and the differences between populations was also significant ($P \leq 0.04$, ANOVA). Inflorescences in Subpopulation 3 had a significantly greater number of flowers (20.6 ± 3.2) than plants in Subpopulations 1 and 2 (15.5 ± 0.7 and 15.3 ± 0.7 respectively). There was no significant interactions effect between year and subpopulation. The total number of mericarps produced was highest in Subpopulations 1 and 2 (Table 1). Although not significant

($P \leq 0.08$, ANOVA), the number of mericarps per inflorescence was higher in the gap subpopulation (19.1 ± 3.2) compared to Subpopulations 1 (13.3 ± 1.1) and 2 (11.1 ± 0.9). There has been no significant subpopulation difference in the number of mericarps that ultimately become seedlings (number of seedlings surviving for at least one year/number of seeds produced): Subpopulation 1 = 16.1%, Subpopulation 2 = 27.2%, Subpopulation 3 = 25.7%.

3. Seed Dispersal

Most mericarps remain attached to the inflorescence,

Table 1. Data on sexual reproduction in the three marked subpopulations of *Cynoglossum virginianum*. Subpopulations 1 and 2 occurred in areas that have not experienced any disturbance while Subpopulation 3 was in an area where a tree gap occurred in 1980.

Subpopulation	# tagged in 1978	# plants flowering at least once	Total # seeds produced	Mean # seeds per plant
1	108	35	799	22.8
2	83	25	545	21.8
3	14	8	383	47.8

which falls to the ground in late summer or early autumn. Most seedlings, consequently, are found near the parents. The distance between seedlings that we have marked and their probable parents (range = 48–78 cm) approximates the average inflorescence height (62.9 ± 1.4 cm, $n = 22$).

Discussion

Tamm (1991) summarized his more than 50 years of observing herbaceous species in permanent plots in Sweden (Inghe and Tamm, 1985, 1988; Tamm, 1948, 1956, 1972a, 1972b) by concluding that "there is no good substitute for long-term observation series (several years and preferably decades) at the level of individual ramets, if we wish to understand vegetation changes...". This 15 year study confirms his conclusion and further demonstrates the complexity and variable nature of long-lived woodland herbaceous species. If we had only sampled the subpopulations in 1978 and 1993, we would have concluded that subpopulation sizes have changed little and that they were quite stable. If we had measured the subpopulations yearly but stopped the study in 1985, we would have concluded that Subpopulation 3 benefited by being in the gap and that Subpopulations 1 and 2 were declining and would also benefit if a tree gap occurred in their area (Whigham and O'Neill, 1988).

Examination of the 15 year data record, however, leads to two salient observations. First, there have been dramatic changes in each subpopulation and the pattern of change has differed between gap and non-gap habitats (Fig. 1). Second, the conclusions that we reached in our 1988 paper (Whigham and O'Neill, 1988) were premature and Subpopulation 3 has received little long-term benefit from being present in the gap and it now appears to be out of flowering synchrony with Subpopulations 1 and 2.

While individuals in Subpopulations 1 and 2 have flowered each year, differences in the number of flowering plants indicates that peaks in flowering may occur at cycles of approximately a decade. Whether or not this pattern is indeed cyclic or related to variations in climatological factors, as Inghe and Tamm (1985) have suggested, will require additional monitoring of the subpopulations. Subpopulation 3 experienced the same increase in flowering in the early 1980's as did Subpopulations 1 and 2 and the percentage of marked individuals that flowered in Subpopulation 3 was greater. Subpopulation 3 did not, however, have a second peak in flowering.

Several factors may be responsible for the differences in the three *C. virginianum* subpopulations. Increased light associated with tree gaps (Endler, 1993) appears to benefit understory herbs in deciduous forests (Collins and Pickett, 1987) but the benefits are often not clear cut or long-term. Understory clonal herbaceous species such as *Aster acuminatus* (Ashmun

Table 2. Comparison of flowering frequency in gap (Subpopulation 3) and non-gap (Subpopulations 1 and 2) plants. Data in the table are percentages of all individuals tagged in 1978 and surviving until 1993.

Number of times flowering	Subpopulation 1	Subpopulation 2	Subpopulation 3
1	54.3	44.0	25.0
2	28.6	32.0	12.5
3	8.6	8.0	37.5
4	5.7	12.0	25.0
5	2.9	0.0	0.0
6	0.0	4.0	0.0

and Pitelka, 1984; Pitelka et al., 1980) may benefit from light gaps more than species that only reproduce by seed. Clonal species can maintain or expand their populations by asexual propagation under a variety of light conditions and they can benefit from gap conditions by increased flowering (Dahlem and Boerner, 1987).

Like *Geranium maculatum* (Dahlem and Boerner, 1987), *C. virginianum* in Subpopulation 3 benefited in the short-term by higher light conditions in the tree gap. Leaf number increased from 2–7 leaves/plant in 1978 to 4–13 leaves/plant by 1981, one year after gap formation (Whigham and O'Neill, 1988). Flowering increased dramatically in 1981 (Fig. 4) and by 1987 the subpopulation was dominated by individuals with one and two leaves that had been recruited into the subpopulation as seedlings, mostly between 1982 and 1985 (Whigham and O'Neill, 1988). The short-term benefits have, however, started to disappear. The subpopulation continues to be dominated by small individuals (Fig. 4) but sexual reproduction has been almost completely absent since 1985, and all but two of the seedlings that were recruited during the period of increased flowering have died.

There are several possible reasons why Subpopulation 3 may have declined in recent years. Reader and Bricker (1992a) have suggested that herbs may not do well in larger tree gaps because of increased competition from woody plants. We have measured the average density of shrubs and small trees (<10 cm DBH) in each of the three *C. virginianum* subpopulations (data not shown) and found no obvious differences. While stem density does not differ between the three areas, increased shoot and leaf production by canopy and understory woody species that were present at the time of gap formation may have resulted in a long-term decrease in light levels in the gap area (Ehrenfeld, 1980). Lower light levels in combination with the high costs of reproduction could have caused plant size to shift toward smaller size classes (Fig. 5) and it seems likely that seedling mortality rates, as occurred in Subpopulation 3, might also be higher under low light conditions of closing gaps.

The high rate of flowering and successful seed production in Subpopulation 3 shortly after the gap was created may also have resulted in the utilization of stored nutrients and energy that have not recovered enough to allow the plants to flower again (Fig. 5). We have shown, for example, that it takes *Tipularia discolor* (Orchidaceae) approximately three years to recover from producing an average number of fruits (Whigham and O'Neill, 1990) and that the cost of reproduction is greater as the number of fruits produced increases (Snow and Whigham, 1989). Dahlem and Boerner (1987) have also suggested that there may be long-term costs associated with increased flowering and seed production in gap habitats. Only continued ob-

servations will allow us to determine if flowering in the three subpopulations will become synchronized again.

The dilemma for *C. virginianum* appears to be that it can respond positively to gap formation (i.e. increased flowering, fruiting, and seedling establishment) but the offspring may ultimately die unless another opening is created near the subpopulation, unless the seeds are dispersed out of the gap, and/or unless seed germination is delayed until more suitable growing conditions exist in the gap area. We have used the *C. virginianum* data in a combined model of forest canopy dynamics and patch-specific demography (Cipollini et al., 1993) to assess the impacts of changes in the rates of gap disturbances, rates of long distance seed dispersal, and patterns of seed dormancy. In summary, the results suggest a small negative impact of increasing the rate of gap disturbances and a small positive effect of long distance dispersal. The model also predicts benefits of enhanced seed dormancy, particularly if seed dormancy is higher in gap areas. We are now testing the model predictions experimentally.

In conclusion, this long-term study of *C. virginianum* lends support to the suggestions (Collins and Pickett, 1987, 1988a, 1988b; Collins et al., 1985; Moore and Vankat, 1986; Reader and Bricker, 1992a, 1992b) that gaps are only of minor importance to the long-term population dynamics of many woodland herbs. Gap formation, however, will have important effects on population structure and, for outcrossing species, and genetic structure. This study supports Tamm's (1991) statement about the importance of long-term studies as it has demonstrated that dynamic changes occur in both gap and non-gap subpopulations. Finally, the study demonstrates that it is difficult, if not impossible, to understand the characteristics of *C. virginianum* in different habitats without monitoring individual genets/ramets for long periods of time.

Acknowledgments The research has been supported by an Environmental Sciences Program grant to D.F. Whigham and a Smithsonian Post-Doctoral Fellowship to M. Cipollini.

References

- Ashmun, J.W. and Pitelka, L.F. 1984. Light-induced variation in the growth and dynamics of transplanted ramets of the understory herb, *Aster acuminatus*. *Oecologia* 64: 255–262.
- Barden, L.W. 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. *Oikos* 35: 16–19.
- Brewer, R. 1980. A half-century of changes in the herb layer of a climax deciduous forest in Michigan. *J. Ecol.* 68: 823–832.
- Brush, G.S., Lenk, C. and Smith, J. 1980. The natural forests of Maryland: an explanation of the vegetation map of Maryland. *Ecol. Monogr.* 50: 77–92.
- Canham, C.F. 1988. An index of understory light levels in

- and around canopy gaps. *Ecology* 69: 1634–1638.
- , C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. and White, P. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. Bot.* 20: 620–631.
- Cipollini, M.L., Whigham, D.F. and O'Neill, J. 1993. Population growth, structure and seed dispersal in the understory herb *Cynoglossum virginianum*: a population and patch dynamics model. *Plant Species Biol.* 8: 117–129.
- Collins, B.S. and Pickett, S.T.A. 1987. Influence of canopy openings on the environment and herb layer in a northern hardwoods forest. *Vegetatio* 70: 3–10.
- . 1988a. Response of herb layer cover to experimental canopy gaps. *Am. Midl. Nat.* 119: 282–290.
- . 1988b. Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. *J. Ecol.* 76: 437–450.
- , Dunne, K.P. and Pickett, S.T.A. 1985. Responses of forest herbs to canopy gaps. In: Pickett, S.T.A. and White, P.S. (eds), *The Ecology of Natural Disturbance and Patch Dynamics*, 217–234. Academic Press, New York.
- Dahlem, T.S. and Boerner, R.E.J. 1987. Effects of canopy light gap and early emergence on the growth and reproduction of *Geranium maculatum*. *Can. J. Bot.* 65: 242–245.
- Davison, S.E. and Forman, R.T.T. 1982. Herb and shrub dynamics in a mature oak forest: a thirty-year study. *Bull. Torrey Bot. Club* 109: 64–73.
- Ehrenfeld, J.G. 1980. Understorey response to canopy gaps of varying size in a mature oak forest. *Bull. Torrey Bot. Club* 107: 29–41.
- Endler, J.A. 1993. The color of light in forests and its implications. *Ecol. Monogr.* 63: 1–27.
- Hibbs, D.E. 1982. Gap dynamics in a hemlock-hardwood forest. *Can. J. Bot.* 12: 522–527.
- Hook, R.A. 1984. Analysis of ground layer vegetation in and around tree-fall gaps in Lilley Cornett Woods, Letcher County, Kentucky. M.S. Thesis, Eastern Kentucky University, Richmond.
- Inghe, O. and Tamm, C.O. 1985. Survival and flowering of perennial herbs. IV. The behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943–1981. *Oikos* 45: 400–420.
- . 1988. Survival and flowering of perennial herbs. V. Patterns of flowering. *Oikos* 51: 203–219.
- McCall, C. and Primack, R.B. 1987. Resources limit the fecundity of three woodland herbs. *Oecologia* 71: 431–435.
- McCune, B., Cloonan, C.L. and Armentano, T.V. 1988. Tree mortality and vegetation dynamics in Hemmer Woods, Indiana. *Am. Midl. Nat.* 120: 416–431.
- Moore, M.R. and Vankat, J.L. 1986. Responses of the herb layer to the gap dynamics of a mature Beech-maple forest. *Am. Midl. Nat.* 115: 336–347.
- Niesenbaum, R.A. 1993. Light or pollen—seasonal limitations on female reproductive success in the understory shrub *Lindera benzoin*. *J. Ecol.* 81: 315–323.
- Pickett, S.T.A. and White, P.S. (eds) 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Pitelka, L.F., Stanton, D.S. and Peckenhams, M.O. 1980. Effects of light and density on resource allocation in a forest herb, *Aster acuminatus*. *Am. J. Bot.* 67: 942–948.
- Reader, R.J. 1987. Loss of species from deciduous forest understorey immediately following selective tree harvesting. *Biol. Conserv.* 42: 231–244.
- and Bricker, B.D. 1992a. Response of five deciduous forest herbs to partial canopy removal and patch size. *Am. Midl. Nat.* 127: 149–157.
- . 1992b. Value of selectively cut deciduous forest for understorey herb conservation: an experimental assessment. *For. Ecol. Manage* 51: 317–327.
- Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests in Eastern North America. *Ecology* 63: 1533–1546.
- . 1984. Development of woody vegetation in treefall gaps in a beech-sugar maple forest. *Holarct. Ecol.* 7: 157–164.
- . 1985. Disturbance regimes in temperate forests. In: Pickett, S.T.A. and White, P.S. (eds), *The Ecology of Natural Disturbance and Patch Dynamics*, 17–33. Academic Press, New York.
- Silvertown, J. and Smith, B. 1988. Gaps in the canopy: the missing dimension in vegetation dynamics. *Vegetatio* 77: 57–60.
- Snow, A.A. and Whigham, D.F. 1989. Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). *Ecology* 70: 1286–1293.
- Tamm, C.O. 1948. Observations on reproduction and survival of some perennial herbs. *Botaniska Notiser* 1948(3): 305–321.
- . 1956. Further observations on the survival and flowering of some perennial herbs. I. *Oikos* 7: 274–294.
- . 1972a. Survival and flowering of some perennial herbs. II. The behaviour of some orchids on permanent plots. *Oikos* 23: 159–166.
- . 1972b. Survival and flowering of some perennial herbs. III. The behaviour of *Primula veris* on permanent plots. *Oikos* 23: 23–38.
- . 1991. Behaviour of some orchid populations in a changing environment: observations on permanent plots, 1943–1990. In: Wells, T.C.E. and Willems, J.H. (eds), *Population Ecology of Terrestrial Orchids*, 1–14. SPB Academic Publishing, The Hague.
- Taylor, R.J. and Pearcy, R.W. 1976. Seasonal patterns of the CO₂ exchange characteristics of understory plants from a deciduous forest. *Can. J. Bot.* 54: 1094–1103.
- Thompson, J.N. 1980. Treefalls and colonization patterns of temperate forest herbs. *Am. Midl. Nat.* 104: 176–184.
- Wallace, L.L. and Dunn, E.L. 1980. Comparative photosynthesis of three gap phase successional tree species. *Oecologia* 45: 331–340.
- Whigham, D.F. and O'Neill, J. 1988. The importance of predation and small scale disturbance to two woodland herb species. In: Werger, M.J.A., van der Aart, P.J.M., During, H.J. and Verhoeven, J.T.A. (eds), *Plant Form and Vegetation Structure*, 243–252. SPB Academic Publishing, The Hague.
- and ———. 1991. The dynamics of flowering and fruit production in two Eastern North American terrestrial orchids, *Tipularia discolor* and *Liparis lilifolia*. In: Wells, T.C.E. and Willems, J.H. (eds), *Population Ecology of Terrestrial Orchids*, 89–101. SPB Academic Publishing, The Hague.