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HABITAT PARTITIONING IN VIOLA SORORIA AND V. FIMBRIATULA

City University of New York

Ph.D. 1984

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HABITAT PARTITIONING IN VIOLA SORORIA AND V. FIMBRIATULA

by

SUSAN E. YOST

A dissertation submitted to the Graduate Faculty
in Biology in partial fulfillment of the requirements
for the degree of Doctor of Philosophy, The City
University of New York.

1984

This manuscript has been read and accepted for the Executive
Committee in Biology in satisfaction of the dissertation
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ABSTRACT

HABITAT PARTITIONING IN VIOLA SORORIA AND V. FIMBRIATULA

by

Susan E. Yost

Advisor: Dr. Dwight T. Kincaid

The overlapping distribution pattern of two violet species in a New York Hudson Highlands study area was found to be related to soil moisture and light conditions. Viola sororia grew in both moist field and woods habitats, where there was no difference in soil moisture content, and it tolerates low light levels. The closely related species, V. fimbriatula, was virtually restricted to the dry, sparsely vegetated areas of the field, apparently because it is more drought-tolerant, has higher light requirements and is a poorer competitor than V. sororia. Although there was some overlap in their distribution, competition between the two species in the field was reduced due to the patchiness of the environment, particularly of the soil texture and moisture content. Neither species grew well in waterlogged soil.

Measurements of environmental and vegetation factors; plant physiological response, size and carbon allocation; as well as experiments with transplants of adults, planted seeds and with soil disturbance were used to help explain the distribution pattern of the two violet species. Factors which appeared to affect the distribution pattern were light; soil factors (moisture, texture, and field capacity); and density, height and

composition of associated vegetation. Other differences between the two species were in mortality of seedlings and adults, leaf water potential and wilting point, leaf shape and thickness, and reproductive rate. In contrast, factors which did not differ between the two species, and therefore probably did not have an effect on the distribution pattern at the study site, included seed germination, leaf predation, and soil pH. For both species, sun leaves were smaller but more numerous than shade leaves, and therefore total leaf surface area per plant was the same between the contrasting habitats of sunny field and shady woods.

Evidence from the transplant and seed experiments for considerable phenotypic plasticity in petiole length strongly indicates that V. fimbriatula is the same species as V. sagittata.

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INTRODUCTION

Studies of habitat partitioning among cooccurring species of plants are common. Studies on coexisting congeneric species are less common, but are more valuable for understanding how plants divide up a habitat in a manner which allows coexistence and reduces competition (Werner, 1979; Sarukhan and Harper, 1973), and also for understanding how they remain genetically distinct (Harper, Clatworthy, McNaughton and Sagar, 1961; Harper and McNaughton, 1962).

The purpose of this study was to investigate the population biology of two closely related species of violets, Viola sororia Willd. and Viola fimbriatula Sm.. Both species grow in large numbers in a field and adjacent woods in the New York Hudson Highlands, but casual observation revealed patchiness in the distribution of the two species in the field, and a predominance of V. sororia in the woods. Therefore, I investigated habitat partitioning of the two species in the field and woods, and described their spatial distribution, morphology, and physiology in relation to the characteristics of environment and vegetation. Experiments with transplants of adults and seed plots yield ecological information on habitat preference, ecotypic differentiation, and phenotypic plasticity, with the taxonomic implication that V. fimbriatula should be included in V. sagittata Ait..

Other studies have described habitat partitioning in coexisting congeners along soil moisture gradients in four species

of Polygonum (Hickman, 1977), two of Typha (Grace and Wetzel, 1981), five of Solidago (Werner, 1979; Werner and Platt, 1976), and in four of Solidago (Abrahamson and Gadgil, 1973). Habitat partitioning has also been described along a temperature gradient in three species of Hieracium (Thomas and Dale, 1976); along a light gradient in two species of Trifolium (Harper and Clatworthy, 1963); and as a result of competition in three species of Plantago (Sagar and Harper, 1961). Other studies on habitat partitioning have involved differences in life histories in two species of Avena (Marshall and Jain, 1967, 1969); of soil characteristics in mosses (Watson, 1980); and of soil moisture and type and competition in five species of Rumex (Harper and Chancellor, 1959). Other studies on cooccurring but unrelated species have revealed habitat partitioning along soil moisture gradients in grasses (Barnes and Harrison, 1982), in Polygonum and Abutilon (Pickett and Bazzaz, 1976), and in Sedum and Minuartia on granite outcrops (Sharitz and McCormick, 1973); and as a result of differences in the use of soil resources and competition in six species of annuals (Parrish and Bazzaz, 1976). In my study, several environmental factors were studied for correlations with distribution patterns, including soil moisture, texture, field capacity, and pH; and light.

Viola sororia and V. fimbriatula lend themselves to a study of habitat partitioning because they are closely related, and yet have distinct differences in morphology and habitat preference, although there is some overlap in their distribution at the study site. Both species lend themselves to experimental manipulation,

as they are easily cloned, have a long blooming and growing season, and are perennials, so that the same plant can be observed over several years.

ECOLOGICAL DESCRIPTION OF THE VIOLA SPECIES

Approximately 51 species of the genus Viola (family Violaceae) occur in the northeastern U.S. (Gleason and Cronquist, 1963), although the number may be as low as 29 species (Cronquist unpublished revision of Gleason and Cronquist, 1963). Violets are either caulescent, or acaulescent (leaves and flowers arise directly from the rhizome or from stolons) (Fernald, 1950). Most species are herbaceous perennials with out-crossing chasmogamous flowers which are violet, yellow, or white, and also self-pollinating cleistogamous flowers which appear later in the season. In addition, the rhizomatous species can spread vegetatively by rhizome division (Solbrig, Newell and Kincaid, 1980), and the stoloniferous species by stolons (Newell, Solbrig and Kincaid, 1981; Newell, 1982).

The two species chosen for this study, V. sororia and V. fimbriatula (figure 1a), are both perennial, acaulescent, violet in petal color, and rhizomatous (non-stoloniferous), with N=27 (Gleason and Cronquist, 1963; Gershoy, 1932). They differ in leaf morphology, habitat preference, and possibly in physiology.

Viola sororia, the dooryard or sister violet (Klaber, 1976), is found in rich woods and moist meadows (Gleason and Cronquist, 1963). Its leaves are round to ovoid, thinner, broader and less drought-resistant than those of V. fimbriatula (Solbrig, Newell and Kincaid, 1980). The geographic range for V. sororia is Quebec and Maine to Minnesota, south to North Carolina and Oklahoma (Gleason and Cronquist, 1963).

Viola fimbriatula, the northern downy violet (Baird, 1942), is found in relatively sunny habitats such as dry fields and hillsides (Gleason and Cronquist, 1963), and occasionally along the edges of dry sterile woods and wood roads (Fernald, 1950; Russell, 1965). Its leaves are oblong, relatively thick, often pubescent, and relatively drought-resistant (Curtis and Kincaid, 1984). The geographic range of V. fimbriatula is from Nova Scotia to Wisconsin, south to Florida and Louisiana (Gleason and Cronquist, 1963).

Early workers on the violets included Gingins (1823), Becker (1910), Gregory (1912), Melchior (1964), Pollard (1896, 1897, 1898), and Wittrock (1896, 1897). Investigations on taxonomic relationships include the work of Russell (1956, 1960, 1965), Brainerd (1904a, 1904b, 1906a, 1906b, 1910, 1921, 1924) who studied violets and their hybrids over a 25 year period, Gershoy (1928, 1932, 1934) who conducted extensive hybridizations, Clausen (1926, 1927, 1929, 1930, 1931, 1962, 1964) who studied the cytology and genetics especially of *Melanium* violets, Baker (1935, 1940, 1949) on the section *Chamaemelanium* in the western U.S., and Miyaji (1929) who investigated the Asiatic violets. The population biology of violets has been investigated by Solbrig and associates in a series of papers, and the pollination biology and seed dispersal by Beattie (1969, 1971, 1972, 1974, 1976, 1978, 1979).

The family Violaceae consists of approximately 16 genera and 800 species of herbs, shrubs, small trees, and lianas of cosmopolitan distribution (Cronquist, 1981; Taylor, 1972). The largest genera are Viola (ca. 450 species), Rinorea (ca. 280

species), and Hybanthus (ca. 80 species) (Engler, 1964; Blake, 1924). The pantropical, woody genus Rinorea is thought to be archaic within the family, and to show a relationship of the Violaceae with the Flacourteaceae (Cronquist, 1981). In North America there are only two genera, Viola and Hybanthus (Gleason and Cronquist, 1963).

The genus Viola is cosmopolitan, but chiefly north temperate, and also with many species in the Andes (Willis, 1973). The genus is mainly herbaceous (Cronquist, 1981), and consists of 11 sections, of which 4 are north temperate, and 7 are tropical. In North America, the acaulescent blue violets (Boreali-Americanæ section) are best developed in the east, and the yellow violets (Chamaemelanium section) are best developed in the west (Baird, 1942; Baker, 1949). The North American species of Viola may have originated from tropical forms, migrating from South America into North America via Mexico, with the Chamaemelanium section (n=6) as the primitive group (Beattie, 1974). The evidence supporting this view is that the greatest number of genera is tropical, and the flowers of the tropical genera are generally of a more primitive type (actinomorphic as opposed to zygomorphic flowers) (Clausen, 1929; Arnal, 1945).

The two study species are in the Boreali-Americanæ group, subsection Plagiostigma, section Nominium (Gershoy, 1934; Clausen, 1929). Most of the members of this group, including V. sororia and V. fimbriatula, have relatively short, thick rhizomes (Baker, 1940). The Boreali-Americanæ violets are hypertetraploids, with an aneuploid chromosome number of $N=27$, and are generally

interfertile (Clausen, 1964). In the view of Brainerd (1906a), the taxa in this group may have formerly occupied distinct niches, and then expanded their territories and hybridized as a result of habitat disruption in North America by humans in the past few centuries.

It is difficult to identify the violets, particularly the blue ones (Pollard, 1896, 1898; Fernald, 1949; McKinney and Blum, 1978; Russell and Risser, 1960; Davidse, 1968). These taxonomic problems have been attributed to hybridization, introgression, and polyploidy (Clausen, 1929, 1962, 1964; Stebbins, 1950; Stebbins et al., 1963; Brainerd, 1904a, 1910; Brizicky, 1961; Kattenhorn, 1976). Hybridization is particularly common within sections; inter-sectional hybrids are rare and usually sterile (Sorsa, 1965). The taxonomic difficulties are compounded by high levels of inbreeding due to self-fertilization of the cleistogamous flowers (Beattie, 1976; Gershoy, 1928). Cleistogamy and also vegetative propagation tend to produce clumps of genetically similar plants causing subdivision of the population (Camp and Gilly, 1943) and is an appropriate strategy for stable habitats; whereas chasmogamy is energetically more "expensive" (Waller, 1979) and results in outbreeding and new genetic combinations (Beattie, 1972, 1976). The establishment of new species through polyploidy is relatively common in the genus; the first example of polyploidy described in a genus was in violets by Miyaji (see Clausen, 1964). Variability due to environmental factors (phenotypic plasticity), and the presence of ecotypes have added

to the taxonomic problems (McKinney and Blum, 1978, 1981; Clausen, 1964).

There have been taxonomic difficulties with both of the species in this study. Cronquist, in an unpublished revision of Gleason and Cronquist (1963), includes V. fimbriatula in V. sagittata; and has V. sororia encompass the formerly recognized species V. affinis, V. floridana, V. langloisii, V. latiuscula, V. missouriensis, V. novae-angliae, V. papilionacea, V. pratincola, V. priceana, and V. septentrionalis.

The chasmogamous flowers are pollinated by a variety of insects including bumblebees, honeybees, solitary bees, hoverflies, beeflies, butterflies, and thrips (Beattie, 1971, 1972; Bernhardt, 1978; Baker, 1935). In a study by Beattie (1974), in a form of V. sororia (V. papilionacea), 64% of the pollinators were solitary bees and 35% bumblebees, syrphids, kombyliids and lepidoptera; and in V. fimbriatula, 95% of the pollinators were solitary bees and 5% bumblebees. Therefore, both violet species are pollinated predominantly by solitary bees, which enter the flower in a supine (inverted) position, and to which the flowers are adapted by the presence of bearded lateral petals which function as footholds (Beattie, 1974). Outbreeding is entirely dependent on insect visits to chasmogamous flowers. Self-pollination of the chasmogamous flowers is usually avoided, although it is more common in the flowers pollinated by short-tongued insects such as solitary bees, and therefore appears to be more common in V. fimbriatula than in V. sororia (Beattie, 1971). Pollinator flight distances for violets are reported to be

leptokurtic in distribution, with a mean pollinator flight distance of only 50 cm (Beattie, 1978). This is in keeping with the restricted gene flow reported for many species of insect-pollinated plants (Levin and Kerster, 1974), and for some wind-pollinated plants (Handel, 1976a).

Most species of violets, including V. sororia and V. fimbriatula, have two modes of seed dispersal (ballistic, and by ants). Both chasmogamous and cleistogamous seeds are forcibly ejected from the capsules as they dry, up to distances of 5 meters; with a mean of 2.1 meters reported for V. papilionaceae (V. sororia). Only 11 Eurasian violet species do not have this ballistic mode of seed dispersal (Beattie and Lyons, 1975). In addition, the seeds contain attractants (diglycerides) and are dispersed by ants (myrmecochory). The ants carry the scattered seeds to their nests to eat the elaiosome, a lipid-filled structure attached to the seed (Handel, Fisch and Schatz 1981). The seeds are then discarded intact, minus the elaiosome, with the nest debris (Gates, 1943; Thompson, 1981; Handel, 1976b). Studies have shown that the majority of seeds are located and removed by the ants within hours after dehiscence, and are discarded by the ants within two days (Beattie and Lyons, 1975). The seeds are thus buried in "safe sites" often 2 cm below the soil surface, and usually some distance from the parent plant (Handel, 1978; Culver and Beattie, 1980). The average distance the seeds are carried by ants is 75 cm, which is less than the average ballistic distance (Culver and Beattie, 1978). There is evidence that seedling emergence is enhanced by removal of the elaiosome, and even more

so by the phosphorous and nitrogen-rich nest environment (Culver and Beattie, 1980; Beattie, 1978). Ant nests are very common (between 60,000 and 100,000 ant nests per acre of various forest floors; Culver and Beattie, 1978); and many ants frequently move the position of their nests (Handel, 1976b). There is no evidence of specialization of a particular ant for a particular violet species (Culver and Beattie, 1978; Beattie, Culver and Pudlo, 1979) or for elaiosome size (Beattie and Lyons, 1975).

Chasmogamous seeds are removed more often than cleistogamous seeds, due to changes in ant diet in summer (Culver and Beattie, 1978). Common sites for ant nests are logs, and myrmecochorous plants are found in these habitats (Handel, 1976b, 1978; Thompson, 1980). Ants therefore appear to play an important role in determining colonization sites and distribution patterns of violets (Handel, 1976b, 1978; Handel, Fisch and Schatz, 1981; Beattie and Culver, 1977).

In violets, pollen movement appears to be greater than seed movement (Beattie, 1979), and pollination appears to be more important than seed dispersal in determining neighborhood area (Beattie and Culver, 1979). The major importance of seed dispersal may be to avoid seed predation (by scattering the seeds randomly), and to improve seed germination and seedling establishment (by ants which deposit the seeds in "safe sites") (Beattie, 1978; Beattie and Culver, 1979). Ants cause clumping, then pollen exchange is also clumped, which is compounded by vegetative propagation and cleistogamy, and this reinforces the distinctness of subpopulations (Beattie, 1976, 1978).

Viola sororia and V. fimbriatula are closely related, share many characteristics, and do hybridize. As has been seen, they are similar morphologically (acaulescent, non-stoloniferous, perennial blue violets, with the same chromosome number), and their geographic distributions overlap considerably. Viola fimbriatula ranges farther south, and somewhat farther north than V. sororia. Both species have ant-dispersed seeds, although V. fimbriatula has smaller and lighter colored seeds than V. sororia. They have similar flowers, and I observed both species blooming at approximately the same time in both field and woods. There is considerable overlap in pollinators, with evidence that both species are pollinated predominantly by solitary bees (Beattie, 1974). Brainerd (1904b) stated that the blue acaulescent violets are likely to produce hybrids if growing together. The hybrid between V. sororia and V. fimbriatula has been described as a separate species, Viola emarginata (Brainerd, 1921). Viola emarginata has been identified as a hybrid between V. fimbriatula or V. sagittata and one of the cordate leaved violets of the "affinis" (sororia) group (Russell and Cooperrider, 1955; Russell and Risser, 1960; Russell, 1965). The hybrid appears to be relatively fertile. Brainerd (1904b, 1924) stated that the hybrid of V. sororia and V. fimbriatula was "less sterile than most hybrids", with no capsule containing more than half the normal number of seeds, apparently basing this comment on observations of one stand of these hybrids, consisting of a few specimens. Other hybrids of other members of the V. sororia group (affinis, latiuscula, papilionacea, septentrionalis) with V. fimbriatula or

V. sagittata are described as "fertile" to "markedly infertile" (1/8 the normal number of seeds) to entirely sterile (Brainerd, 1904b, 1924). Gershoy defined "fertile" much more broadly than Brainerd, with "sterile" plants being those with at least 95% failure of seed set. Gershoy produced many hybrids experimentally using a minimum of 10 pollinations per cross. F1 hybrids of V. sororia and V. fimbriatula were "vigorous and fertile" (Gershoy 1934). He also described hybrids of members of the V. sororia group (sororia, affinis, papilionacea, septentrionalis, latiuscula) with V. fimbriatula or V. sagittata as "thrifty plants" (Gershoy (1928, 1932).

DESCRIPTION OF THE STUDY SITE

The study site is an open, grassy field and adjacent woods (figure 1b), adjoining the Harvard Black Rock Forest in the New York Hudson Highlands. It is approximately 50 miles north of N.Y.C. on the the west side of the Hudson River (74 degrees 2' longitude, 41 degrees 25' latitude), at an elevation of 215 meters. The field is aproximately 400 meters south of the intersection of route 9W and Mountain Road. The field slopes downhill on the west side of a road which goes from the intersection of route 9W and Mountain Road, southwards to the Upper Reservoir of the Black Rock Forest. The vegetation of the area was described by Raup (1938). The soils of the area are formed on a glacial till deposited on a granitic bedrock (Scholz, 1931; Denny, 1938).

In the open field both V. sororia and V. fimbriatula are abundant, but in the adjacent woods V. sororia remains abundant while V. fimbriatula is scarce. The field is approximately 150 meters long and 40 meters wide, and is surrounded by a mixed deciduous forest. It is on a west/northwest-facing hillside with an average incline of 10 degrees as measured by an Abney level; with a road at the head, a stream at the base, and an old stone wall along the north side. The southern side of the field is shaded by trees due to the position of the sun in our hemisphere. The old stone wall is evidence of agricultural or grazing activities in the past, and topographic maps show that the field was present at least as early as 1957. It was last cleared of small trees and shrubs approximately 15 years ago, and mowed

approximately 10 years ago (Jack Karnig, personal communication). One of the larger tree saplings (Carya sp.) had five growth rings in 1982. The field is still in an early stage of succession with herbaceous plants predominating and the relatively few trees generally less than 30 cm tall.

SPATIAL DISTRIBUTIONS AND CORRELATIONS

INTRODUCTION

The open field was analyzed by quadrats to determine the distribution and characteristics of the violets and associated vegetation. In addition, light and soil characteristics were measured in the field and woods.

METHODS AND MATERIALS

The open field was mapped systematically, using a 1 m X 1 m frame. A systematic sampling is more advantageous than a random sampling for investigating variability within an area (Grieg-Smith, 1964). A total of 714 meter-square plots were sampled by making 47 transects across the field, and sampling every other meter across the width of the field and every third meter down the length of the field. These plots represent about 1/6 of the total surface area of the field. In each plot, the number of genets of V. sororia, V. fimbriatula and hybrids was recorded, as well as the names of all other species of plants (with the exception of some grasses). Hybrids were identified on the basis of morphological characters intermediate between those of the parents. In addition, the largest plant of each violet species in each plot was measured for number of leaves, and reproductives (flowers and/or capsules); and for size (length, width and petiole) of the largest leaf. Vegetation height and coverage were approximated for each plot. Vegetation height was measured as the estimated average height of the vegetation, and coverage was rated qualitatively on a scale from 1 (sparse vegetation with bare ground) to 5 (dense vegetation). In

addition, plots in which the soil was soggy were rated as wet. This study was conducted in the summers of 1981 and 1982. The spatial pattern of the violets in the field was analyzed using coefficients of dispersion and G-tests; and correlations between all the variables measured in the 714 field plots were determined. All the data in this research project were analyzed using BASIC programs written after Sokal and Rohlf (1981) and Rohlf and Sokal (1981), by Miller and Kincaid (1982), and by myself (G-test, Mann Whitney U test for ties), and implemented on Apple II+ computers; and by release 79.5 of the Statistical Analysis System (SAS, Box 8000, Cary, N.C. 27511) on our mainframe IBM computers. For the entire study, the data were tested for normality and other assumptions of parametric methods; and where appropriate, non-parametric tests were used. The type I error employed in all tests was 0.05.

The distribution of the violets within the shady woods was not analyzed in such a detailed fashion. Two 1 m X m plots were established and the number of V. sororia recorded. In addition, other plant species growing in the woods study area were recorded.

For collecting environmental data, the open sunny field was divided into 8 areas, based on the clumped distribution of the two species, with 4 V. sororia-dominated areas, 3 V. fimbriatula-dominated areas, and one area at the bottom of the field where violets are noticeably absent. Two additional V. sororia sites were chosen in the shady woods immediately adjacent to the field. These 10 areas were sampled at regular intervals throughout the 1982 growing season for solar noontime

photosynthetically active radiation (PAR, 400-700 nm), and soil moisture content; and the soil was analyzed for field capacity, particle size and pH.

PAR was measured at solar noon in the 10 areas on 20 days, in micrcinsteins/sq.m/sec with a Licor #180 sensor.

For soil moisture content, measured as percent of dry weight, soil was collected in the 10 areas on 10 days, in #4 soil tins with 3 replicates per site. Implanted plaster resistance blocks (Slavik, 1974) failed to measure soil moisture accurately in this soil of high rock content, and were abandoned.

Field capacity, which is a measure of the water storage capacity of the soil after the loss of gravitational water (Larcher, 1980; Peters, 1965), was determined after Oosting (1956). Eighteen #4 tins of soil were analyzed for field capacity for each of the ten sites.

Soil particle size was analyzed using sieves of 2, 1, 0.5, 0.25, 0.125, 0.063, and < 0.063 mm mesh openings. Approximately equal volumes of soil were collected from each of 8 of the 10 sites in the study area; three V. fimbriatula sites in the field (on average 1350 gm dry weight of soil per site), two V. sororia sites in the field (on average 859 gm dry weight of soil per site), two V. sororia sites in the woods (on average 1145 gm dry weight of soil per site), and one site at the bottom of the field where violets are absent (692 gm dry weight).

Soil pH was analyzed for the same 8 field and woods sites as for soil particle size, with 3 replicates per site. A soil slurry was formed of 1 part water:2 parts soil, and the pH determined

using a Beckman pH meter (Coleman and Thomas, 1967). A pH meter is the most accurate method of determining soil pH (Brady, 1974).

RESULTS

DISTRIBUTION OF VIOLETS AT THE STUDY SITE

DISTRIBUTION IN THE FIELD

There were 2,867 total violets in the plots in the field, consisting of 2,078 V. fimbriatula, 736 V. sororia, and 53 putative hybrids (V. sororia X V. fimbriatula). Since the plots represent about 1/6 of the total area of the field, there may be approximately 17,200 violets in the entire field, consisting of approximately 12,500 V. fimbriatula, 4,400 V. sororia and 300 hybrids. Of the 714 plots, 449 (63%) had violets present, consisting of 250 (35%) with V. sororia, 278 (39%) with V. fimbriatula, only 84 (12%) with both species, and 42 (6%) with hybrids present. Figure 2 represents the violets in the 714 plots in the field, and for purposes of statistical analysis the plots were described by their X and Y coordinates with the lower left corner of the field as the origin.

Although both species were distributed widely throughout the field, their distributions and especially that of V. fimbriatula were clumped; the coefficient of dispersion (variance/mean) is 4.54 for V. sororia, and 16.07 for V. fimbriatula. In a Poisson or random distribution the coefficient of dispersion is 1 (Sokal and Rohlf, 1981). G-tests, which compare observed frequencies with expected Poisson frequencies, were used to test the significance of deviations from randomness. The distributions of both V. sororia and V. fimbriatula are highly significantly different ($p < .001$) from a random distribution ($G = 406.57$ for V. sororia (5 classes), and $G = 2021.63$ for V. fimbriatula (9

classes)). Figure 3 presents the correlation coefficients (Spearman correlation) and levels of significance between the various factors measured in the 714 field plots. Based on correlations with the X and Y axes of the field, it can be seen that both violet species (but especially V. sororia) were more common in the upper (eastern) as opposed to the lower part of the field; they differ in that V. fimbriatula was more common in the sunnier north side of the field, and V. sororia was more common in the south side of the field.

Within a square meter plot the number of individual plants of V. sororia ranged from 1 to 18 with a mean of 2.92, of V. fimbriatula from 1 to 98 with a mean of 7.45, and of hybrids from 1 to 3 with a mean of 1.26 (within plots occupied by these species). The distributions of the two species are significantly skewed to the right and leptokurtic, with a large number of plots with few or no individuals. For V. sororia $G_1=3.5$ and $G_2=15.8$, and for V. fimbriatula $G_1=6.1$ and $G_2=63.4$ ($n=714$, $p<.001$ in all cases). Although individuals of V. sororia and V. fimbriatula grew as close as 1 cm in the field, they were found in the same plot only 12% of the time, and plots with a high density of one species usually had a low density of the other species. In the 447 plots containing one or both species, there is a highly significant negative correlation between the densities per plot of the two species (Spearman $r = -.67$, $p < .001$) (figure 3).

Hybrids were most common in the southern and eastern parts of the field (upper part of the hill, on the shadier side), as there is a positive correlation between the number of hybrids and the X

and Y axes of the field (figures 2 and 3). The distribution of hybrids in the field is related to the distribution of the parent species. Of the 42 plots containing hybrids, 40 (95%) also contained V. sororia and/or V. fimbriatula, 22 (52%) contained both parents, 5 (12%) contained only V. sororia, and 13 (31%) contained only V. fimbriatula. This means that the percentage of plots containing no parent species is only 5% of the hybrid plots, as opposed to 37% of all the plots in the field. The correlation between densities of hybrids and V. sororia and/or V. fimbriatula per plot for the 714 plots is low but statistically significant (Spearman $r = 0.16$, $p < .001$). Of the 53 hybrids present in the 714 plots, 51 (96%) were found in plots containing V. sororia and/or V. fimbriatula, and 30 hybrids (57%) were found in plots containing both parents.

The distribution of hybrids is correlated with both V. sororia and V. fimbriatula individually. In terms of numbers of plants, hybrids occurred with the same percentage (9%) of the V. sororia and V. fimbriatula plants in the field. The correlation between numbers of hybrids and numbers of V. sororia and of V. fimbriatula per plot in the 714 field plots is low but significant (for V. sororia, Spearman $r = 0.13$, $p < .001$; and for V. fimbriatula Spearman $r = 0.19$, $p < .001$). In terms of presence/absence of plants per plot, there is a similar correlation. Hybrids were found in 11% of the V. sororia and 13% of the V. fimbriatula plots in the field (for V. sororia, Spearman $r = 0.15$, $p < .001$; and for V. fimbriatula, Spearman $r = 0.23$, $p < .001$) (figure 3).

DISTRIBUTION IN THE WOODS

In the woods around the field, V. sororia was abundant in a few areas, and densities of 18 and 51 plants were recorded in two 1 m X 1 m plots. The density in the latter plot is more than twice as dense as in any V. sororia plot in the field.

In contrast, V. fimbriatula was found in small numbers and only in one area of the woods a few meters from the edge of the field, with a total of approximately 30 plants. No hybrids were found in the woods.

CORRESPONDENCE OF DISTRIBUTION PATTERN WITH OTHER PLANT SPECIES

Within the field plots, the two violet species differ in the types of other plant species with which they occur. Of the approximately 91 other species present in the 714 plots, some are highly associated with either V. sororia or V. fimbriatula, others are associated with both V. sororia and V. fimbriatula, while yet other species are associated with the absence of violets (Table 1). Nomenclature and taxonomy follow Gleason and Cronquist (1963).

Species associated with V. sororia include Rhus radicans which occurs with 30.7% of the V. sororia in the plots sampled in the field, and with only 4.3% of the V. fimbriatula. Other species are Pycnanthemum flexuosum, Daucus carota, Fragaria virginiana and Oxalis stricta which occur with 13.5, 10.1, 12.6 and 20 % of the V. sororia respectively, and with only 1.9, 2.3, 4.1 and 7.8 % of the V. fimbriatula respectively.

Species associated with V. fimbriatula are generally typical of and indicators of dry soils. They include Lechea intermedia,

Cladonia cristatella, Betula lenta, B. populifolia, Solidago hispida and S. graminifolia, which occur with 27.4, 10.8, 20.9 and 24.5 % of the V. fimbriatula and with only 0.5, 0.7, 10.1 and 13.3 % of the V. sororia in the field, respectively.

Other species of plants are associated with both V. sororia and V. fimbriatula. Rubus arundelanus is found growing with 51.5% of the V. sororia and 38.6% of the V. fimbriatula in the plots sampled in the field. Similarly, Achillea millefolium and Potentilla intermedia occur with 28.9 and 13.7% of the V. sororia and 17.5 and 16.8% of the V. fimbriatula in the field, respectively.

Species of plants found in plots where violets are absent are generally plants typical of relatively wet soil such as Impatiens biflora, Mimulus ringens, Onoclea sensibilis, Pilea pumila, Polygonum hydropiperoides, Thelypteris noveboracensis and Thelypteris palustris which occur with 0, 0, 3.4, 0, 0, 0.3, 0.3 % of the V. sororia in the field respectively, and with 0% of the V. fimbriatula in the field.

In addition to violets, the most common species in terms of the number of field plots they occupy, are Rubus arundelanus (281 plots), Achillea millefolium (154 plots) and Rhus radicans (148 plots). Of the 91 species in the field, only 10 are trees, of which Betula lenta and B. populifolia are the most common (70 plots). In the 714 field plots, the total number of species in a plot ranged from 1 to 11, with a mean of 5.2. There is a significant positive correlation between densities of both V.

sororia and V. fimbriatula and total number of all species per plot (figure 3).

In the woods, the species associated with violets in the area of the experimental sites were also recorded (table 2). Of these, the majority were also present in the field (the exceptions were Ostrya, Alliaria and Circaea spp.).

CORRESPONDENCE OF DISTRIBUTION PATTERN WITH LIGHT REGIMES

Midday PAR readings throughout the 1982 growing season in the 10 representative sites indicate that V. sororia growing in the woods receives significantly less light than either species growing in the field, as expected, although light levels are relatively high in the woods early in the season before the canopy closes. In the field, V. sororia receives significantly less light than V. fimbriatula (one-way Anova) (figure 4, table 3), because it generally grows in microsites with denser vegetation (figure 3). On average for the entire growing season, V. sororia receives approximately 12% of full sunlight in the woods, and approximately 70% of full sunlight in the field. After the canopy closes, V. sororia in the woods receives only about 50 microE/sq. m/sec, or 3% of full sun. Fluctuations in light, especially in the field, are due to sunny and shady days. Light measurements made from dawn to dusk on a day in late summer of 1980 (figure 49), and described more fully later, show some variation in light in the woods due to sunflecks. Viola sororia also is exposed to variable light in the field due to movement of the adjacent vegetation. Viola fimbriatula, in contrast, is generally exposed

to a relatively constant diurnal regime of full sunlight, because there is little adjacent vegetation.

CORRESPONDENCE OF DISTRIBUTION PATTERN WITH SOIL CHARACTERISTICS:

MOISTURE, PARTICLE SIZE, FIELD CAPACITY AND PH

Soil analyses of the 10 representative sites in field and woods show that on average V. fimbriatula grows in sites where soils are significantly drier, more coarsely-textured, and which have a lower field capacity than those of V. sororia.

Soil moisture content over time (Aug. 1981 to July 1982) is not different for V. sororia between sites in the woods and in the field. Also there is a highly significant difference between V. sororia (both in woods and field) and V. fimbriatula (one-way Anova) (figures 5 and 6, table 4; with values for V. sororia in the woods and field expressed both separately and merged). Viola sororia grows in soils that are on average almost twice as wet as V. fimbriatula soils (34% as opposed to 19% soil water content). The soils in the area at the bottom of the field in which violets are mostly absent are significantly wetter than the upper slope violet sites and have up to 76% soil water content, with a mean of 61%. These findings are supported by the results of the subjective rating of the 714 field plots as "wet" or "not wet". Ninety plots, located entirely at the bottom of the field were wet. Of these, only 10 plots had violets present, of which 9 had V. sororia (28 plants) and only 1 had V. fimbriatula (2 plants). Therefore, 13% of the plots in the field are wet, but they contain less than 4% of the V. sororia, and less than 1% of the V. fimbriatula plants. There is a significant negative rank correlation between presence of "wet" plots and presence of V. sororia, V. fimbriatula and hybrids per plot (figure 3).

Soil texture analysis shows that V. fimbriatula grows in coarser soil than V. sororia; V. fimbriatula soils have 43% gravel-sized and larger (>2 mm) particles, or three times more than those of V. sororia in either field or woods. Viola sororia soils in both field and woods are similar in composition in terms of soil particle size and have a relatively large amount of medium sand-sized particles (0.25 - 0.5 mm) (figure 7).

Analysis of the field capacity of the soil indicates that V. fimbriatula grows in soils that have a significantly lower field capacity than that of V. sororia, and that there is no significant difference in field capacities between V. sororia sites in the woods and in the field (table 5).

The soil is quite acid (pH 4 to 5) at all the V. sororia and V. fimbriatula sites tested in the field and woods (table 6). There is no significant difference among these sites.

CORRESPONDENCE WITH VEGETATION HEIGHT AND VEGETATION DENSITY

In the 714 field plots, vegetation height ranged from 7.6 to 120 cm, with a mean of 37.6 cm. Cover ranged from 1 (sparse) to 5 (dense), with a mean of 3.2 (medium density) (figure 3).

Viola sororia generally grows in denser plots with taller vegetation, whereas V. fimbriatula grows in barer plots with shorter vegetation. Density per plot of V. sororia had a highly significant positive correlation with both vegetation height and cover, Spearman $r = 0.45$ and 0.42 respectively ($p < .001$, $n = 444$, for both). Density per plot of V. fimbriatula, on the other hand, has a highly significant negative correlation with both vegetation height and cover, $r = -0.57$ and -0.58 respectively ($p < .001$, $n =$

444, for both. Species diversity decreases with increase in cover, as there is a significant negative correlation between the total number of all species/plot, and vegetation cover (figure 3).

Based on measurements of the largest plant in each plot, the correlation between number of leaves per plant and vegetation height and cover is significantly positive for V. sororia and significantly negative for V. fimbriatula (figure 3). The size of the largest leaves (blade length and width, and petiole length) is significantly positively correlated with vegetation height and vegetation density for both V. sororia and V. fimbriatula ($p < .001$ in most cases). The only exception is the leaf blade length of V. fimbriatula which is not significantly correlated with vegetation height.

There is no significant correlation between number of reproductives/plant and vegetation height or cover, for either species.

SIZE OF PLANT

Based on measurements of the largest plant in each plot in the field, V. fimbriatula had on average two times the number of leaves as V. sororia (V. fimbriatula had 5.3 leaves per plant with a maximum of 22 leaves per plant, whereas V. sororia had only 2.6 leaves per plant with a maximum of 10 leaves per plant). Viola fimbriatula also had six times more reproductives on average as V. sororia (0.99 as opposed to 0.15 reproductives/plant). There are significant correlations between number of leaves/plant, number of reproductives/plant, and density per plot, for both species (figure 3).

In the field as a whole, V. sororia has longer petioles and wider leaf blades, and V. fimbriatula has longer leaf blades. Average leaf dimensions (length X width X petiole) in mm are 38 x 45 x 103 for V. sororia, and 44 X 25 X 52 for V. fimbriatula, and for each species there are positive correlations among the three leaf dimensions. For V. sororia, the more V. sororia plants per plot the larger the leaf size; and for V. fimbriatula, the more V. fimbriatula plants per plot the smaller the petiole size (figure 3).

OTHER CORRELATIONS

Another way of interpreting the data from the quadrat analysis of the field is to compare all the plots in the field, with plots which contain only one species ("pure V. sororia" and "pure V. fimbriatula" plots), with plots which contain both species together (table 7). The results are in keeping with the other results in this study. In terms of number of plants per plot, both V. sororia and V. fimbriatula had a greater density in their own "pure" plots than in the plots containing both species. For V. sororia the largest leaves and somewhat more leaves and reproductives per plant were in the "pure V. sororia" plots. In contrast to V. sororia, for V. fimbriatula the petioles were smallest in the "pure V. fimbriatula" plots. Values of average vegetation height and cover were highest in the "pure V. sororia" plots, low in the "pure V. fimbriatula" plots, and intermediate in the plots containing both species which in turn were somewhat lower than the value for all the plots in the field. Hybrids grew in plots with even shorter vegetation (mean 13.1, range 6-24 cm)

but with greater cover (mean 2.7, range 1-5 cm) than V. fimbriatula on average.

DISCUSSION

The clumped spatial distribution of V. sororia and V. fimbriatula in the field, the negative correlation of the densities per plot of the two species, and the virtual absence of V. fimbriatula from the woods, correspond to soil moisture and light intensity. Aggregated distributions have been observed in other populations of violets in other studies (Schellner, Newell and Solbrig, 1982; Newell, 1983).

Viola sororia grows more often and in greater density in sites in which the soil is relatively moist, which is in turn related to the finer texture and higher field capacity of the soil as compared with soils of V. fimbriatula-dominated microsites. Of particular interest is the fact that there is no significant difference in average soil moisture content or field capacity between the field and woods microsites of V. sororia, indicating that habitat preference in this species may be largely determined by soil moisture. Viola sororia grows in both sunny field and shady woods habitats in the study area, and therefore tolerates a relatively wide range of light levels. In the woods after the canopy closes, V. sororia receives approximately only 3% of full sunlight, which is comparable to the 1 to 13% reported for this species by Solbrig, Newell and Kincaid (1980). Even in the field, V. sororia is not often exposed to full solar radiation, receiving on average 70% of full sunlight. This is because it generally

grows in areas where the vegetation is relatively tall and dense, and also is more common on the shadier southern side of the field. The light regime during the growing season varies somewhat in the woods due to sunflecks (Anderson, 1964), but generally is more variable in the field due to clouds and movement of the surrounding vegetation. Within the field, V. sororia has more leaves and is more abundant in taller denser vegetation (based on correlations in all the field plots, as well as on observations of the "pure V. sororia" plots), indicating greater success in this habitat. The density of plants per plot and the numbers of leaves and reproductives, which are all positively correlated for this species in the field, can be used to assess the "success" of plants (Harper and Chancellor, 1959). A positive correlation between number of leaves and reproductives is not surprising since flowers are produced in the axils of leaves (Solbrig, Newell and Kincaid, 1980), and larger violets tend to have more reproductives (Solbrig, 1981).

In contrast to V. sororia, V. fimbriatula occurs more often and in greater density in the more exposed sparsely vegetated areas of the open field where the soil is relatively dry, which is in turn related to the relatively coarse texture and low field capacity of the soil. In these sites, V. fimbriatula is generally exposed to full sunlight, and it is also most common on the sunnier north side of the field. Viola fimbriatula therefore is relatively tolerant of drought and of high light levels. As in V. sororia, there is a positive correlation between density of V. fimbriatula per plot, and numbers of leaves and reproductives per

plant. Within the field, this species has more leaves and is most abundant in the plots with shorter, less dense vegetation indicating greater "success" in this habitat. In a study of several grasses in a sandhill prairie, Barnes and Harrison (1982) also found that the distributions of the species were related to a soil moisture gradient, which was in turn related to the texture and water-holding capacity of the soil. The very infrequent occurrence of V. fimbriatula in the woods in the study area implies a requirement for relatively high light levels as compared with V. sororia. Viola fimbriatula may be interpreted as consisting of a central population in the dry-field, with a very marginal representation in the edge of the woods (see Antonovics, 1976). The absence of V. fimbriatula from the moister, more densely vegetated V. sororia-dominated parts of the open field may be related to the significantly lower light levels of these microsites or to competitive exclusion.

Both species are present in large numbers at the study site. They are present in approximately the same number of plots in the field, but V. fimbriatula occurs at 2.5 times the density per plot, and 3 times the density in the field, as V. sororia. This may be the result of lower competition from other plants due to drought stress in V. fimbriatula microsites, as compared with the moist but densely vegetated V. sororia microsites. Intraspecific competition may be more important for V. fimbriatula, and interspecific competition for V. sororia. There are fewer total species/plot in the most densely vegetated plots, which have relatively moist soil. Platt and Weiss (1977) also found that

when a resource is abundant, competition increases and species abundance decreases. Another reason for the larger numbers of V. fimbriatula in the field may be because this species has >6X more reproductives per plant than V. sororia (measured on the largest plant per plot). Viola fimbriatula has 2X more leaves and also a greater maximum number of leaves than V. sororia (on average for the largest plant per plot), which may help compensate for its relatively small leaf surface area.

Both species have larger leaf blades and petioles in the more densely vegetated and hence shadier parts of the field, and smaller leaf blades and petioles in the barer more exposed parts of the field, as expected for sun versus shade leaves (Givnish, 1979). Givnish (1982) states that competition for light may be the most important selection pressure for leaf height, with taller plants growing in areas of dense vegetation and most competition for light. Viola sororia has 2X the average petiole length, and greater minimum (4X) and maximum petiole lengths, than V. fimbriatula, which may either be the result of, or a contributing factor to, the habitat preferences of the two species. The correlation between petiole length and vegetation height and cover is particularly high for V. fimbriatula. The very short petioles which may be found in V. fimbriatula appear to be related to its ability to grow in the bare exposed field sites, where it would be advantageous for a plant to be close to the ground (either to conserve water by creating a protected, moister microclimate beneath the leaves, or to avoid the direct sun by growing beneath the shade of other plants). The relatively long petioles of V.

sororia may allow this species to overtop and outcompete V. fimbriatula for sun in the same habitat, and probably compete better with tall vegetation such as is frequently found in the V. sororia plots of the field. Viola fimbriatula has a longer blade than V. sororia, but this difference is relatively small, and does not compensate for the differences in petiole length between the two species in terms of the total height of the plant.

The association of V. sororia and V. fimbriatula with particular species of plants in the 714 field plots and in the woods, corroborates the evidence from the independent analysis of soil moisture. Viola fimbriatula is commonly found growing with species typical of dry soil such as pinweeds, British soldiers lichen, birches and goldenrod. In contrast, V. sororia, which grows in relatively moist soil, is found in the field predominantly with certain other plants such as the third most common species (poison ivy), and in the woods with species which are also mostly associated with V. sororia in the field. Other plants, including the two most common species in the field (blackberry and yarrow), are found growing with both violet species. In the woods, V. sororia is growing in what Raup (1938) and Ross (1958) have described for the Black Rock Forest as a mixed hardwood association.

Both V. sororia and V. fimbriatula are only rarely found growing in the wet soil at the bottom of the field, implying that both species and especially V. fimbriatula are intolerant of water-logged soils, or that the seeds are not dispersed there in the first place, or that the seedlings fail to survive. The

species of plants found growing in plots where violets are absent, or nearly absent, are plants typical of moist to wet soil, such as ferns.

The number of hybrids in the field is relatively low compared with the number of parent species (2%). The occurrence of hybrids in the field is significantly correlated with the distribution of both parent species. A high proportion (26%) of the 84 plots in the field which contain both parent species also contain hybrids, even though hybrids are found in only a small fraction (6%) of all the plots in the field. The leaf morphology of the hybrid looks intermediate between that of V. sororia and V. fimbriatula and it appears that the hybrid also has a habitat preference for the microsites occupied by both parents (although the vegetation in hybrid plots is low, generally more characteristic of V. fimbriatula than of V. sororia microsites). These results are consistent with a study of two stemmed violet species, Viola striata and Viola conspersa, in which the hybrids overlapped the range of the parents in soil moisture and pH (Kattenhorn, 1976). Anderson (1948, 1949) states that the first generation hybrid tends to be adapted to habitats intermediate between that of the two parent species. In addition to habitat preference, an obvious factor in the distribution of the hybrids in the field is the increased likelihood of interspecific cross-pollination in microsites where the two parent species are in close proximity to each other. Levin and Kerster (1974) report on fairly restricted gene flow in a number of insect pollinated plants, and Beattie (1976) found that in Viola papilionacea (a glabrate form of V.

sororia, Russell 1965), 50% of flights were within 30 cm, and the great majority within 100 cm. If the seeds are not dispersed far, there would tend to be a clustering of hybrids in and near plots where V. sororia and V. fimbriatula occur together. Other factors increasing the likelihood of cross-pollination between V. sororia and V. fimbriatula are that they share some of the same pollinators (Beattie, 1974), and bloom in the early spring when there is little competition from other plants for insect vectors (Beattie, 1972). In addition, pollinator activity is particularly high on sunny west-facing slopes (Beattie, 1969) and when plant density is high (Beattie, 1976); and there are generally more pollinators and hybridizations in disturbed and marginal habitats (Anderson, 1954; Beattie, 1969). Beattie (1969) reported frequent interspecific and intraspecific pollen transfer in 3 violet species in England.

No hybrids were found in the woods. This may be related to relatively high light requirements of the hybrid, or to factors reducing the production of hybrids such as the near-absence of one parent (V. fimbriatula), or the exclusion of many insects by deep shade (Beattie, 1969).

Soil pH does not appear to be an important factor in the distribution of the violets at the study site. The soil pH is quite acid (pH 4-5) in all the violet sites; a pH of 4 to 7 is ordinarily the range for acid soils (Coleman and Thomas, 1967), and the range of tolerance for most vascular plants is a pH of 3.5 to 8.5 (Larcher, 1980). Violets in general seem to show a preference for acid soil (Brizicky, 1961). McCullough (1941)

found similar results in several localities in W. Pennsylvania and W. Virginia, with soil pH ranging from 5 to 6.2 for V. sororia, and from 4.8 to 5.1 for V. fimbriatula, and with quality of growth apparently unrelated to pH value. Mycorrhizae may play a role in violet distribution, as they have been reported in Viola palustris and V. biflora (Brizicky, 1961).

EXPERIMENTS WITH TRANSPLANTS OF ADULTS,
EXPERIMENTAL SEED PLOTS, AND DISTURBANCE PLOTS

Field experiments were set up to help explain why V. sororia is abundant in both woods and moist areas of the field, but V. fimbriatula is abundant only in the dry areas of the field.

Experiments involving reciprocal transplants of adult plants, and other experiments involving seed germination and seedling establishment were carried out in the two contrasting habitats of shady woods and dry sunny field. The woods are considered the control habitat for V. sororia, and the dry field the control habitat for V. fimbriatula. Survivorship of seedlings and adults, predation, number and phenology of leaves and reproductives, phenotypic plasticity and convergence in leaf size and shape, and ecotypic differentiation were compared for the two species.

Another set of transplant experiments was established to investigate the absence of both species of violets in the wet soil at the bottom of the field.

In addition, seven plots in which the soil was disturbed were set up to assess the seed bank of the soil in both woods and field.

TRANSPLANTS BETWEEN WOODS AND DRY FIELD

INTRODUCTION

Viola sororia and V. fimbriatula were transplanted into dry-field and woods sites in order to investigate the phenotypic responses, mortality, and predation of the two species in relation to different environmental conditions; and to help explain the absence of V. sororia from the former site and of V. fimbriatula from the latter site.

METHODS AND MATERIALS

I did two transplant experiments involving V. sororia and V. fimbriatula. The first set of transplants, referred to as reciprocal transplant #1, was established in 1980, and clones were used so that the same genotype could be observed for environmentally-caused phenotypic differences. The second set of transplants, referred to as reciprocal transplant #2, was established in 1981. It replicated reciprocal transplant #1, but instead of using clones, plants of comparable sizes were used, and the V. sororia originated entirely from the woods whereas in reciprocal transplant #1 the V. sororia originated from both the woods and field habitats.

Reciprocal transplant #1: Plants of V. sororia and V. fimbriatula were collected in both field and woods, and cloned to produce a total of 100 ramets (see Harper, 1977), which were transplanted into the field and woods so that each genotype was growing in both habitats (control and experimental). The duration of this experiment was almost 3 years. The plants were collected in May

and early June of 1980, taken to the greenhouse where they were divided by cutting the rhizome, and grown in peat pots for three weeks. They were transplanted in July 1980, and observed through the spring of 1983. Twenty genets (see Harper, 1977) of V. fimbriatula from the field were cloned and transplanted so that one ramet of each genet was in a dry area of the field (control) and one ramet of each genet in the woods (experiment), for a total of 40 ramets. Thirty genets of V. sororia were cloned and transplanted so that one ramet of each genet was in the woods, and one ramet in a dry area of the field. Of these 30 V. sororia, 20 originated in the field and 10 originated in the woods. The purpose of using plants of V. sororia which originated in the two different habitats is to determine whether ecotypic differentiation exists. Plants were placed in rows at 30 cm intervals, and marked for identification with a numbered plastic stick on two sides of each plant.

Reciprocal transplant #2: A second set of reciprocal transplants involving another 100 ramets was begun on September 22, 1981, and observed through the spring of 1983. Since these plants were not cloned, they were matched for leaf number and size and rhizome size, (ANOVA, $p > .05$, no significant difference, for all the factors), and transplanted directly into their "native" and "foreign" habitats as control and experimental plants. A total of 50 V. fimbriatula were taken from the field, and 25 placed in the field (control) and 25 matched plants placed in the woods (experimental). A total of 50 V. sororia were taken from the woods, and transplanted with 25 control plants in the woods and 25

matched experimental plants in the field. Plants were again placed in otherwise undisturbed soil in rows across the woods and in a dry area of the field, at 30 cm intervals, and again marked with plastic sticks.

Throughout 1981 and 1982 for reciprocal transplant #1, and throughout 1982 for reciprocal transplant #2, the plants were censused approximately biweekly for number of leaves, number and type of reproductives, and mortality. A total of 1,927 plant-censuses were made. In addition, leaves were numbered consecutively as they appeared throughout the growing season, and, approximately monthly, the leaf dimensions (length, width and petiole) were measured, amount of predation per leaf estimated (7/8, 3/4, 1/2, 1/4, 1/10 or less of the leaf area eaten), and leaf senescence recorded. A total of 9,277 leaf dimension measurements, and 7,222 leaf predation estimates, were made.

RESULTS

MORTALITY OF PLANTS

In both transplant experiments, there was little mortality in the control plants and high mortality in the experimental plants.

In reciprocal transplant #1, on May 31 1983, almost 3 years after the transplant experiment commenced, for V. sororia, 80% of the plants in the woods (control) were alive, as opposed to only 57% in the dry area of the field (experimental); whereas for V. fimbriatula, 90% in the dry area of the field (control) were alive, as opposed to only 35% in the woods (experimental) (figure 8). Decline in plants present at the end of a growing season may be due either to senescence or death. In order to facilitate

interpretation of mortality, in reciprocal transplant #1, table 8 represents the maximum % of plants alive each year, and figure 9 is a bar graph of survivorship two years after the experiment commenced. For V. fimbriatula in the woods, mortality was highest in the winter in both 1980 and 1981; and for V. sororia in the field, mortality was highest during the growing season (June and July) in both 1981 and 1982. Mortality is spread out over the experimental period; V. fimbriatula in the woods lost approximately equal numbers of plants each year for the first 2 years and none over the winter of 1982, and V. sororia in the field lost no plants over the first winter, and approximately equal numbers over the next 2 years. Senescence begins relatively early for V. sororia in the woods (late August).

For reciprocal transplant #2 (figure 10), 1.5 years after the transplants were initiated (May 1983), for V. sororia, 100% of the plants in the woods (control) were alive, as compared with only 56% of the plants in the dry field (experimental) where most of the mortality (28%) again occurred during the growing season (May). For V. fimbriatula, 84% of the plants in the field (control) were alive, as opposed to only 64% of the plants in the woods (experimental). Senescence of the whole plant began approximately in August. Mortality was again highest for V. fimbriatula in the woods late in the season (August and later), and for V. sororia in the field earlier during the growing season (May).

NUMBER OF LEAVES PER PLANT

In both transplant experiments, leaves first appeared in early to mid April, and remained present until first snowfall (a few leaves were still present as late as Nov. 21, 1981) (figures 11, 12). Peak leaf production was May to July for reciprocal transplant experiment #1, and May to August for reciprocal transplant experiment #2; the plants in this latter experiment experiencing two peaks of leaf production, May for the woods and August for the field.

Throughout most of the growing season V. fimbriatula had more leaves than V. sororia (in both habitats), and the results of analysis of variance (2-way, no replication design) show that this difference is significant ($p < .05$) for average leaf number over the time of the experiment (table 9, 10). The greatest number of leaves present on a single plant of V. fimbriatula at any one time was 8 in the woods, and 7 in the field, in August 1982.

A comparison between plants of the same species growing in the two contrasting habitats generally shows no significant difference in average number of leaves per plant over time. In reciprocal transplant #1, there is no significant difference in average leaf number between control and experimental plants for either V. sororia (approximately 2.2 leaves) or for V. fimbriatula (approximately 3.7 leaves) (table 9). In reciprocal transplant #2, for V. fimbriatula there is again no significant difference between control and experimental plants (approximately 4.4 leaves), but V. sororia had significantly more leaves in the field (3.8 leaves) than in the woods (2.3 leaves) (table 10).

PHENOLOGY OF LEAF PRODUCTION AND SENESCENCE

In the transplant experiments, in 1982, each individual leaf was numbered with an indelible pen indicating the order of emergence of the leaves. It was therefore possible to follow the production and senescence of each individual leaf (figures 13 - 16). In general, the timing of leaf production and total number of leaves produced in one growing season were noticeably different between the woods and field habitats for both species. In the field, as contrasted to the woods, more new leaves were produced (about 2X as many) and they were produced much later into the growing season. In the field some V. sororia plants produced as many as 20 leaves each (reciprocal transplant #2), and some V. fimbriatula plants produced as many as 25 and 23 leaves each (reciprocal transplant #1 and #2 respectively). In contrast, in the woods, the maximum number of new leaves produced on an individual plant was only 8 for V. sororia (reciprocal transplant #2), and only 14 and 12 for V. fimbriatula (reciprocal transplant #1 and #2 respectively). The single exception was V. sororia in reciprocal transplant #1 which produced approximately the same number of leaves in the field and in the woods (10 and 12 leaves respectively).

Leaf production was staggered over the growing season, but ended earlier in the woods than in the field. In the field, new leaves were still produced in October in both V. sororia and V. fimbriatula (except in V. sororia in reciprocal transplant #1 which produced its last new leaves in August). In contrast, in the woods new leaves were produced only up to July in all cases.

More new leaves were produced each month in the field than in the woods, but most of the difference in the number of new leaves produced in the two habitats was due to the continued production of new leaves from August through October in the field only.

The width of the lines in figures 13-16 indicates the number of leaves present of a particular leaf sequence number. The majority of the plants produced leaf #1 and #2 and sometimes #3. Leaf sequence numbers higher than 3 are represented by thinner lines indicating that fewer plants produced these leaves. Generally, only 1 or 2 plants produced the very highest number of new leaves in any given habitat.

The senescence of leaves was also staggered over the growing season. Generally, leaves #1 and #2 senesced by July. Only in one plant (V. sororia in the woods, reciprocal transplant #1) did the second leaf remain the entire growing season. Some leaves produced early in the year outlived leaves produced later in the year.

SIZE OF LEAVES

Leaves were larger in the woods than in the field in length, width and petiole measurements for both V. sororia and V. fimbriatula at all times in both transplant experiments (figures 17-23). Figure 20 is an illustration of average leaf dimensions in reciprocal transplant #1, on a June day approximately two years after the transplant experiment began. Analysis of variance indicates that the differences in leaf dimensions are significant on average over the two year period (tables 9, 10).

Comparing the two species within the same habitats (woods, field), V. fimbriatula had significantly longer leaf blades, but V. sororia had significantly wider leaf blades and longer petioles. Viola sororia petioles were approximately 1.5 X longer in the woods, and approximately 2 X longer in the field, than those of V. fimbriatula.

Maximum leaf size for all transplants was achieved in July and August. Leaves were small at the beginning of the growing season, and leaves present in the autumn were smaller than in mid-summer.

NUMBER OF REPRODUCTIVES PER PLANT

Chasmogamous flowers appeared in April in both woods and field habitats in both transplant experiments (figures 24-33). Figures 26-33 illustrate the phenology and number of chasmogamous and cleistogamous reproductives. In general, both species, but especially V. fimbriatula, produced more cleistogamous than chasmogamous reproductives. In the field, the cleistogamous fruits usually remained present as long as the leaves (October).

Viola fimbriatula produced significantly more reproductives (flowers and fruits) per plant than V. sororia in both field and woods on average in both transplant experiments (figure 24, 25) (table 9, 10). When comparing control plants with experimental plants, for both V. sororia and V. fimbriatula, there was no significant difference in average number of reproductives over time.

In all transplant experiments, there were peaks in number of reproductives in the spring and again in late summer,

corresponding to chasmogamous and cleistogamous forms. For V. fimbriatula, in the woods the greatest peak was in spring and early summer, whereas in the field the greatest peak was later in the summer. For V. sororia, there is a peak in number of reproductives in the spring for both woods and field plants, with the woods again preceeding the field slightly; and in addition a mid summer peak in the woods (1982).

PREDATION

The average percent of leaf area eaten was lowest at the beginning and end of the season, and highest from June to early September, in both transplant experiments (figures 34, 35).

Predation was higher in the woods than in the field for both species. In particular, V. sororia in the woods had conspicuously and significantly higher predation (% leaf area eaten) than any of the other plants throughout the growing seasons in both transplant experiments (tables 11, 12). This frequently took the form of removal of the entire blade, leaving a bare petiole. On average annually, V. sororia in the woods had the highest predation not only in terms of % leaf area eaten (approximately 20%, or at least 2X as high as in any other group), but also in terms of percent leaves which were eaten at all (+ or - predation) (approximately 27%, or 2x as high), and in terms of percent of the leaves with bare petioles (approximately 18%, or at least 3X as high).

Predation was lowest for V. fimbriatula in the field, where there were few bare petioles (less than 1%), and the percent of leaf area eaten was less than 3%.

DISCUSSION

The results of both transplant experiments make sense in terms of the distribution pattern observed at the study site. For V. sororia, mortality was greatest in the dry field sites where it does not generally occur; and for V. fimbriatula mortality was greatest in the woods sites where it occurs only rarely. It is interesting that mortality occurred at different times of the year for the two species. For V. sororia in the field, mortality was highest in summer, the period of greatest growth and also highest temperatures and drought. This is evidence that V. sororia is intolerant of dry sunny conditions. Summer was also found to be the period of greatest mortality in a population of this species in Massachusettes (Solbrig, Newell and Kincaid, 1980), and also of Ranunculus sp. (Sarukhan and Harper, 1973), Plantago lanceolata and Salvia lyrata (Fowler and Antonovics, 1981), and of other species of plants (White, 1980). For V. fimbriatula in the woods mortality appears to be highest in late summer and in winter, which may indicate that this species develops a carbon deficit under the low light levels of this habitat and has inadequate food reserves to form overwintering buds. There is no obvious, consistent correspondence between mortality of these transplants and periods of low monthly precipitation (figure 38).

Average number of leaves produced per plant is used as a non-destructive measure of plant size and performance in violets (Solbrig, 1981; Waller, 1981), and in other species (Lewis and Zenger, 1982). In the transplant experiments there were generally no significant differences in number of leaves or reproductives

between control and experimental plants for either V. sororia or V. fimbriatula, and therefore these factors do not yield information as to habitat preference in this set of experiments. The only exception is that V. sororia in reciprocal transplant #2 produced more leaves per plant in the field than in the woods.

The reproductive pattern followed the same general pattern in both species. Chasmogamous (open, insected-pollinated) flowers were produced in spring (April, May), which then produced fruits (May, June). The chasmogamous flowers were followed by cleistogamous (closed, self-pollinated) flowers which were produced for the rest of the growing season (late May to autumn), and these cleistogamous flowers also produced fruits (June to autumn). This pattern is typical of that described for many species of violets (Darwin, 1877). Cleistogamous flowers have been studied extensively in violets, where they were first described as early as 1660 (see Uphof, 1938). The cleistogamous flowers are initiated by long-days, and the chasmogamous flowers by short-days (Evans, 1956; Russell, 1960). This is true even in some southern hemisphere violets (Holdsworth, 1966), and is related to photoperiod and temperature (Lord, 1980, 1981).

There were generally more cleistogamous than chasmogamous flowers and fruits produced in both transplant experiments, and this was especially true for V. fimbriatula. This may be the result of the longer period of time during which cleistogamous reproductives were produced and also because in V. fimbriatula more cleistogamous reproductives were produced per month. The large number of cleistogamous flowers and therefore high levels of

self-fertilization, and the comparatively low production of chasmogamous fruits appears to be common in violets and has been reported in 3 English species (Beattie, 1972), and in V. sororia (Solbrig, 1981), V. pubescens and several species of acaulescent blue violets (McKinney and Blum, 1981).

Viola fimbriatula produces more leaves and reproductives than V. sororia in both habitats, indicating that this is a characteristic difference between the two species, and may be related to the different life history strategies of the two species. The two species behave similarly in that they both produced more new leaves later into the season in the field than in the woods.

Leaf predation was significantly higher for V. sororia in the woods than in any other transplant. Since this species is found in abundance in the woods, and survivorship in the transplant experiments was high, V. sororia appears to be adapted not only to growing under relatively low light levels, but also to functioning with 1/5 of its leaf area eaten. Similarly high values for predation of V. sororia, also after the first month of growth, were reported by Solbrig, Newell and Kincaid (1980). Viola fimbriatula may be less palatable than V. sororia, as it was less frequently eaten, and this may be in part related to its thicker and more pubescent leaf. There was more predation in the woods than in the field for both species, and this may be due to differences in types and numbers of predator species, or to differences in leaf morphology between the two habitats. Leaves of both species are thicker (greater leaf specific weight) in the

field than in the woods (as discussed later in the section on plant size and carbon allocation). Violets are susceptible to slugs, caterpillars and other predators (Hudak, 1976; Coon, 1977) which may be more abundant in the woods than in the field. Beattie and Lyons (1975) report that slugs rarely leave the humidity and shade near the substrate in order to feed. Some of the plants, particularly in the woods, had all the leaves cropped to just below the blade, apparently by rabbits or deer. Predation of plant parts other than leaves has been documented. Rhizomes of V. papilionaceae have been found in vole nests (Gates and Gates, 1980); and in my study, death of one V. fimbriatula in the woods of reciprocal transplant #2 was due to the tunnel of a rodent.

Viola sororia had significantly longer petioles than V. fimbriatula within the same habitat, which would mean that if the two plants are growing in close proximity, as occasionally occurs in the field, V. sororia may overtop and shade V. fimbriatula. Viola sororia may outcompete V. fimbriatula under such conditions, as V. fimbriatula appears to have relatively high light requirements. The relatively long petioles of V. sororia may allow it to survive in the field sites with tall dense vegetation, by enabling it to receive adequate sunlight. Givnish and Vermeij (1976) point out the advantage of long petioles in preventing mutual shading. Conversely, the very short petioles of V. fimbriatula in the field (approximately half as long as those of V. sororia in the same habitat), would seem appropriate in the dry exposed field sites where this species predominates.

Both species have bigger leaves in the shady woods than in the exposed, sunny, dry areas of the field, which is consistent with concepts of sun and shade leaves (Parkhurst and Loucks, 1972). The smaller leaves produced in the early spring and late fall may be the result of shorter photoperiods (Russell, 1960).

Similar reports of phenotypic plasticity in other plant species are common in the literature (Antonovics, 1976; White, 1980; Stebbins, 1979; Mack and Harper, 1977). In transplant experiments carried out by Clausen and Hiesey (1958), some of the characters which were highly modified by the environment were size of leaves and stem, and total growth. Other "plastic" characters are pubescence, and number of shoots, leaves and flowers (Bradshaw, 1965).

EVIDENCE FOR ECOTYPES

Ecotypes or ecological races of a species are genetically adapted to certain environmental conditions, and remain different when transplanted into a common garden. This was demonstrated by extensive experiments with several species of plants, including Viola tricolor, by Clausen, Keck and Hiesey (1940, 1947, 1948); Clausen and Hiesey (1958); and Clausen (1962).

Viola sororia is abundant in both woods and field habitats in the study area, and, as has been discussed, there is significantly more sunlight in the field than the woods, but no difference in soil moisture (on average over time). Viola sororia plants grade without real interruption from field into woods in some areas, but the edge of the field provides a fairly abrupt ecological boundary, especially in terms of light. Selection for different genotypes of V. sororia may have occurred in the two habitats in terms of morphological characteristics such as leaf size, leaf number or reproductive number, or of some other factors affecting survival.

As stated earlier for reciprocal transplant #1, some of the V. sororia plants used in that experiment originated in the woods, and others originated in the field. Plants of both types were cloned and transplanted so that one ramet of each genet was in the woods habitat, and the other ramet of each genet was in the dry V. fimbriatula-dominated area of the field. Twenty V. sororia genets originated in the field, and ten genets originated in the woods, for a total of 60 ramets. Thus far, the V. sororia plants have been treated regardless of origin.

However, a closer look at the characteristics of the V. sororia plants based on their habitat of origin may cast some light on the possibility of ecotypic differentiation between the woods and field individuals of V. sororia. For these purposes, V. sororia plants which were transplanted back into their habitat of origin will now be considered the "control" plants, and the plants which were transplanted into the foreign habitat will be considered the "experimental" plants. Survivorship was recorded on June 3, 1983, almost 3 years after the date of transplant; and number of leaves and reproductives, and leaf size were measured on July 1, 1982, 2 years from the date of transplant.

There is some evidence for ecotypic differentiation in terms of survivorship after almost 3 years, as more of the "control" plants survived in both woods and field. Of the V. sororia plants transplanted into the woods, 90% of those from the woods as opposed to only 75% of those from the field survived; and of the V. sororia transplanted into the field, 60% of those from the field as opposed to only 50% of those from the woods survived.

In terms of numbers of leaves per plant, of the V. sororia plants growing in the field, there were significantly more leaves per plant in the transplants from the field (control) than from the woods. In terms of number of reproductives per plant, there was no significant difference between control and experimental plants (table 13).

In terms of leaf size, there appears to be selection for larger plants in the woods. Plants originating in the woods as compared with those originating in the field had significantly

larger leaves in terms of blade width and petiole length (but not blade length) in both woods and field habitats. Two-way analysis of variance demonstrates that these differences are significant on average over a period of two years (table 13). In addition, these measurements are significantly different on 4 out of the 8 dates on which measurements were made.

In summary, there is some evidence for ecotypic differentiation between woods and field plants of V. sororia in terms of survivorship, number of leaves and size of leaves, but not in terms of number of reproductives.

More of the "control" plants survived and had more leaves in comparison with "experimental" plants, indicating that there may be adaptation to each habitat (with the exception of leaf number in the woods). Similar results with greater survivorship of "native" plants were obtained in reciprocal transplants of Anthoxanthum odoratum (Davies and Snaydon, 1976), and of Ranunculus flammula (Cook and Johnson, 1968).

It appears that for V. sororia, there has been selection for plants with larger leaves in the woods, and for plants with relatively smaller leaves in the field. These results are consistent with the fact that plants receive less light in the woods than in the field, and larger leaves would be adaptive in the woods for increasing photosynthetic leaf surface area at lower light levels. In the field, light levels are higher, and therefore the adaptive value of smaller leaves would be to reduce heat load and transpiration (Givnish, 1979; Givnish and Vermeij, 1976), at the cost of photosynthetic leaf surface area. Since

light levels are much higher in the field than in the woods this is probably a reasonable tradeoff, as heat load is probably more of a limiting factor than photosynthetic rate in the field. It is particularly interesting that, in addition to the leaf phenotypic plasticity already discussed where leaves of both species grow larger in shady versus sunny habitats, there also appears to be a genetic element to leaf size in the two contrasting habitats, with selection for plants with larger leaves in the woods.

There is evidence for similar local ecotypic differentiation in other plant species such as Plantago lanceolata and Salvia lyrata (Fowler and Antonovics, 1981). Some studies report ecotypic differentiation over short distances such as 10 meters (Bradshaw, 1965), and a few meters (Cook and Johnson, 1968), and in 1 to 2 meters (Jain and Bradshaw, 1966). Ecotypes of Anthoxanthum odoratum have been found to have differentiated in less than 1 meter and in less than 60 years, in response to soil metal concentrations. Experiments with reciprocal transplants of Anthoxanthum odoratum found that, as in this study, selection was also influenced by different light conditions, and "native" plants had higher survival and better "performance" (dry matter, # tillers) than "alien" plants (Davies and Snaydon, 1976). Much evidence for ecotypic differentiation over sharp boundaries and within short periods of time, comes from studies of several species of plants growing on heavy-metal contaminated soils around mines (Cook, Lefebvre and McNeilly, 1972; Hickey and McNeilly, 1975; Jain and Bradshaw, 1966; Antonovics et al, 1971; Antonovics, 1976).

SEED PLOTS

INTRODUCTION

Seed plots were established in the woods and dry areas of the field in order to examine the importance of seed germination and seedling establishment on the distribution of V. sororia and V. fimbriatula at the study site. The distribution patterns observed in the adult plants may largely reflect factors which were operating at the seedling stage (Sagar and Harper, 1961; Harper, 1977). Monthly rainfall data were obtained in order to investigate the effect of drought on seedling survivorship.

METHODS AND MATERIALS

Two sets of seed plots were established. Seeds of V. sororia and V. fimbriatula were planted in 50 cm X 50 cm plots in both the shady woods and dry-field sites, in 1980 (seed plot #1) and also in 1981 (seed plot #2). They differ in that seed plot #1 was observed over a two year period, and seed plot #2 over a one year period; fewer seeds were planted per plot in seed plot #2; and also that seed plot #1 involved cleared plots only, whereas seed plot #2 involved both cleared plots and undisturbed plots.

Seed plot # 1: In October, 1980, approximately 790 V. sororia and 720 V. fimbriatula seeds were planted separately in each 50 cm X 50 cm plot. In all the plots, the vegetation was completely removed and the soil loosened, and the seeds were planted under a thin layer of soil.

Seed plot #2: In October, 1981, 113 V. sororia and 426 V. fimbriatula seeds were planted separately in each 50 cm x 50 cm

plot in both field and woods. The number of seeds planted was determined by availability of seeds. One set of plots had soil cleared of vegetation ("disturbed") and the seeds planted under a thin layer of soil as in seed plot #1, and in the other set of plots the vegetation was left untouched ("undisturbed") and the seeds scattered on the surface.

Throughout 1981 and 1982 for seed plot #1, and throughout 1982 for seed plot #2, the plots were observed approximately every two weeks for number of plants. Percent germination and percent mortality were calculated for each plot. In seed plot #1 only, approximately monthly throughout 1981 and 1982, 10 (occasionally 5) plants were selected randomly and measured for number of leaves per plant, and for leaf size (length, width and petiole). A total of 212 plant censuses, and 1,414 leaf dimension measurements, were made.

Monthly precipitation data for 1980-1983 for West Point, New York (approximately 3 miles from the study area) were obtained from the National Oceanic and Atmospheric Administration (NOAA) (figure 39).

RESULTS

Germination and Mortality of Plants:

Seed plot #1: Germination (May 1981) was approximately the same in all plots in both woods and field (26%). In the first year (by Aug. 11, 1981) many more V. sororia (92%) died in the field plot than in any other plot (46% for V. sororia in the woods, 57% for V. fimbriatula in the woods, and 60% for V. fimbriatula in the field) (figure 36). In the second year (by late July 1982), the

highest mortality was in both "experimental" plots: V. sororia in the field (214 out of 221 cohorts, or 97%) and V. fimbriatula in the woods (168 out of 194 cohorts, or 87%). In contrast, there was relatively low mortality in both of the "control" plots: V. sororia in the woods (111 out of 168 cohorts or 66%), and V. fimbriatula in the field (159 out of 209 cohorts or 76%).

Mortality was the highest in the early part of the growing season (May, early June), especially in the first year when the plants were seedlings. In the second year, there was relatively little mortality in the field plots; most of the plants that survived the first year in the field also survived the second year. In contrast, in the woods plots, V. sororia showed a moderate decline in the woods especially in late May, and V. fimbriatula showed a sharp decline which continued through the growing season.

Seed plot #2: In the field, germination was much lower (1/10) in the undisturbed than in the disturbed plots; whereas in the woods, germination was similar in the disturbed and undisturbed plots (Table 14). Because germination was so low in the undisturbed plots in the field, the ensuing results refer only to the disturbed seed plots.

As in the first year of seed plot #1, mortality (as of July 31, 1982) was highest in V. sororia in the field (28 out of 31 cohorts, or 90%), and lower for both V. sororia in the woods (16 out of 36 cohorts, or 44%) and for V. fimbriatula in the woods (39 out of 93 cohorts, or 42%) (figure 37). However in contrast to seed plot #1, mortality was also fairly high in V. fimbriatula in the field (58 out of 70 cohorts, or 83%). Mortality was highest

again in the early part of the growing season (May) when the seedlings were very small, and this was especially true in the field plots. Figure 38 represents survivorship in the undisturbed seed plots.

Size of Plants:

In the measurement of randomly selected plants in seed plot #1, there was no significant difference in number of leaves per plant either between species in the same habitat, or between the two habitats for the same species, on average over the first two seasons of growth from seeds (figure 40, table 15). These plants were selected randomly using X-Y coordinates from computer-generated random numbers. There were on average 2-3 leaves per plant. There does not appear to be any noticeable increase in average number of leaves per plant over time; even 1 month old seedlings have an average number of leaves per plant comparable to that of plants after 2 seasons of growth. In the plants selected randomly, only 1 reproductive was observed in the first year of growth (cleistogamous flower on V. sororia in the field).

Leaf size for seedlings was consistently and significantly different both between species, and between habitats; and these differences generally were obvious from the inception of the observations when the seedlings were only 1-2 months old (figures 41-43, table 15). Leaves are larger in length, width and petiole measurements in the woods than in the field for both species. Within the same habitat, V. sororia has wider leaves, and V.

fimbriatula has longer leaves, but petiole length is the same for both species.

DISCUSSION

Seedlings in all cases exhibited highest mortality in the first month after germination when the plants were small and only the cotyledons and 1 to 2 small leaves were present. Plants over one year old exhibited relatively low mortality. This pattern of mortality has been observed by other workers, and the high seedling mortality rate linked to drought (soil moisture, competition) or to herbivores (Cook, 1979a, 1979b). The mortality rates in the first year of the control seedling plots were similar to that reported for a natural population of a different violet species (Viola blanda) which had 64% mortality in the first year of growth (Cook, 1983). Survival of violet seedlings is strongly size dependent (Solbrig, 1981), and seedlings which germinate early are relatively large and have high survivorship as adult plants (Cook, 1980; Ross and Harper, 1972). Some of the mortality observed in this experiment may be due to density-dependent "self-thinning" (Harper, 1980; White, 1980).

Mortality is generally consistent with what might be expected from the distribution pattern observed at the study site where V. sororia is absent from the dry areas of the field and V. fimbriatula is largely absent from the woods. In both seed plot experiments, mortality for V. sororia was highest in the dry field, and lowest in the woods. For V. fimbriatula, mortality in the field was low as expected in seed plot #1, but is surprisingly high in seed plot #2. This may be the result of fairly high precipitation (figure 39) in May 1981 when seed plot #1 plants were seedlings, and abnormally low precipitation in May 1982 when

seed plot #2 plants were in the very vulnerable early seedling stage and when most of the mortality of V. fimbriatula in the field occurred. Plants that do survive the first year generally survive the second year. Drought is cited as a major cause of seedling mortality in V. sororia (Solbrig, Newell and Kincaid, 1980), as well as competition and predation (Newell, Solbrig and Kincaid, 1981). The ability of V. fimbriatula to occupy dry field microsites may be largely related to its ability to withstand drought as a seedling, provided conditions are not more severe than usual. Viola fimbriatula is rarely found in the woods, and it is therefore surprising that mortality in V. fimbriatula in the woods was low in the first year (in both seed plots). However, in the second year, mortality was high, as expected, and these results may be interpreted as pointing to higher light requirements for adult plants as opposed to seedlings in V. fimbriatula. The limiting factor for V. fimbriatula in the woods may be relatively high light requirements for adult plants. Cook and Lyons (1983) found that two populations of V. fimbriatula in tree blowdowns went to extinction in six years as the canopy filled in, supporting the idea that light may be an important factor in survivorship.

For the disturbed plots in both experiments, percent germination was approximately the same for both species in both habitats, so it appears that habitat (woods versus field) does not affect germination and that the distribution pattern is not related to differential germination rates of the two species provided that there is some soil disturbance.

Lack of soil disturbance appears to be a limiting factor in seed germination in the field, but not in the woods, for both species. In the woods germination was approximately the same in the undisturbed as in the disturbed plots, whereas in the field germination rates were strikingly lower in the undisturbed plots as compared with the disturbed plots. This difference in germination in the two habitats appears to be due to differences in soil characteristics. The relatively loose soil and sparse vegetation in the woods even when the soil is left undisturbed is conducive to seed germination. In contrast, the relatively compacted dry soil with matted vegetation in the field when the soil is left undisturbed makes seedling germination and establishment difficult. Disturbing the plots mimics natural conditions as violets often grow in disturbed sites (Solbrig, Newell and Kincaid, 1980). A disturbance such as a tree blow-down causes light, soil moisture, temperature, and soil nutrient content to rise (Cook, 1983), and light has been shown to cause germination of buried seed (Harper, 1977). Several studies on violets and other species, both with sown seed and with naturally occurring seedlings, have shown that more plants become established on disturbed soil than in mature vegetation (Cook, 1979b; Cook and Lyons, 1983). Competition from grasses caused inhibition of germination and high seedling mortality in teasel (Werner, 1977), and affected survivorship of seedlings of 3 coexisting Plantago species (Sagar and Harper, 1961).

For V. sororia, the average number of leaves per plant is similar in the seedling and 2-year old plants (seed plot

experiments) and adult plants (transplant experiments). In contrast, for V. fimbriatula the seedlings and 2-year old plants (seed plot experiments) have not yet developed as many leaves per plant as are found in adult plants (transplant experiments), in either woods or field.

The size of the leaves of the plants throughout the first 2 years of growth is consistent with what has been observed in the transplant experiments, and obvious even in one month old seedlings. Leaves are larger in the woods than in the field, as expected. The small leaves and short petioles of V. fimbriatula may be adaptive to dry field conditions, and conversely the relatively large leaves of V. sororia may be adaptive to the shady woods environment.

Only one reproductive was observed in the first year in the plants being randomly sampled, probably because field conditions are relatively severe. Reproductive output and onset of reproduction is more related to size or vigor than to age (White, 1980), and decreased fecundity and plant size due to increased density stress is well documented (Harper, 1977; Palmblad, 1968). Formation of reproductives in violet seedlings is rare in nature (Cook, 1983), but under "ideal" greenhouse conditions an 8-week old V. sororia seedling was observed to produce several fruits and 21 leaves (Solbrig, 1981).

TRANSPLANTS BETWEEN WOODS AND WET FIELD

INTRODUCTION

A third set of transplants, involving only V. sororia, was also established in order to investigate the absence of violets at the bottom of the field where the soil is so wet that water was visible throughout much of the summer of 1982.

METHODS AND MATERIALS

On June 1, 1982, 10 genets of V. sororia were matched with another 10 genets for leaf size and number, and rhizome size. All of these plants originated in the woods. Without a stay in the glasshouse, one set was transplanted into the woods (control), and the other set of matched plants was transplanted into the wet soil at the bottom of the field (experimental). These plants were placed in rows at 15 cm intervals and each plant marked with two numbered plastic sticks for identification. Plants were censused through May 1983.

RESULTS

Approximately one year after this transplant experiment was initiated (May 1983), mortality was much higher in the wet field (experimental) than in the woods (control). In the woods, 100% of the plants were still alive, whereas in the wet field only 40% of the plants were still alive. Of the 6 plants that died in this latter site, 3 plants died within the first 3 months and the other 3 plants died during the winter. Viola sororia was also more

productive in the woods than in the wet field in number of reproductives. In May 1983, the time of spring flowering, there were 1.3 reproductives per plant in the woods and 0 reproductives in the wet field site. The number of leaves produced per plant on average over time was the same in the two transplant experiments ($p=.56$), with approximately 2 leaves per plant.

Predation (percent leaf area eaten) in August was 29% in the woods as opposed to only 16% in the wet field, and in September was 61% in the woods as compared to only 44% in the wet field.

DISCUSSION

The results of this transplant experiment, with high mortality and low reproductive rate in the wet soil at the lower end of the field, make sense in terms of the distribution of violets at the study site as there were very few violets present in this habitat. The most obvious cause of this mortality is the water-logged soil (soil moisture content of up to 80%, figure 5). This experiment demonstrated high mortality of adult plants, but seed and seedling mortality may also play an important role in the exculsion of violets from this site. Also, it is possible that fewer seeds are dispersed into this area, because ants aid in violet seed dispersal and ants probably avoid such wet microsites. However, it seems that some seeds must arrive at this site through forcible ejection from the capsules, or simply by washing down from the uphill parts of the field. This experiment was carried out only with V. sororia, but the results would probably be even more dramatic with V. fimbriatula since it grows in even drier

soils than V. sororia and occurs even less frequently in this wet part of the field. Predation of leaves was apparently not an important factor in the survivorship rates, as predation was higher in the woods site than in the wet field site.

DISTURBANCE PLOTS

INTRODUCTION

Disturbance plots, in which the vegetation was removed and the soil turned over, were established in order to assess the violet seed bank of the soil, and to observe colonization of disturbed habitats by violets. Violet seeds can stay dormant in the soil for years (Solbrig, 1981; Cook and Lyons, 1983). Longevity of 400 years has been reported for seeds of Viola arvensis, and 31 years for V. tricolor (Harrington, 1972). Soil disturbance brings buried seeds closer to the surface where they germinate, and also may reduce competition (Solbrig, Newell and Kincaid, 1980; Solbrig, 1981). An average density of 250 seeds per square meter was measured for V. sororia in Massachusetts (Solbrig, 1981). These disturbance plots simulate events occurring in nature, such as a blow-down.

METHODS AND MATERIALS

In the spring of 1980 seven 1 meter X 1 meter permanent disturbance plots were established in the study area (5 plots in the field and 2 in the woods). The plots were marked off with corner stakes and wire, all the vegetation including violets was removed, and the soil turned over to a depth of 25 cm. These plots were then censused for violets over a two year period (June 1980 to August 1982).

RESULTS

Of the field plots, 3 originally contained mostly V. fimbriatula, and 2 contained mostly V. sororia (table 16). One of these V. sororia plots became so overgrown with vegetation that it was lost after the first year. A single V. sororia plant grew in 4 of the 5 field plots, early in the experiment. These V. sororia plants died, so that at the end of the two year period, all plots contained only V. fimbriatula (up to 40 plants), including the plot which had originally contained mostly V. sororia. Two of the field plots added approximately equal numbers of V. fimbriatula in each of the two years, another plot gained 9 V. fimbriatula in the first year and lost 4 of them by the second year, and the other field plot which had originally contained mostly V. sororia had 40 V. fimbriatula in the second year.

Of the woods plots, one originally contained only V. sororia, and the other was in an area of the woods where no violets were present. The woods plot which originally contained only V. sororia also had only V. sororia present throughout the two years, gaining 1 V. sororia in the first year, and an additional 7 in the second year. The woods plot which originally contained no violets, still had no violets after two years.

DISCUSSION

In the field, both V. sororia and V. fimbriatula are present in the soil seed bank. In the field, V. fimbriatula appears to be a better colonizer of bare, disturbed soil than V. sororia, even in the site which had formerly been dominated by V. sororia. This

may mean that V. fimbriatula has a larger seed bank than V. sororia. The greater drought tolerance of V. fimbriatula would be advantageous in these denuded plots which were directly exposed to the sun in the first year as they became revegetated.

In the woods, only V. sororia grew in the disturbed plots, and this is in keeping with the abundance of this species in this habitat. It appears that there may be few V. fimbriatula seeds in the soil in the woods, since the seed plot experiments demonstrated that if seeds are present, both V. fimbriatula and V. sororia will germinate and survive in the woods at least the first year. The total absence of violets from the other woods plot which did not originally contain violets is somewhat perplexing as it is only 5-6 meters from the edge of the field where both species of violets grow, and conceivably seeds could have been dispersed there by forcible ejection from the capsule and by ants. Ants were very common in the study area, and were particularly noticeable in the dry areas in the field. Seeds of a form of V. sororia (V. papilionacea), have been observed to travel across open areas by ballistic dispersal along a mean distance of 2.8 meters, with a maximum of 4.8 meters (Beattie and Lyons, 1975). The absence of violets from this disturbed plot in the woods may be due to absence of seeds in the soil, or possibly to some microclimatic factor inhibiting germination or establishment of seedlings.

PLANT SIZE AND CARBON ALLOCATION

INTRODUCTION

Plants of both species were collected in the field and woods, and were measured and tested for differences in plant size and weight, in carbon allocation to plant parts, and in leaf blade area and thickness. These comparisons should shed some light on plant responses and relative "fitness" in the contrasting habitats.

METHODS AND MATERIALS

In August 1982 a total of 46 violet plants was collected from the woods and field, with 12 V. sororia and 11 V. fimbriatula plants from each habitat. The number of leaves and reproductives per plant, and the length and width of the rhizomes were recorded.

The 136 leaves from these plants, plus an additional 50 leaves collected from other plants, for a total of 186 leaves of the two species in the two habitats were measured (27 leaves of V. sororia in the woods, 42 leaves of V. sororia in the field, 45 leaves of V. fimbriatula in the woods, and 72 leaves of V. fimbriatula in the field). The leaves were measured for length and width of the blade, and length of the petiole (the latter measured only on the 136 leaves from the whole plants collected). Each leaf was traced on a digitizing surface (Graphics Tablet, Apple Computer Corp.) by projection of a film negative, and the average surface area determined. In addition, the average shapes of the leaves in each set were determined using the leaf boundary method and Fourier analysis of Kincaid and Schneider (1983).

Somewhat fewer leaves of V. fimbriatula were used (43 leaves from the woods, and 65 leaves from the field), and the number of V. sororia leaves were the same as mentioned above. Each leaf was dried and weighed, and the leaf specific weight calculated as dry weight/surface area, to be used as an indicator of the thickness of the leaf.

The plants were also divided into leaf blades, petioles, rhizomes, roots and reproductives, which were dried in an oven, and weighed. The mean dry weight and the percent carbon allocation (dry weight of plant part/dry weight of whole plant) for each plant part were calculated. The data were subjected to analysis of variance, with a total of 88 pairwise comparisons.

RESULTS

The results will be divided into two sections: data for the whole plant, and for individual leaves. The results will first be compared between the woods and field for V. sororia and V. fimbriatula, and then between the two species growing in the same habitat. In contrast to the transplant and seed plot experiments, this analysis involves plants as they occur naturally in the woods and field. The "field" is different for the two species, since V. sororia and V. fimbriatula generally grow in different microsites, as already described. The statistics, and results of analysis of variance are in tables 17 and 18. Figures 44 and 45 represent the dry weights and percent carbon allocation of the plant parts, respectively.

WHOLE PLANT

For V. sororia and V. fimbriatula there were significantly more leaves per plant in the field than in the woods. Within the same habitat, V. fimbriatula had significantly more leaves/plant (2X) than V. sororia.

Viola fimbriatula had significantly more reproductives/plant (>4x) in the field than in the woods. There was no significant difference for V. sororia between the two habitats. Within the same habitat, V. fimbriatula had significantly more reproductives per plant than V. sororia.

For V. fimbriatula, the rhizome was significantly longer and wider in the field than in the woods, whereas there is no significant difference in the rhizome dimensions in V. sororia between field and woods habitats. Within both the field and woods, V. sororia had a significantly larger rhizome than V. fimbriatula.

There is no significant difference in total leaf surface area per plant between the two habitats for either species, or between the species in the same habitat.

For V. fimbriatula, the dry weight of the whole plant was significantly greater (>2 X as great) in the field than in the woods. In contrast, there is no significant difference between the dry weights of the V. sororia plants in the two habitats. Within the woods habitat, V. sororia weighed significantly more than V. fimbriatula (almost 2X), whereas within the field there is no significant difference between the dry weights of the two species.

The heaviest plant part was the rhizome for V. sororia, and the leaf blades for V. fimbriatula, in both woods and field.

For V. sororia, the leaf blades and petioles weighed more in the field than in the woods (almost 2x), and there was no difference in the weight of any of the other plant parts between the two habitats. For V. fimbriatula, all the plant parts except the petioles weighed more in the field than in the woods (leaf blades 2X, rhizomes 2X, roots 3X, and reproductives 9X).

In the woods, V. sororia had significantly heavier rhizomes and roots than V. fimbriatula, and there was no difference between the two species in the weight of the other plant parts. In the field, V. sororia had significantly heavier petioles and rhizomes, and V. fimbriatula had heavier reproductives, and there was no difference between the two species in the weight of the leaf blades or roots.

For V. sororia, percent carbon allocation to the roots was significantly greater in the woods than in the field. For V. fimbriatula, percent carbon allocation was significantly greater for the petioles in the woods than in the field (>2X), and for the reproductives in the field than in the woods (>4X).

In the woods, percent carbon allocation to leaf blades and petioles was greater for V. fimbriatula than for V. sororia. In the field percent carbon allocation to petioles was greatest for V. sororia, and to roots and reproductives was greatest for V. fimbriatula. In both woods and field, percent carbon allocation to rhizomes was greater for V. sororia than for V. fimbriatula. There was no significant difference between the two species in

percent carbon allocation to roots or reproductives in the woods, or to leaf blades in the field.

INDIVIDUAL LEAVES

Figure 46 represents the average computer-generated leaves in each group. For both V. sororia and V. fimbriatula, the leaf blades were significantly bigger in the woods than in the field, and in V. fimbriatula the petiole was longer in the woods (>2X) than in the field. It follows that individual leaf blade area was significantly greater in the woods than in the field for both species.

Within each of the two habitats, V. sororia had a significantly wider leaf, greater individual leaf blade surface area (>2X greater), and also longer petioles (>3X in the field) than V. fimbriatula. There was no difference in leaf blade length between the two species.

For both species, the leaves were significantly thicker (greater leaf specific weight) in the field than in the woods. The leaf of V. fimbriatula was significantly thicker than V. sororia in the field only.

The average shapes of the leaves, independent of areas, were significantly different between the two habitats, for both species (Friedman's Method, testing the Fourier amplitudes for $n=30$ frequencies in a two-way test, $p<.001$).

DISCUSSION

WOODS VERSUS FIELD FOR BOTH SPECIES:

Both species exhibit differences in their growth response to the contrasting habitats of woods and field, reflecting either phenotypic plasticity and/or genotypic differentiation (ecotypes).

Viola fimbriatula seems particularly successful in the field as compared with the woods, as may be expected, since the field is its major habitat. Not only were there significantly more leaves and reproductives and larger rhizomes per plant in the field as opposed to the woods, but the entire plant weighed more (2X), as did all the plant parts except the petioles. The reproductive effort of V. fimbriatula in the field is particularly striking. The reproductives were 4X greater in number, 9X greater in weight, and had a greater percent carbon allocation, than in the woods. Plant dry weight and fecundity have been used as a measure of fitness in other studies (Hickey and McNeilly, 1975; Cook, Lefebvre and McNeilly, 1972; Harper and Chancellor, 1959).

For V. sororia, on the other hand, there was no significant difference between woods and field in the total plant weight nor in the weight of any plant parts except the leaves, which weighed more and were more numerous in the field. There was also no difference in number of reproductives per plant or in rhizome size. Similarly, there was no significant difference in percent carbon allocation to any plant parts (except to the roots). This suggests that V. sororia was relatively successful in both field and woods, which corresponds to its abundance in both habitats.

Both species had larger leaves in the woods than in the field. This is in keeping with the concept of sun and shade leaves. Viola fimbriatula had longer petioles and a greater percent carbon allocation to the petioles in the woods than in the field, which would allow it to avoid self-shading and compete better for the low light of the woods (see Abrahamson and Gadgil, 1973). Holler and Abrahamson (1977) also found a greater percent of plant biomass in petioles (and blades) as a result of increased shading in Fragaria virginiana. The relatively short petioles in the dry exposed areas of the field may enable V. fimbriatula plants to conserve moisture by creating a moist microclimate beneath the leaves close to the ground, and also may reduce heat load through shading by surrounding vegetation. Viola sororia, on the other hand, had equally long petioles in woods and field, which may be in response to the low light levels in both the woods and the densely vegetated areas of the field.

It is particularly interesting that there was no significant difference in total leaf area per plant between the woods and field habitats, for either species. This is because there were fewer but larger leaves in the woods, and more numerous but smaller leaves in the field. As a result, the total leaf surface area available for photosynthesis was the same for the two habitats. However, there are other factors besides total leaf surface area involved in photosynthetic capacity. Sun leaves are generally characterized by higher photosynthetic rates, more cells with more abundant chloroplasts, thicker leaves (thicker mesophyll, cuticle, epidermis), higher transpiration rates, and

greater stomatal and vein density. In contrast, shade leaves have lower photosynthetic rates, but perform more efficiently at low light intensities; larger chloroplasts with higher concentrations of chlorophyll and accessory pigments, although the chlorophyll content per leaf area is lower; and thinner leaves (Boardman, 1977; Larcher, 1980). Both species have significantly thinner leaves in the woods as opposed to the sunny field, a well known response to lowered light intensity (Harper, 1977). Similar results, with thicker, smaller and more pubescent leaves formed in the sun as opposed to the shade were found in Arnica cordifolia (Young and Smith, 1980); and thicker leaves were found in sun leaves of Fragaria virginiana (Chabot, Jurik and Chabot, 1979). Optimal leaf size may be related to trade-offs between photosynthesis, and leaf temperature and water loss (Parkhurst and Loucks, 1972). There was no difference in the weight of the individual leaves for either species between the woods and field habitats, probably because the leaves are larger but thinner in the woods, and smaller but thicker in the field.

Average leaf shape as determined by Fourier analysis was different between habitats. Leaf shape is often measured by a "length to breadth" ratio, or by more cumbersome means (Russell, 1956). Differences in leaf shapes in contrasting habitats have been found in other species such as Ranunculus (Cook and Johnson, 1968).

VIOLA SORORIA VERSUS V. FIMBRIATULA WITHIN THE SAME HABITAT:

The two species differ consistently in certain characteristics, regardless of habitat. Such characters are

apparently species-specific, as opposed to other characters which reflect relative fitness in a particular habitat. Viola sororia always had larger, heavier rhizomes with a greater percent carbon allocation; and always had larger leaf blades (width, area and weight) and also petiole length, than V. fimbriatula. Viola fimbriatula, on the other hand, always had more leaves and more reproductives than V. sororia. The more numerous leaves of V. fimbriatula compensate for their small size, as the total leaf surface area is the same for both species. The longer petioles of V. sororia mean that if the two species grow close together, V. sororia could outcompete V. fimbriatula for light.

In the woods, V. sororia appears to be more successful than V. fimbriatula in that the whole plant weighed significantly more, as did the below-ground plant parts (rhizome and roots). There was no difference in the weight of the reproductives, leaf blades, or petioles (V. fimbriatula had more leaves per plant). Percent carbon allocation to roots and reproductives was the same for the two species, whereas V. sororia allocated a greater percent of its carbon to rhizomes, and V. fimbriatula to leaves in this habitat.

In the field, there was less difference between the two species, the whole plant and also the leaf blades and roots were the same in weight. This corresponds with the abundance of both species in the field (as opposed to the woods). In addition, in the field, V. sororia had a greater percent of its carbon allocated to rhizomes and petioles than V. fimbriatula, whereas V. fimbriatula had a greater percent of its carbon allocated to reproductives and roots. Greater carbon allocation to roots is

correlated with drier soil (Jordan and Miller, 1980; Weibe, 1980; Abrahamson and Gadgil, 1973), because the plants can then extract more water from the soil (Ludlow, 1980); and also with sun versus shade plants (Young and Smith, 1980). This greater carbon allocation to roots may explain the greater drought tolerance of V. fimbriatula and its ability to grow in dry soil, as has been found in male plants of Rumex acetosella (Zimmerman and Lechowicz, 1982).

Both species have the same total leaf surface area and total blade weight per plant, meaning that the plants have the same leaf area exposed to the sun for photosynthesis. This is because V. fimbriatula has smaller but more numerous leaves than V. sororia in the same habitat. Both species also have the same blade weight per plant. Viola fimbriatula has thicker leaves than V. sororia in the field, related to its sunnier drier microsite within the field.

PHYSIOLOGICAL DATA

Responses of V. sororia and V. fimbriatula to environmental factors were examined. These include leaf water potential and diffusion resistance, in relation to solar radiation, air temperature, relative humidity, and soil moisture content. This ecophysiological approach clarifies some aspects of the distribution of V. sororia and V. fimbriatula.

LEAF WATER POTENTIAL

INTRODUCTION

Leaf water potential is a measure of the energetic availability of water to the plant tissues (Larcher, 1980). Leaf water potential is determined by the rate of water supply from the soil and roots, and the rate of water loss through the stomates and cuticle (Chabot and Bunce, 1979). In order to investigate the drought tolerance of the two species, the leaf water potential at the temporary wilting point was measured in the laboratory for both species. In addition, in order to determine the relative values of the leaf water potential of the two species in the field and woods, and also to determine whether either species is near its temporary wilting point under natural field conditions, the leaf water potential of both species was measured in the two habitats at the study site on two days in mid-summer.

METHODS AND MATERIALS

Water was withheld from plants of V. sororia and V. fimbriatula which had been growing in the greenhouse. The water

potential of the leaves was determined at the temporary wilting point for 16 leaves of V. sororia and 15 leaves of V. fimbriatula, using a Scholander-type pressure chamber (Model 3000, Soil Moisture Equipment Corporation, Santa Barbara) (Slavik, 1974).

Leaf water potential was measured on two mid-summer days (July 16 and August 19, 1982) for V. sororia and V. fimbriatula growing in woods and field habitats. Measurements were made at mid-day when leaf water potentials are usually near a minimum (Richter, 1976). July 16 was a hot day (30 degrees) during a period of drought, and 40 leaves were analyzed. August 19 was a cooler day (22.5 degrees), and 77 leaves were analyzed. In addition to leaf water potential, photosynthetically active radiation using a Licor #180 sensor (July 16 only), and soil moisture content (3 replicates per site) were measured for each site.

RESULTS

In the laboratory experiment, V. fimbriatula had a lower leaf water potential at the temporary wilting point than V. sororia (-18.1 ± 2.3 bars versus -13.1 ± 1.1 bars, $p < .001$).

In the field experiments, on both days, leaf water potential was significantly lower in the field than in the woods for both species, and there was no significant difference in leaf water potential between the two species within the field (tables 19, 20). Soil moisture content of the V. fimbriatula site in the field was much lower than in any other site (1/3 as dry in July, and 1/2 as dry in August).

DISCUSSION

Viola fimbriatula is more drought tolerant than V. sororia, as it wilted at a lower leaf water potential. A fully hydrated leaf has a water potential of close to zero, and the more dehydrated the leaf the more negative the leaf water potential (Slavik, 1974). The difference in leaf water potential at the temporary wilting point for the two species is consistent with the previous findings of -22.9 ± 5.4 bars for V. fimbriatula (Curtis and Kincaid, 1984) and -15.0 ± 2.6 bars for V. sororia (Solbrig, Newell and Kincaid, 1980) in Massachusetts.

In the sunny field, it is particularly interesting that in spite of the fact that V. fimbriatula was growing in much drier soil than V. sororia (especially on July 16), it still developed the same leaf water potential as V. sororia on both days, suggesting that V. fimbriatula is better either at obtaining or at conserving water, or both (tables 19, 20). In addition, on the hot dry day in July, V. sororia at -12 bars was close to its temporary wilting point of -13 bars, whereas V. fimbriatula at -12 bars was still far from its temporary wilting point of -18 bars. As expected, V. fimbriatula had a higher leaf water potential in the woods, than in the field. Viola sororia also had a higher leaf water potential in the woods, as compared with the field.

DIURNAL LEAF DIFFUSION RESISTANCE, AIR TEMPERATURE,
RELATIVE HUMIDITY, AND LIGHT

INTRODUCTION

Leaf diffusion resistance is the resistance of the leaf to gas exchange, and is the result of stomatal, boundary layer and cuticular resistances (Larcher, 1980). Diurnal leaf resistance to the diffusion of water vapor was measured in V. sororia and V. fimbriatula growing in close proximity in the field. Leaf diffusion resistance is an important factor in photosynthetic rate. If diffusion resistance is high, water loss is reduced, but there is a tradeoff in terms of lowered photosynthesis (Orians and Solbrig, 1977; Gates, 1976) and increased leaf temperature (Mooney and Gulman, 1979).

METHODS AND MATERIALS

On September 19, 1980, diurnal leaf diffusion resistance of the upper and lower surfaces of the blade was measured on one leaf of V. sororia and 2 leaves of V. fimbriatula in the sunny field. These measurements were made every hour from 9:45 to 17:45 EDST (eastern daylight savings time) using a porometer (Licor, model Li 60). In addition, measurements of total solar radiation, relative humidity, and air temperature at violet height (2.5 cm from the ground) were made in the field and woods every 1/2 hour from 7:00 to 18:00 EDST. Total solar radiation was measured with an Eppley precision radiometer. A thermistor and capacitance sensor were used to measure air temperature and humidity (Weather Measure, model HT-1001-R).

RESULTS

In both species, leaf diffusion resistance was higher in the upper surface than in the lower surface of the leaf blade (figures 47, 48).

In both species there was more fluctuation in diffusion resistance in the upper surface of the leaf as opposed to the lower surface. There was no great difference in diffusion resistance between the two species in the lower leaf surface, and resistance was similar in the upper leaf surface early in the day but the stomates in the upper leaf surface closed earlier in the day in V. fimbriatula than in V. sororia.

In the woods light levels remained low throughout much of the day, except for a rise due to a sunfleck in the afternoon as a result of a gap in the canopy. Air temperature was approximately the same in both field and woods. Relative humidity in both field and woods was highest early in the day (100%), and dropped to approximately 60% by mid-afternoon, and rose again towards dusk (figure 49).

DISCUSSION

Both V. sororia and V. fimbriatula showed a pattern of high leaf diffusion resistance early in the day, followed by a decrease in midmorning, with a gradual rise in the afternoon. These results are similar to those of Solbrig, Newell and Kincaid (1980) for V. sororia growing in Massachusetts; and of Curtis and Kincaid (1984) who found rapid stomatal closure for V. fimbriatula at 16:00 solar time which may have been related to heat load.

It is interesting that leaf diffusion resistance was similar in the two species. The relatively high diffusion resistance of the upper leaf surface of V. fimbriatula in mid-afternoon may be the result of stomatal closure due to high temperature and light at this time of day. There is some disagreement in the literature about whether drought-tolerant genotypes respond to water stress by keeping their stomates open even at low leaf water potentials, or by closing their stomates (Jones, 1980). According to Chabot and Bunce (1979), dry-habitat species are able to maintain photosynthesis at more negative leaf water potentials, are able to resume photosynthetic activity rapidly when rewatered, and often close their stomates at lower leaf water potentials than more mesic species. Drought-related stomatal closure could be a factor in the drought-tolerance and also the apparent high light requirements of V. fimbriatula; the increased resistance would decrease the water loss through the stomates but slow down photosynthesis (Chabot, Jurik and Chabot, 1979).

Diurnal air temperature and relative humidity were similar in both field and woods, whereas the field received more light than the woods. Humidity appears to be inversely proportional to temperature in both habitats (temperature rose throughout the day, whereas humidity fell).

DISCUSSION

The two closely related species, V. sororia and V. fimbriatula, appear to divide the habitats of woods and open field along a soil moisture and light gradient. As a result, the adults are seldom in direct competition. Both species grow abundantly in the field, but occur in the same meter square plot only 12% of the time; and only V. sororia grows in significant numbers in the woods. Viola sororia grows predominantly in the moist, shaded areas of both the woods and densely vegetated parts of the field, where competition from other plants is high. Viola fimbriatula grows predominantly in the sunny, dry, sparsely vegetated areas of the field, where environmental conditions are relatively severe but competition is low. Soil moisture content, which is in turn related to soil texture and water-holding capacity, appears to be the controlling factor affecting the distribution pattern in the field, whereas light appears to be the controlling factor in the woods.

The distribution pattern of V. sororia may be due largely to intolerance of dry soil particularly in the seedling stage, and also to tolerance of low light levels and of competition. This species appears to require moist soil in both seedling and adult stages; mortality in the dry field was 97% for seedlings (seed plot experiment), and 40% for adults (reciprocal transplant experiment), after two years. Viola sororia appears to tolerate shade, and to be a better competitor than V. fimbriatula, as it grows in the densely vegetated parts of the field, and also in the

woods, where it competes with other plants for light, water and nutrients.

In contrast, the distribution pattern of V. fimbriatula appears to be due to drought tolerance in both seedlings and adults, and high light requirements and poor competitive ability in adults. Seedlings germinate and grow well in both dry field and woods, whereas adults have high mortality in the woods (in both transplant and seed plot experiments). It appears that V. fimbriatula is physiologically able to grow in both the dry and moist areas of the field, but is restricted to the drier parts of the field by its poor competitive ability. In studies of Sedum and Linum on granite outcrops, Sharitz and McCormick (1973) have shown that a species capable of growing under moderate conditions may be restricted in nature to more severe environmental conditions because of interspecific competition. In other studies, heavy-metal-tolerant ecotypes of several plant species have been shown to be capable of growing in normal soil, if it were not for competitive displacement (Cook, Lefebvre and McNeilly, 1972; Hickey and McNeilly, 1975; Cook, 1981).

Viola fimbriatula may be virtually excluded from the woods because adult plants cannot maintain a positive carbon balance under low light conditions (Chabot, Jurik, and Chabot, 1979). Viola fimbriatula appears to be relatively xerophytic in comparison with V. sororia. It has a relatively high carbon allocation to roots in the field. Its leaves are narrow and thick with a relatively small surface area, and it withstands high water stress. Smaller leaves have the advantage of reduced water loss

and heat load, but the disadvantage of reduced photosynthetic surface area, for which V. fimbriatula compensates by producing more numerous leaves (total leaf surface area was the same in the woods and field). However, there also is evidence that xerophytic leaves have lower maximum rates of photosynthesis, and tend to be competitive only under dry conditions (Orians and Solbrig, 1977; Chabot and Bunce, 1979). Therefore, V. fimbriatula may do well in very dry sunny habitats, but cannot maintain itself in shade because of its low photosynthetic rate.

Seed germination does not appear to be a factor in the exclusion of V. fimbriatula from the woods, or of V. sororia from the field, as seeds of both species germinated readily when planted in both habitats, particularly if the soil was disturbed in the field. Seed availability in the field is probably not a major factor in the distribution pattern, as seeds of both species are probably widely dispersed around the field, by forcible ejection and by ants. Ants are common in the study area, and do not show a preference for seeds of a particular species (Culver and Beattie, 1978; Beattie, Culver and Pudlo, 1979). In contrast, in the woods, seed availability may be a factor in the absence of V. fimbriatula, since seedlings should have been present (naturally, or in the disturbance plots) if the seeds had been present. Finally, the relatively large seed size of V. sororia may have survival advantage under conditions of high density and competition, as in the V. sororia microsites in the field (see Harper, 1977; Hickman, 1977).

Predation can play an important role in the balance of species in a community (Huffaker, 1971; Harper, Clatworthy, McNaughton and Sagar, 1961), including violets (Cook, 1979b). However, predation appears to be less important than drought, low light levels or competition for survival of V. sororia and V. fimbriatula at the study area. Predation is highest for V. sororia in the woods, where this species is quite successful. However, predation may be a contributing factor in the virtual exclusion of V. fimbriatula from the woods, as predation is higher in this habitat. Schellner et al. (1982) and Solbrig (1981) also found that environmental factors and competition were major factors determining growth rate and plant size in violets.

Hybrids are present in the field in fairly low numbers relative to the numbers of V. sororia and V. fimbriatula. They show a preference for plots occupied by both parent species, with over half the hybrids found in plots which contain the parental species. Factors that may help maintain the distinctiveness of the two species include their spatial and ecological separation, the large amount of selfing by cleistogamous flowers, probable differences in pollinators (Beattie, 1974), and the reportedly reduced fertility of the hybrids (Brainerd, 1904b, 1924). One of the earliest reported cases of ecological isolation was by Clausen (1926), between Viola arvensis and V. tricolor in which hybridization was reduced due to spatial separation by soil pH (see Stebbins, 1950).

Both species exhibit great variability in leaf size in different environments, related primarily to phenotypic plasticity

but also to some degree of genotypic differentiation, as seen in the reciprocal transplants of clones of V. sororia originating in sun and shade habitats. When the two species do occur together in the field, V. sororia could probably outcompete V. fimbriatula for resources, particularly light, since it has longer petioles than V. fimbriatula in the same habitat. Further studies involving competition experiments between the two species would be informative.

The plasticity exhibited in leaf size has taxonomic significance, and indicates that V. fimbriatula should be included in V. sagittata. Several taxonomic descriptions use petiole length as one of the characters distinguishing V. fimbriatula from V. sagittata, with the petiole longer than the blade in V. sagittata, and shorter than the blade in V. fimbriatula (Brainerd, 1906b; Klaber, 1976; Gleason and Cronquist, 1963; Russell, 1965). In addition, V. sagittata is described in the literature as growing in moister soils than V. fimbriatula (Pollard, 1898; Baird, 1942; Russell, 1960, 1965; Gleason and Cronquist, 1963). I found that petiole length varied greatly with environment, particularly with light and soil moisture conditions, and therefore is not a good taxonomic character. This is in agreement with Cronquist's unpublished revision of Gleason and Cronquist (1963) in which V. fimbriatula is included in V. sagittata (Cronquist, personal communication). In the woods, the petioles were generally as long as, or longer than the blades, or more like V. sagittata. In contrast, in the field, the petioles were only 1/3 to 3/4 as long as the blades, or more like V. fimbriatula.

(table 21). This is because petioles of V. fimbriatula were consistently and significantly longer in the shady woods than in the dry, sunny field (table 21). These results apply to all the groups studied: reciprocal transplant #1 (using clones), reciprocal transplant #2, in plants collected from where they occur naturally in the two habitats, and in the seed plots. I have used the specific epithet "fimbriatula" instead of "sagittata" in this manuscript since this is not a taxonomic treatment, and because V. fimbriatula is the name in current usage in manuals (Gleason and Cronquist, 1963; Radford et al., 1968; Fernald, 1950) and in ecological studies (Solbrig, Newell and Kincaid, 1980; Cook and Lyons, 1983; Curtis and Kincaid, 1984).

The number of leaves per plant is related to the "fitness" of the plant (Solbrig, 1981), and it was greater in sites where the plants were also most abundant as evidenced by the field quadrat analysis, and by plants collected in the field and woods. Viola fimbriatula has more leaves and more reproductives than V. sororia. On average, in plants occurring naturally, there were approximately 1.5 to 3 leaves per plant for V. sororia (woods, and field) which is similar to the 1 to 2 leaves per plant reported for this species by Solbrig, Newell and Kincaid (1980); as contrasted with approximately 5 to 6 leaves per plant for V. fimbriatula (field).

Viola fimbriatula appears to be more of an "r" selected species, and V. sororia appears to be more of a "K" selected species, based on the following characteristics which have been associated with these strategies (Pianka, 1978; Solbrig, 1971;

Solbrig and Simpson, 1974, 1977; Jain, 1979; Beattie and Lyons, 1975). Viola fimbriatula has a higher reproductive rate, smaller seeds, smaller leaves, and is more adapted to a less stable and harsher environment where mortality is probably density-independent and where intraspecific competition is probably stronger than interspecific competition. It may be more inbred, and according to Cook and Lyons (1983) has earlier seed production and more rapid growth than V. sororia. In contrast, V. sororia has some characteristics typical of "K" selection: lower reproductive rate, larger seeds, larger leaves, and is adapted to a more stable, mature and equable habitat where mortality is probably density-dependent and where interspecific competition is probably stronger than intraspecific competition. It may be more outbred, has high predation, and is rather long-lived (>10 years, Solbrig, Newell and Kincaid, 1980).

CONCLUSIONS

Habitat partitioning corresponds to morphological and physiological differences in V. sororia and V. fimbriatula. Viola sororia does not grow in the dry microsites in the field due to its broad thin leaves and poor drought-resistance, but it is a better competitor for light in the densely-vegetated field sites and in the woods. Evidence indicates that coexistence in the field occurs because V. fimbriatula is more drought-resistant but a poorer competitor, and has a dry-soil refuge.

This study documents the existence of different microhabitats within the superficially uniform field, and demonstrates habitat partitioning along environmental gradients, particularly soil moisture and light.

The data indicate that V. fimbriatula should be included in V. sagittata, based on plasticity in petiole length. This illustrates how ecological studies can be of value to taxonomy, by distinguishing between genotypic and phenotypic variation.

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TABLE 1. PLANT SPECIES IN THE 714 1 m X 1 m PLOTS IN THE FIELD.

SPECIES	ASSOCIATION WITH <u>V. SORORIA</u> AND <u>V. FIMBRIATULA</u>		
	% OF TOTAL <u>V. SORORIA</u>	# OF PLANTS OF <u>V. FIMBRIATULA</u>	# PLOTS
<u>Acalypha</u> sp.	0.8 %	0.4 %	3
<u>Acer</u> sp.	3.9	1.8	16
<u>Achillea millefolium</u>	28.9	17.5	154
<u>Amphicarpa bracteata</u>	1.5	0.7	23
<u>Antennaria plantaginifolia</u>	1.4	3.7	20
<u>Apocynum</u> sp.	1.0	0	2
<u>Artemisia vulgaris</u>	0.3	0.4	2
<u>Asparagus officinalis</u>	0	0	1
<u>Athyrium felix-femina</u>	0	0	1
<u>Berberis thunbergii</u>	0.4	0.3	7
<u>Betula</u> (<u>lenta</u> , <u>populifolia</u>)	10.1	20.9	70
<u>Botrychium</u> sp.	0.1	0	1
<u>Bryoandersonia illecebra</u>	0.5	0.1	4
<u>Carya</u> sp.	3.0	3.6	22
<u>Carex</u> sp.	0	0	1
<u>Chrysanthemum leucanthemum</u>	0.1	0.1	1
<u>Cirsium arvense</u>	0.1	0	4
<u>Cladonia cristatella</u>	0.7	10.8	17
<u>Cladonia pyxidata</u>	0.1	0.2	1
<u>Cornus</u> sp.	4.2	2.1	22
<u>Cyperus strigosus</u>	3.3	0.1	18
<u>Daucus carota</u>	10.1	2.3	31
<u>Dennstaedtia punctilobula</u>	2.9	0.1	12
<u>Dianthus armeria</u>	2.0	1.6	2
<u>Epilobium ciliatum</u>	0	0	2
<u>Equisetum arvense</u>	0.4	0.1	5
<u>Fragaria virginiana</u>	12.6	4.1	51
<u>Fraxinus americana</u>	1.0	0.1	2
<u>Galium obtusum</u>	0.1	0	3
<u>Geranium maculatum</u>	3.5	0	14
<u>Gnaphalium obtusifolium</u>	0.1	0	2
<u>Hamamelis virginiana</u>	1.0	0.1	2
<u>Hedeoma pulegioides</u>	0.5	6.7	21
<u>Hieracium</u> sp.	3.1	0.5	7
<u>Hypericum</u> sp.	1.5	0.1	5
<u>Impatiens biflora</u>	0	0	5
<u>Juncus effusus</u>	0	0	1
<u>Lechea intermedia</u>	0.5	27.4	52
<u>Linaria vulgaris</u>	5.0	3.7	40
<u>Liquidambar styraciflua</u>	2.9	0.8	12
<u>Liriodendron tulipifera</u>	3.7	0.9	33
<u>Lobelia spicata</u>	1.4	1.0	8
<u>Lonicera japonica</u>	0	0.1	4
<u>Lycopus americanus</u>	9.8	0.5	60
<u>Medicago lupulina</u>	0.1	0	1
<u>Mimulus ringens</u>	0	0	11

<u>Mitchella repens</u>	0.4	0.2	1
<u>Oenothera perennis</u>	0	0	5
<u>Onoclea sensibilis</u>	3.4	0.1	33
<u>Osmunda claytonia</u>	0	0	2
<u>Oxalis stricta</u>	20.0	7.8	77
<u>Panicum dichotomum</u>	1.2	6.1	26
<u>Parthenocissus quinquefolia</u>	6.1	0.5	19
<u>Pilea pumila</u>	0	0	4
<u>Plantago rugelii</u>	0	0	1
<u>Polygonum hydropiperoides</u>	0	0	4
<u>Polygonum sagittatum</u>	3.3	0	28
<u>Polystichum acrostichoides</u>	0.4	0	7
<u>Polytrichum commune</u>	11.1	8.7	42
<u>Potentilla intermedia</u>	13.7	16.8	66
<u>Prunella vulgaris</u>	1.4	0.2	13
<u>Pycnanthemum flexuosum</u>	13.4	1.9	53
<u>Pycnanthemum virginianum</u>	0.1	0	13
<u>Quercus sp.</u>	0.7	0.9	6
<u>Ranunculus acris</u>	2.6	0.1	21
<u>Rhus radicans</u>	30.7	4.3	148
<u>Rosa sp.</u>	0.1	0	4
<u>Rubus arundelanus</u>	51.5	38.6	281
<u>Rudbeckia hirta</u>	0.7	0.8	5
<u>Rumex acetosella</u>	1.0	0.2	80
<u>Satureja vulgaris</u>	8.0	0.5	67
<u>Scutellaria laterifolia</u>	0.3	0	8
<u>Silene sp.</u>	0	0	1
<u>Sisyrinchium graminoides</u>	1.1	0	4
<u>Solanum carolinense</u>	0.1	0.5	7
<u>Solidago bicolor</u>	0.7	0.5	8
<u>Solidago carolinense</u>	0.1	0.5	7
<u>Solidago (hispida, graminifolia)</u>	13.3	24.5	109
<u>Spiraea tomentosa</u>	0	0	1
<u>Thelypteris noveboracensis</u>	0.3	0	15
<u>Thelypteris palustris</u>	0.3	0.1	18
<u>Thuidium delicatulum</u>	0	0	1
<u>Trifolium agrarium</u>	3.3	1.8	27
<u>Trifolium pratense</u>	2.2	0.3	4
<u>Triodia flava</u>	0.3	0	1
<u>Tsuga canadensis</u>	0.3	0.2	1
<u>Vaccinium vacillans</u>	0.8	1.4	10
<u>Veronica officinalis</u>	1.4	0.7	9
<u>Vicia sp.</u>	5.8	0	13
<u>Viola fimbriatula</u>	22.7	100.0	278
<u>Viola sororia</u>	100.0	24.4	250
<u>Viola sororia x fimbriatula</u>	8.8	8.6	42
<u>Vitis sp.</u>	2.9	3.6	8

TABLE 2. PLANT SPECIES IN THE WOODS

TREES AND SHRUBS

Acer rubrum
Betula lenta
Cornus florida
Fraxinus americana
Hamamelis virginiana
Liriodendron tulipifera
Ostrya virginiana

HERBS

Alliaria officinalis
Berberis thunbergii
Circaea quadrisulcata
Dennstaedtia punctilobula
Fragaria virginiana
Hedeoma pulegioides
Lobelia inflata
Lobelia spicata
Oxalis stricta
Parthenocissus quinquefolia
Polygonum sp.
Rubus sp.
Veronica officinalis
Viola fimbriatula
Viola sororia
Vitis sp.

TABLE 3. PHOTOSYNTHETICALLY ACTIVE RADIATION (microE/m sq./sec)

Each site measured at solar noon, on 20 days (5/3/82-11/2/82).

See figure 4.

	<u># SITES</u>	<u>MEAN</u>	<u>SD</u>	<u>N</u>
SOR - WOODS	2	183	298.4	40
SOR - FIELD	4	1045	394.8	51
FIM - FIELD	3	1498	453.5	60
VIOLETS ABSENT - FIELD	1	910	360.0	20

ONE-WAY ANOVA TABLE
(overall ANOVA significant, $p < .001$)

	<u>F</u>	<u>V1,V2</u>	<u>p</u>	
SOR-WOODS vs SOR-FIELD	131.52	1,89	0	***
SOR-WOODS vs FIM-FIELD	260.62	1,98	0	***
SOR-FIELD vs FIM-FIELD	30.96	1,109	.00001	***
VIOLETS ABSENT-FIELD vs SOR-WOODS	68.73	1,78	0	***
VIOLETS ABSENT-FIELD vs SOR-FIELD	1.78	1,69	NS	
VIOLETS ABSENT-FIELD vs FIM-FIELD	27.79	1,78	.00002	***

TABLE 4. SOIL MOISTURE CONTENT.

Water content as percent of dry weight.

Sampled on 10 days; 8/81, 4/82 - 10/82; 3 replicates/site.

See figures 5, 6.

	<u># SITES</u>	<u>MEAN</u>	<u>SD</u>	<u>N</u>
SOR - WOODS	2	32.02	11.92	58
SOR - FIELD	4	35.76	9.81	77
FIM - FIELD	3	18.90	6.91	87
VIOLETS ABSENT - FIELD	1	61.18	14.28	30

ONE-WAY ANOVA TABLE *
(overall ANOVA significant, $p < .001$)

	<u>F</u>	<u>V1,V2</u>	<u>p</u>	
SOR-WOODS vs SOR-FIELD	4.0	1,133	.05	NS
SOR-WOODS vs FIM-FIELD	70.18	1,143	0	***
SOR-FIELD vs FIM-FIELD	164.84	1,162	0	***
VIOLETS ABSENT-FIELD vs SOR-WOODS	103.24	1,86	0	***
VIOLETS ABSENT-FIELD vs SOR-FIELD	110.82	1,105	0	***
VIOLETS ABSENT-FIELD vs FIM-FIELD	458.04	1,115	0	***

* Dunn-Sidak method, all pairwise comparisons,

p' for $p = .05$ with 6 pairs = 0.0085.

TABLE 5. SOIL FIELD CAPACITY.

18 samples per site.

	# SITES	MEAN	SD	N
SOR - WOODS	2	.7547	.08	36
SOR - FIELD	4	.7582	.09	72
FIM - FIELD	3	.4190	.11	54
VIOLETS ABSENT - FIELD	1	.6854	.11	18
SOR - WOODS + FIELD	6	.7571	.09	108

ONE-WAY ANOVA TABLE
(overall ANOVA significant, $p < .001$)

	F	V1,V2	p
SOR-WOODS vs SOR-FIELD	.04	1,106	.8430 NS
SOR-WOODS vs FIM-FIELD	236.00	1,88	0 ***
SOR-FIELD vs FIM-FIELD	347.76	1,124	0 ***
VIOLETS ABSENT-FIELD vs SOR-WOODS	11.25	1,52	.0019 **
VIOLETS ABSENT-FIELD vs SOR-FIELD	10.76	1,88	.0019 **
VIOLETS ABSENT-FIELD vs FIM-FIELD	93.49	1,70	0 ***
SOR-W & F vs FIM-FIELD	440.28	1,160	0 ***
SOR-W & F vs VIOLETS ABSENT	11.51	1,124	.0013 **

TABLE 6. SOIL PH

	<u>MEAN</u>	<u>SD</u>	<u>N</u>
SOR - WOODS	4.4	.0	3
SOR - FIELD	4.5	.20	6
FIM - FIELD	4.6	.17	9
VIOLETS ABSENT - FIELD	5.1	.06	3

ONE-WAY ANOVA TABLE
(overall ANOVA significant, $p < .001$)

	<u>F</u>	<u>V1,V2</u>	<u>p</u>	
SOR-WOODS vs SOR-FIELD	.78	1,7	.571	NS
SOR-WOODS vs FIM-FIELD	4.75	1,10	.052	NS
SOR-FIELD vs FIM-FIELD	1.06	1,13	.323	NS
VIOLETS ABSENT-FIELD vs SOR-WOODS	400.00	1,4	0	***
VIOLETS ABSENT-FIELD vs SOR-FIELD	24.08	1,7	.002	**
VIOLETS ABSENT-FIELD vs FIM-FIELD	29.26	1,10	.001	***

TABLE 7. FIELD QUADRAT ANALYSIS.

A comparison of factors between the following sets of plots: all the plots in the field, the plots containing only *V. sororia*, the plots containing only *V. fimbriatula*, and the plots containing both *V. sororia* and *V. fimbriatula*.

See Figures 2, 3.

	PLOTS IN FIELD			
	ALL PLOTS	PURE SOR	PURE FIM	BOTH
	(714 plots)	(168 plots)	(195 plots)	SOR & FIM (84 plots)
	MEAN (SD) (min-max)	MEAN (SD) (min-max)	MEAN (SD) (min-max)	MEAN (SD) (min-max)
# <i>V. SORORIA</i> /PLOT		3.4 (3.2) (1-18)		2.0 (1.4) (1-8)
# <i>V. FIMBRIATULA</i> /PLOT			8.1 (8.3) (1-63)	6.0 (1.4) (1-98)
VEG HT (cm)	37.6 (14.6) (8-122)	42.7 (11.7) (15-91)	27.2 (10.9) (8-61)	31.8 (14.2) (10-61)
VEG COVER	3.3 (1.3) (1-5)	3.7 (.9) (1-5)	2.3 (1.1) (1-5)	2.5 (1.7) (1-5)
<i>V. SORORIA</i> (largest plant)				
# LVS	2.6 (1.4) (1-10)	3.1 (1.5) (1-10)		2.6 (1.2) (1-7)
# REP	.15 (.5) (0-4)	.2 (.5) (0-4)		.16 (.4) (0-1)
LEAF DIMENSIONS (largest leaf, mm)				
L	37.7 (13.5) (10-95)	41.4 (14.5) (13-95)		35.5 (13.1) (12-70)
W	45.5 (14.6) (13-93)	48.5 (15.0) (17-90)		42.5 (12.7) (13-75)
PET	103.0 (33.8) (25-210)	110.0 (33.8) (47-210)		96.1 (32.6) (40-165)
<i>V. FIMBRIATULA</i> (largest plant)				
#LVS	5.3 (3.2) (1-22)		5.7 (3.3) (1-19)	5.6 (3.6) (1-22)
#REP	.99 (1.2) (0-6)		.97 (1.1) (0-5)	1.26 (1.5) (0-6)
LEAF DIMENSIONS (largest leaf, mm)				
L	44.0 (12.5) (10-82)		44.1 (12.1) (10-80)	46.0 (13.4) (17-82)
W	24.9 (6.0) (7-46)		24.7 (5.8) (7-40)	26.0 (6.5) (12-46)
PET	51.5 (26.8) (6-160)		47.4 (25.8) (6-125)	54.6 (27.3) (11-113)

TABLE 8. SURVIVORSHIP, reciprocal transplant #1, 9/80 - 5/83.

See figure 8.

	MAXIMUM % ALIVE EACH YEAR			
	<u>SOR-WOODS</u>	<u>SOR-FIELD</u>	<u>FIM-FIELD</u>	<u>FIM-WOODS</u>
1980	100%	100%	100%	100%
1981	96%	100%	95%	70%
1982	93%	80%	95%	35%
1983	80%	57%	90%	35%

TABLE 9. STATISTICS, RECIPROCAL TRANSPLANT #1, 1980-1982.

See figures 11, 17-20, 24.

	<u>SOR-WOODS</u>			<u>SOR-FIELD</u>			<u>FIM-FIELD</u>			<u>FIM-WOODS</u>		
	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>
NUMBER PER PLANT:												
LVS	2.1	.6	(393)	2.3	1.0	(325)	3.7	2.0	(292)	3.8	2.8	(157)
REP	.14	.19	"	.08	.17	"	.52	.46	"	.47	.44	"
LEAF DIMENSIONS (mm):												
L	26.9	2.9	(339)	15.2	6.4	(275)	21.2	4.8	(525)	30.3	6.7	(233)
W	34.9	3.5	(344)	21.2	8.4	(270)	13.5	2.7	(530)	19.4	3.7	(239)
P	49.3	9.1	(426)	20.6	10.0	(530)	11.7	3.4	(530)	31.7	11.9	(233)

2-WAY ANOVAS NO REPLICATION

	<u>F</u>	<u>V1,V2</u>	<u>p</u>
<u>#LEAVES/PLANT</u>			
SOR-WOODS vs SOR-FIELD	.94	1,19	NS
FIM-WOODS vs FIM-FIELD	.02	1,19	NS
SOR-WOODS vs FIM-WOODS	22.24	1,19	<.001 ***
SOR-FIELD vs FIM-FIELD	17.56	1,19	<.001 ***
<u>#REPRODUCTIVES/PLANT</u>			
SOR-WOODS vs SOR-FIELD	1.38	1,19	NS
FIM-WOODS vs FIM-FIELD	.12	1,19	NS
SOR-WOODS vs FIM-WOODS	17.27	1,19	<.001 ***
SOR-FIELD vs FIM-FIELD	21.64	1,19	<.001 ***
<u>BLADE LENGTH</u>			
SOR-WOODS vs SOR-FIELD	47.52	1,7	<.001 ***
FIM-WOODS vs FIM-FIELD	36.41	1,7	<.001 ***
SOR-WOODS vs FIM-WOODS	3.61	1,7	NS
SOR-FIELD vs FIM-FIELD	10.11	1,7	<.05 *
<u>BLADE WIDTH</u>			
SOR-WOODS vs SOR-FIELD	25.81	1,7	<.005 **
FIM-WOODS vs FIM-FIELD	34.59	1,7	<.001 ***
SOR-WOODS vs FIM-WOODS	1727.64	1,7	<.001 ***
SOR-FIELD vs FIM-FIELD	8.73	1,7	<.05 *
<u>PETIOLE LENGTH</u>			
SOR-WOODS vs SOR-FIELD	73.87	1,7	<.001 ***
FIM-WOODS vs FIM-FIELD	35.21	1,7	<.001 ***
SOR-WOODS vs FIM-WOODS	151.38	1,7	<.001 ***
SOR-FIELD vs FIM-FIELD	8.71	1,7	<.05 **

TABLE 10. STATISTICS, RECIPROCAL TRANSPLANT #2, 1982.

See figures 12, 21-23, 25.

<u>SOR-WOODS</u>			<u>SOR-FIELD</u>			<u>FIM-FIELD</u>			<u>FIM-WOODS</u>		
<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>
NUMBER PER PLANT:											
LVS	2.3	1.2 (182)	3.8	1.0 (145)		4.9	1.5 (238)		3.9	2.3 (195)	
REP	.3	.4 (182)	.4	.5 (145)		1.3	.8 (238)		.6	.6 (195)	
LEAF DIMENSIONS (mm):											
L	26.9	7.2 (270)	18.7	4.4 (278)		22.9	8.5 (568)		32.7	12.5 (459)	
W	34.1	8.1 (271)	24.4	6.3 (279)		13.7	4.1 (572)		18.5	5.1 (460)	
P	41.2	6.9 (324)	17.7	7.2 (279)		7.7	5.5 (572)		26.5	16.4 (471)	

2-WAY ANOVAS NO REPLICATION

	<u>F</u>	<u>V1,V2</u>	<u>p</u>
<u>#LEAVES/PLANT</u>			
SOR-WOODS vs SOR-FIELD	8.48	1,9	<.025 *
FIM-WOODS vs FIM-FIELD	1.83	1,9	NS
SOR-WOODS vs FIM-WOODS	14.14	1,9	<.07 **
SOR-FIELD vs FIM-FIELD	19.25	1,9	<.005 **
<u>#REPRODUCTIVES/PLANT</u>			
SOR-WOODS vs SOR-FIELD	.18	1,9	NS
FIM-WOODS vs FIM-FIELD	3.74	1,9	NS
SOR-WOODS vs FIM-WOODS	6.17	1,9	<.05 *
SOR-FIELD vs FIM-FIELD	7.68	1,9	<.05 *
<u>BLADE LENGTH</u>			
SOR-WOODS vs SOR-FIELD	19.43	1,4	<.05 *
FIM-WOODS vs FIM-FIELD	27.09	1,4	<.01 **
SOR-WOODS vs FIM-WOODS	1.31	1,4	NS
SOR-FIELD vs FIM-FIELD	2.86	1,4	NS
<u>BLADE WIDTH</u>			
SOR-WOODS vs SOR-FIELD	19.53	1,4	<.05 *
FIM-WOODS vs FIM-FIELD	48.86	1,4	<.005 ***
SOR-WOODS vs FIM-WOODS	36.70	1,4	<.01 **
SOR-FIELD vs FIM-FIELD	64.74	1,4	<.01 **
<u>PETIOLE LENGTH</u>			
SOR-WOODS vs SOR-FIELD	45.79	1,4	<.005 **
FIM-WOODS vs FIM-FIELD	14.43	1,4	<.025 *
SOR-WOODS vs FIM-WOODS	14.32	1,4	<.05 *
SOR-FIELD vs FIM-FIELD	12.15	1,4	<.05 *

TABLE 11. LEAF PREDATION, reciprocal transplant #1, 1980-1982.
See figure 34.

	N	% AREA EATEN	% EATEN AT ALL	% BARE PETIOLES
SOR - WOODS	1104	19.4 %	26.7 %	17.9 %
SOR - FIELD	975	5.9	9.6	4.6
FIM - WOODS	659	7.1	14.9	4.6
FIM - FIELD	1267	1.2	5.0	0.2

2-WAY ANOVA NO REPLICATION, % LEAF AREA EATEN

	F	V1,V2	p	
SOR-WOODS vs SOR-FIELD	20.34	1,19	<.001	***
FIM-WOODS vs FIM-FIELD	10.05	1,19	<.01	**
SOR-WOODS vs FIM-WOODS	20.42	1,19	<.001	***
SOR-FIELD vs FIM-FIELD	5.09	1,19	<.05	*

TABLE 12. LEAF PREDATION, reciprocal transplant #2, 1982.
See figure 35.

	N	% AREA EATEN	% EATEN AT ALL	% BARE PETIOLES
SOR - WOODS	595	22.5 %	33.8 %	19.0 %
SOR - FIELD	541	3.6	15.0	0
FIM - WOODS	902	4.7	9.3	3.9
FIM - FIELD	1179	2.7	13.0	0

2-WAY ANOVA NO REPLICATION, % LEAF AREA EATEN.

	F	V1, V2	p	
SOR-WOODS vs SOR-FIELD	6.18	1,9	<.05	*
FIM-WOODS vs FIM-FIELD	2.20	1,9	NS	
SOR-WOODS vs FIM-WOODS	10.80	1,9	<.01	**
SOR-FIELD vs FIM-FIELD	1.95	1,9	NS	

TABLE 13. V. SORORIA - EVIDENCE FOR ECOTYPIC DIFFERENTIATION

reciprocal transplant #1, 1980-1982

<u>IN WOODS</u>								
	<u>CONTROL</u> (IN WOODS-FROM WOODS)			<u>EXPERIMENTAL</u> (IN WOODS-FROM FIELD)			2-WAY ANOVA NO REPLICATION	
	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>F</u>	<u>V1,V2</u> <u>p</u>
#LVS/PL	2.3	.98	(136)	2.5	.99	(252)	1.57	1,19 NS
#REP/PL	0.13	.31	(136)	.15	.20	(252)	.08	1,19 NS
LEAF DIMENSIONS								
LENGTH	29.2	5.5	(130)	25.1	3.0	(216)	3.85	1,7 NS
WIDTH	38.7	6.3	(130)	32.8	3.1	(214)	8.42	1,7 <.05*
PET.	61.1	16.0	(138)	42.9	8.6	(286)	11.13	1,7 <.05*

<u>IN FIELD</u>								
	<u>CONTROL</u> (IN FIELD-FROM FIELD)			<u>EXPERIMENTAL</u> (IN FIELD-FROM WOODS)			2-WAY ANOVA NO REPLICATION	
	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>F</u>	<u>V1,V2</u> <u>p</u>
#LVS/PL	2.5	1.3	(210)	1.9	1.2	(105)	18.02	1,19 <.001***
#REP/PL	.07	.17	(210)	.05	.16	(105)	.10	1,19 NS
LEAF DIMENSIONS								
LENGTH	25.5	6.9	(196)	16.3	2.0	(73)	.15	1,7 NS
WIDTH	20.0	8.9	(196)	23.0	2.8	(74)	7.11	1,7 <.05 *
PET.	18.9	10.7	(197)	27.6	3.0	(76)	7.3	1,6 =.05 *

TABLE 14. % SEED GERMINATION, DISTURBED VERSUS UNDISTURBED SOIL,
SEED PLOT #2, 1982

		% GERMINATION/PLOT	
		DISTURBED	UNDISTURBED
IN WOODS			
SOR	113	31.9%	28.3%
FIM	426	22.1%	13.6%
IN FIELD			
SOR	113	27.4%	2.7%
FIM	426	16.4%	1.6%

TABLE 15. STATISTICS, SEED PLOT #1, 1981-1982

See figures 40-43.

<u>SOR-WOODS</u>			<u>SOR-FIELD</u>			<u>FIM-FIELD</u>			<u>FIM-WOODS</u>			
<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	<u>MEAN</u>	<u>SD</u>	<u>(N)</u>	
NUMBER PER PLANT:												
LVS	2.4	.5	(55)	2.2	.4	(47)	2.5	.7	(55)	2.4	.9	(55)
LEAF DIMENSIONS (mm): Length (L), Width (W), Petiole (P):												
L	16.4	5.0	(127)	13.1	4.1	(100)	15.5	3.0	(130)	21.4	7.4	(129)
W	21.4	5.0	(126)	17.2	4.3	(101)	10.7	2.4	(130)	15.7	3.3	(128)
P	36.3	11.8	(117)	16.8	9.7	(90)	10.7	8.2	(116)	32.8	19.8	(120)

TWO-WAY ANOVAS NO REPLICATION

	<u>F</u>	<u>V1,V2</u>	<u>p</u>	
<u>#LEAVES/PLANT</u>				
SOR-WOODS vs SOR-FIELD	4.51	1,6	NS	
FIM-WOODS vs FIM-FIELD	.05	1,6	NS	
SOR-WOODS vs FIM-WOODS	.12	1,6	NS	
SOR-FIELD vs FIM-FIELD	3.11	1,6	NS	
<u>BLADE LENGTH</u>				
SOR-WOODS vs SOR-FIELD	17.03	1,6	<.01	**
FIM-WOODS vs FIM-FIELD	7.65	1,6	<.05	*
SOR-WOODS vs FIM-WOODS	7.07	1,6	<.05	*
SOR-FIELD vs FIM-FIELD	11.87	1,6	<.025	*
<u>BLADE WIDTH</u>				
SOR-WOODS vs SOR-FIELD	9.71	1,6	<.025	*
FIM-WOODS vs FIM-FIELD	47.22	1,6	<.001	***
SOR-WOODS vs FIM-WOODS	21.06	1,6	<.01	**
SOR-FIELD vs FIM-FIELD	73.04	1,6	<.001	***
<u>PETIOLE LENGTH</u>				
SOR-WOODS vs SOR-FIELD	161.97	1,5	<.001	***
FIM-WOODS vs FIM-FIELD	19.69	1,5	<.01	**
SOR-WOODS vs FIM-WOODS	.69	1,5	NS	
SOR-FIELD vs FIM-FIELD	5.73	1,5	NS	

TABLE 16. DISTURBANCE PLOTS (established 5/80)

Plots were disturbed by removing all vegetation, including violets; and turning soil over to a depth of 25 cm. (five plots in the field, and two plots in the woods; each 1 meter X 1 meter).

		# VIOLETS PER PLOT			
<u>BEFORE DISTURBANCE</u>		<u>6/19/80</u>	<u>4/25/81</u>	<u>8/21/81</u>	<u>8/19/82</u>
<u>SOR, FIM</u>		<u>SOR, FIM</u>	<u>SOR, FIM</u>	<u>SOR, FIM</u>	<u>SOR, FIM</u>
FIELD					
5, 43		0, 0	0, 1	0, 8	0, 15
2, 12		0, 0	1, 2	0, 7	0, 13
10, 34		0, 0	0, 0	1, 9	0, 5
58, 0		1, 0	1, 0	plot lost	
26, 2		0, 0	0, 0	1, 0	0, 40
WOODS					
18, 0		0, 0	0, 0	1, 0	8, 0
0, 0		0, 0	0, 0	0, 0	0, 0

TABLE 17. COMPARISON OF PLANTS OF V. SORORIA AND V. FIMBRIATULA
COLLECTED IN WOODS AND FIELD (8/1982)

(12 plants V. sororia, and 11 plants V. fimbriatula per habitat).
See figures 44,45.

	WOODS			FIELD		
	MEAN	SD	N	MEAN	SD	N
PER PLANT (MEANS)						
# LEAVES						
SOR	1.58	.51	12	2.50	1.09	12
FIM	3.00	1.48	11	5.27	2.15	11
# REPROD.						
SOR	.25	.46	12	1.00	1.34	11
FIM	.64	.69	11	2.73	1.84	11
RHIZOME LENGTH (mm)						
SOR	20.08	6.61	12	23.75	7.58	12
FIM	9.09	5.87	11	15.82	2.64	11
RHIZOME WIDTH (mm)						
SOR	5.92	.90	12	6.58	1.60	12
FIM	3.91	.70	11	5.09	1.04	11
TOTAL LEAF AREA (mm ²)						
SOR	2657.17	754.51	12	3068.00	1411.60	12
FIM	2154.36	1155.24	11	2424.09	1498.69	11
TOTAL DRY WEIGHT (gm)						
SOR	.32	.14	12	.48	.27	11
FIM	.17	.07	11	.36	.14	11
PLANT PARTS DRY WEIGHTS (MEAN PER PLANT, gm)						
LEAF BLADES						
SOR	.07	.02	12	.13	.06	11
FIM	.06	.04	11	.12	.07	11
PETIOLES						
SOR	.03	.02	12	.05	.03	12
FIM	.03	.01	11	.02	.02	11
RHIZOMES						
SOR	.17	.09	12	.25	.16	12
FIM	.05	.04	11	.10	.05	11
ROOTS						
SOR	.05	.02	12	.05	.04	12
FIM	.02	.01	11	.06	.04	11
REPRODUCTIVES						
SOR	.011	.02	12	.009	.02	12
FIM	.007	.01	11	.062	.06	11
PLANT PARTS % CARBON ALLOCATION:						
LEAF BLADES						
SOR	22.73	7.8	12	29.18	9.5	11
FIM	37.51	11.1	11	33.16	14.4	11

PETIOLES							
SOR	9.71	2.7	12	12.21	4.1	11	
FIM	18.24	5.2	11	6.75	3.2	11	
RHIZOMES							
SOR	48.88	10.7	12	47.66	11.7	11	
FIM	26.34	16.3	11	29.18	16.0	11	
ROOTS							
SOR	15.87	3.8	12	9.12	4.5	11	
FIM	14.22	4.5	11	16.43	10.7	11	
REPRODUCTIVES							
SOR	2.85	6.2	12	1.85	3.6	11	
FIM	3.70	4.4	11	14.50	10.6	11	

PER LEAF (MEANS):

BLADE WEIGHT (gm)							
SOR	.05	.03	27	.05	.04	41	
FIM	.02	.02	45	.03	.01	72	
BLADE AREA (sq.mm)							
SOR	2093.28	911.69	27	1325.65	803.86	42	
FIM	862.53	433.82	43	556.65	215.89	65	
BLADE SPECIFIC WT (gmX.00001/sq.mm)							
SOR	2.58	.28	27	3.71	.75	41	
FIM	2.73	.58	43	4.79	1.08	65	
BLADE LENGTH (mm)							
SOR	41.52	11.72	27	33.05	12.80	42	
FIM	41.24	13.53	45	35.00	9.04	72	
BLADE WIDTH (mm)							
SOR	55.19	13.64	27	44.67	14.15	42	
FIM	25.09	6.09	45	19.93	4.16	72	
PETIOLE (mm)							
SOR	90.35	30.12	17	81.55	37.74	29	
FIM	66.66	28.55	32	25.69	9.35	58	

TABLE 18. ANOVA TABLE for factors in table 17.

PLANTS OF V. SORORIA AND V. FIMBRIATULA
COLLECTED IN WOODS AND FIELD (8/1982)

	F	V1,V2	p

PER PLANT (MEANS)			

# LEAVES			
SOR-WOODS vs SOR-FIELD	6.97	1,23	.014 *
FIM-WOODS vs FIM-FIELD	8.33	1,21	.009 **
SOR-WOODS vs FIM-WOODS	9.71	1,22	.005 **
SOR-FIELD vs FIM-FIELD	15.66	1,22	.001 ***
# REPROD.			
SOR-WOODS vs SOR-FIELD	3.61	1,22	.068 NS
FIM-WOODS vs FIM-FIELD	13.09	1,21	.002 **
SOR-WOODS vs FIM-WOODS	4.28	1,22	.05 *
SOR-FIELD vs FIM-FIELD	7.73	1,21	.011 *
RHIZOME LENGTH			
SOR-WOODS vs SOR-FIELD	1.59	1,23	.22 NS
FIM-WOODS vs FIM-FIELD	12.01	1,21	.003 **
SOR-WOODS vs FIM-WOODS	17.64	1,22	.001 **
SOR-FIELD vs FIM-FIELD	10.80	1,22	.004 **
RHIZOME WIDTH			
SOR-WOODS vs SOR-FIELD	1.64	1,23	.21 NS
FIM-WOODS vs FIM-FIELD	9.71	1,21	.006 **
SOR-WOODS vs FIM-WOODS	35.13	1,22	0 ***
SOR-FIELD vs FIM-FIELD	7.10	1,22	.014 *
TOTAL LEAF AREA			
SOR-WOODS vs SOR-FIELD	.79	1,23	.62 NS
FIM-WOODS vs FIM-FIELD	.22	1,21	.65 NS
SOR-WOODS vs FIM-WOODS	1.55	1,22	.22 NS
SOR-FIELD vs FIM-FIELD	1.13	1,22	.30 NS
TOTAL DRY WEIGHT			
SOR-WOODS vs SOR-FIELD	3.20	1,22	.09 NS
FIM-WOODS vs FIM-FIELD	17.12	1,21	.001 **
SOR-WOODS vs FIM-WOODS	11.58	1,22	.003 **
SOR-FIELD vs FIM-FIELD	1.68	1,21	.21 NS
PLANT PARTS DRY WEIGHT/PLANT			

LEAF BLADES			
SOR-WOODS vs SOR-FIELD	11.72	1,22	.003 **
FIM-WOODS vs FIM-FIELD	5.35	1,21	.03 *
SOR-WOODS vs FIM-WOODS	.06	1,22	.81 NS
SOR-FIELD vs FIM-FIELD	.08	1,21	.79 NS
PETIOLES			
SOR-WOODS vs SOR-FIELD	5.17	1,23	.03 *
FIM-WOODS vs FIM-FIELD	.97	1,21	.67 NS
SOR-WOODS vs FIM-WOODS	.008	1,22	.91 NS
SOR-FIELD vs FIM-FIELD	8.93	1,22	.007 **

RHIZOMES

SOR-WOODS vs SOR-FIELD	2.82	1,23	.10	NS
FIM-WOODS vs FIM-FIELD	8.68	1,21	.008	**
SOR-WOODS vs FIM-WOODS	16.35	1,22	.001	***
SOR-FIELD vs FIM-FIELD	10.16	1,22	.005	**

ROOTS

SOR-WOODS vs SOR-FIELD	.12	1,23	.74	NS
FIM-WOODS vs FIM-FIELD	6.37	1,21	.01	**
SOR-WOODS vs FIM-WOODS	15.62	1,22	.001	***
SOR-FIELD vs FIM-FIELD	.59	1,22	.54	NS

REPRODUCTIVES

SOR-WOODS vs SOR-FIELD	.07	1,23	.79	NS
FIM-WOODS vs FIM-FIELD	9.27	1,21	.006	**
SOR-WOODS vs FIM-WOODS	.45	1,22	.52	NS
SOR-FIELD vs FIM-FIELD	8.58	1,22	.008	**

PLANT PARTS % CARBON ALLOCATION:

LEAF BLADES

SOR-WOODS vs SOR-FIELD	3.27	1,22	.08	NS
FIM-WOODS vs FIM-FIELD	.63	1,21	.56	NS
SOR-WOODS vs FIM-WOODS	13.75	1,22	.002	**
SOR-FIELD vs FIM-FIELD	.60	1,21	.55	NS

PETIOLES

SOR-WOODS vs SOR-FIELD	3.04	1,22	.09	NS
FIM-WOODS vs FIM-FIELD	38.74	1,21	0	***
SOR-WOODS vs FIM-WOODS	24.73	1,22	0	***
SOR-FIELD vs FIM-FIELD	12.22	1,21	.003	**

RHIZOMES

SOR-WOODS vs SOR-FIELD	.07	1,22	.80	NS
FIM-WOODS vs FIM-FIELD	.17	1,21	.69	NS
SOR-WOODS vs FIM-WOODS	15.62	1,22	.001	***
SOR-FIELD vs FIM-FIELD	9.59	1,21	.006	**

ROOTS

SOR-WOODS vs SOR-FIELD	15.13	1,22	.001	***
FIM-WOODS vs FIM-FIELD	.40	1,21	.54	NS
SOR-WOODS vs FIM-WOODS	.90	1,22	.65	NS
SOR-FIELD vs FIM-FIELD	4.35	1,21	.05	*

REPRODUCTIVES

SOR-WOODS vs SOR-FIELD	.23	1,22	.64	NS
FIM-WOODS vs FIM-FIELD	10.24	1,21	.005	**
SOR-WOODS vs FIM-WOODS	.15	1,22	.71	NS
SOR-FIELD vs FIM-FIELD	14.74	1,21	.001	***

PER LEAF (MEANS):

BLADE WEIGHT

SOR-WOODS vs SOR-FIELD	.06	1,67	.81	NS
FIM-WOODS vs FIM-FIELD	.82	1,116	.37	NS
SOR-WOODS vs FIM-WOODS	38.67	1,71	.0001	***
SOR-FIELD vs FIM-FIELD	24.38	1,112	.0001	***

BLADE AREA			
SOR-WOODS vs SOR-FIELD	13.49	1,68	.0005***
FIM-WOODS vs FIM-FIELD	23.58	1,107	.0001***
SOR-WOODS vs FIM-WOODS	57.88	1,69	.0001***
SOR-FIELD vs FIM-FIELD	53.75	1,106	.0001***
BLADE SPECIFIC WT.			
SOR-WOODS vs SOR-FIELD	56.83	1,67	.0001***
FIM-WOODS vs FIM-FIELD	131.47	1,107	.0001***
SOR-WOODS vs FIM-WOODS	1.69	1,69	.20 NS
SOR-FIELD vs FIM-FIELD	31.42	1,105	.0001***
BLADE LENGTH			
SOR-WOODS vs SOR-FIELD	7.68	1,68	.007 **
FIM-WOODS vs FIM-FIELD	8.97	1,116	.003 **
SOR-WOODS vs FIM-WOODS	.01	1,71	.93 NS
SOR-FIELD vs FIM-FIELD	.91	1,113	.34 NS
BLADE WIDTH			
SOR-WOODS vs SOR-FIELD	9.34	1,68	.003 **
FIM-WOODS vs FIM-FIELD	29.58	1,116	.0001***
SOR-WOODS vs FIM-WOODS	165.48	1,71	.0001***
SOR-FIELD vs FIM-FIELD	192.53	1,113	.0001***
PETIOLE LENGTH			
SOR-WOODS vs SOR-FIELD	.67	1,45	.42 NS
FIM-WOODS vs FIM-FIELD	100.66	1,89	.0001***
SOR-WOODS vs FIM-WOODS	7.36	1,48	.009 **
SOR-FIELD vs FIM-FIELD	114.36	1,86	.0001***

TABLE 19. LEAF WATER POTENTIAL.

7/16/82 10:15-1:15 solar time air temp. 30

	LEAF WATER POTENTIAL, BARS			SOIL WATER, %	PAR, $\mu\text{E}/\text{m}^2/\text{s}$
	MEAN	SD	N		
FIM - FIELD	-12.2	2.2	23	8.8	1460
FIM - WOODS	- 6.9	1.2	10		80
SOR - FIELD	-12.0	2.4	23	25.9	1380
SOR - WOODS	- 9.5	1.2	21	25.7	80

ANOVA TABLE
(overall ANOVA significant, $p < .001$)

	F	V1, V2	p	
SOR-WOODS vs SOR-FIELD	19.20	1,42	.00021	***
FIM-WOODS vs FIM-FIELD	52.04	1,31	0	***
SOR-WOODS vs FIM-WOODS	34.48	1,29	.00003	***
SOR-FIELD vs FIM-FIELD	.07	1,44	NS	
SOR-WOODS vs FIM-FIELD	24.98	1,42	.00006	***
SOR-FIELD vs FIM-WOODS	42.07	1,31	.00001	***

TABLE 20. LEAF WATER POTENTIAL.

8/19/82 11:15-12:15 solar time air temp. 22.5

	LEAF WATER POTENTIAL, BARS			SOIL WATER, %
	MEAN	SD	N	
FIM - FIELD	-10.4	1.5	11	13.6
FIM - WOODS	- 6.9	1.4	10	26.7
SOR - FIELD	-10.6	1.7	10	29.1
SOR - WOODS	- 8.6	1.1	9	20.6

ANOVA TABLE
(overall ANOVA significant, $p < .001$)

	F	V1, V2	p	
SOR-WOODS vs SOR-FIELD	9.75	1,17	.00624	**
FIM-WOODS vs FIM-FIELD	31.32	1,19	.00008	***
SOR-WOODS vs FIM-WOODS	8.98	1,17	.00799	**
SOR-FIELD vs FIM-FIELD	.03	1,19	NS	
SOR-WOODS vs FIM-FIELD	9.65	1,18	.00614	**
SOR-FIELD vs FIM-WOODS	29.90	1,18	.00011	***

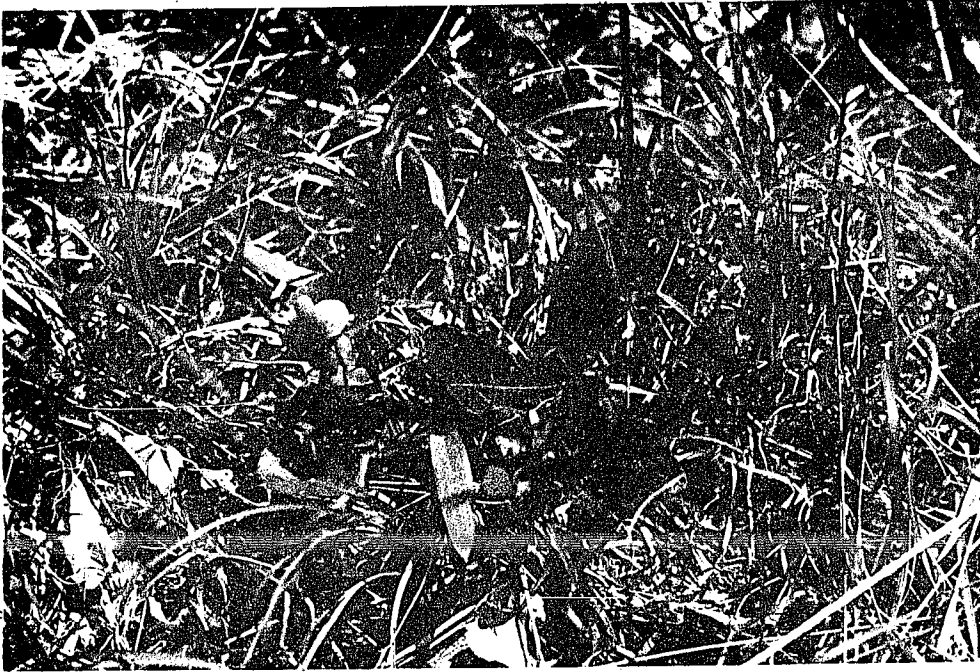
TABLE 21. PHENOTYPIC PLASTICITY IN PETIOLE LENGTH FOR
V. FIMBRIATULA.

	<u>RATIO OF</u> <u>PETIOLE LENGTH/BLADE LENGTH</u>	
	<u>WOODS</u>	<u>FIELD</u>
RECIPROCAL TRANSPLANT #1 (clones):	1.04	0.6
RECIPROCAL TRANSPLANT #2:	0.8	0.3
NATURALLY OCCURRING PLANTS:	1.6	0.7
SEED PLOT #1:	1.5	0.7

	<u>RATIO OF PETIOLE LENGTHS</u> <u>WOODS/FIELD</u>
RECIPROCAL TRANSPLANT #1 (clones):	2.7
RECIPROCAL TRANSPLANT #2:	3.4
NATURALLY OCCURRING PLANTS:	2.6
SEED PLOT #1:	3.1

FIGURE 1a. VIOLA SORORIA (left), AND V. FIMBRIATULA (right).

1b. FIELD STUDY SITE, as seen from the foot of the field.



1a.



1b.

FIGURE 2. MAPPED FIELD, 714 METER-SQUARE PLOTS.

Each of the 714 meter-square plots is 1 meter apart across the width of the field, and 2 meters apart down the length of the field.

Each open circle is one V. sororia genet (total 736), each black circle is one V. fimbriatula genet (total 2,078). Plots colored yellow contain hybrids (total 53 hybrids in 42 plots).

The field is surrounded by woods, and has a stream at the base, old stone wall on the north, and a road at the east (top) side of the slope.

See Figure 3 and Table 7 for statistical analysis.

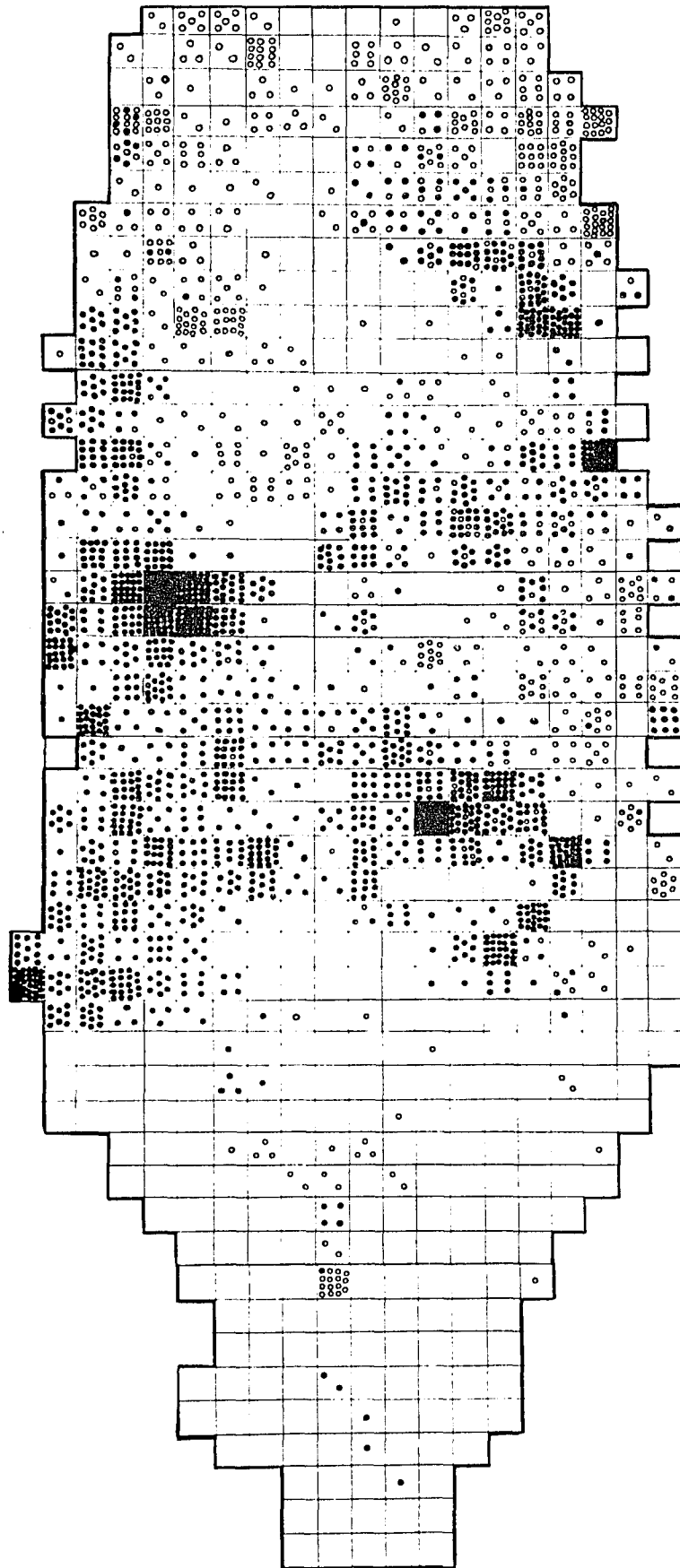


FIGURE 3. STATISTICS FOR THE FIELD QUADRAT ANALYSIS.

Correlations, means, standard deviations, and ranges for the 26 factors measured in the field plots (see Figure 2).

The boxes contain the correlation coefficients (Spearman r) and the levels of significance: blank box, not significant $p > .05$;

* $p < .05$; ** $p < .01$; *** $p < .001$. The upper boxes represent the total 714 plots mapped, and the lower boxes represent the 447 plots which contain V. sororia and/or V. fimbriatula.

X, Y = position of the plots represented by their X and Y coordinates with the origin at the lower left corner of the field;

SOR = number of V. sororia per plot; SPRES = plots with

V. sororia present; %SOR = number of V. sororia per plot as a percent of the total number of V. sororia and V. fimbriatula;

FIM = number of V. fimbriatula per plot; FPRES = plots with

V. fimbriatula present; %FIM = number of V. fimbriatula per plot

as a percent of the total number of V. sororia and V. fimbriatula;

#S&F = number of V. sororia and V. fimbriatula per plot; S&F PRES =

plots with V. sororia and/or V. fimbriatula present; #HYB =

number of hybrids present in a plot; HYBPRES = plots with hybrids

present; SOR #LVS = number of leaves on the largest plant of

V. sororia in a plot; SOR #REP = number of reproductives on the

largest plant of V. sororia in a plot; SOR L = length (cm) of the

largest leaf of the largest plant of V. sororia per plot; SOR W =

width (cm) of the largest leaf of the largest plant of V. sororia

per plot; SOR P = petiole length (cm) of the largest leaf of the

largest plant per plot; FIM #LVS = number of leaves on the largest

plant of V. fimbriatula per plot; FIM L = length (cm) of the

largest leaf of the largest plant of V. fimbriatula per plot; FIM

W = width (cm) of the largest leaf of the largest plant of V.

fimbriatula per plot; FIM P = petiole length (cm) of the largest

leaf of the largest plant of V. fimbriatula per plot; VEG HT =

average height (cm) of the vegetation per plot; VEG COVER =

average coverage of the vegetation per plot (1 = sparse

vegetation, to 5 = dense vegetation); WET = plots subjectively

rated as wet; #SP = total number of species, including violets,

per plot.

FIGURE 4. PHOTOSYNTHETICALLY ACTIVE RADIATION.

Photosynthetically active radiation (PAR) in microeinsteins per meter square per second (microE/m sq./s), from May to October 1982, at noon eastern daylight savings time. Points are means of several sites, except the single site where violets are absent. See Table 3 for statistical analysis.

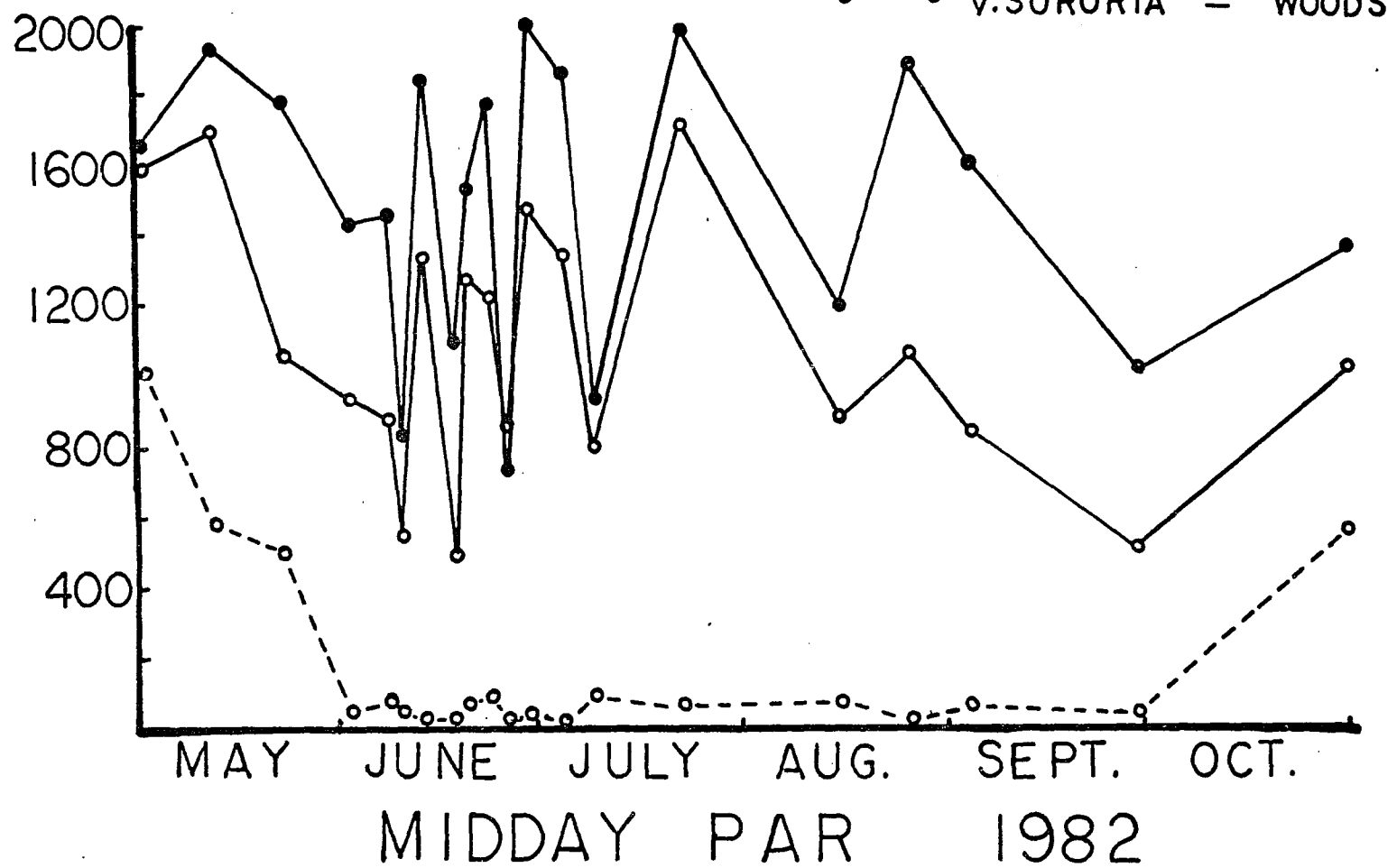


FIGURE 5. SOIL MOISTURE CONTENT.

Percent soil moisture content, from August 1981 to October 1982. Points are means of replicates from several sites, except the single site where violets were absent. The means are significantly differently ($p < .001$), except for V. sororia in the woods and V. sororia in the field which are the same. Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods. See Table 4 for statistical analysis.

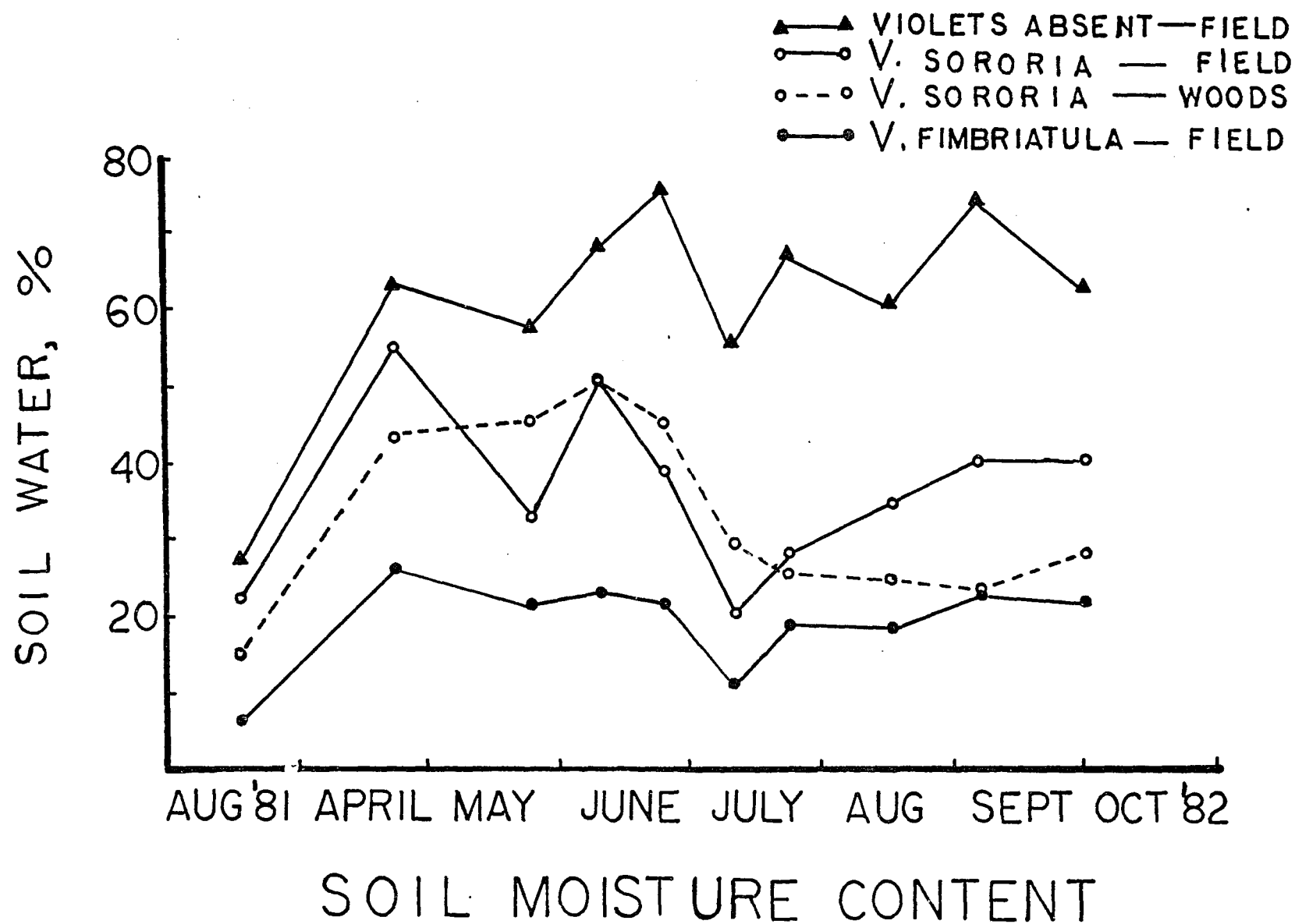


FIGURE 6. SOIL MOISTURE CONTENT.

Percent soil moisture content. The means are significantly different ($p < .001$). Same graph as figure 5 except that the values for V. sororia in the woods and in the field are merged because the means were not significantly different.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 4 for statistical analysis.

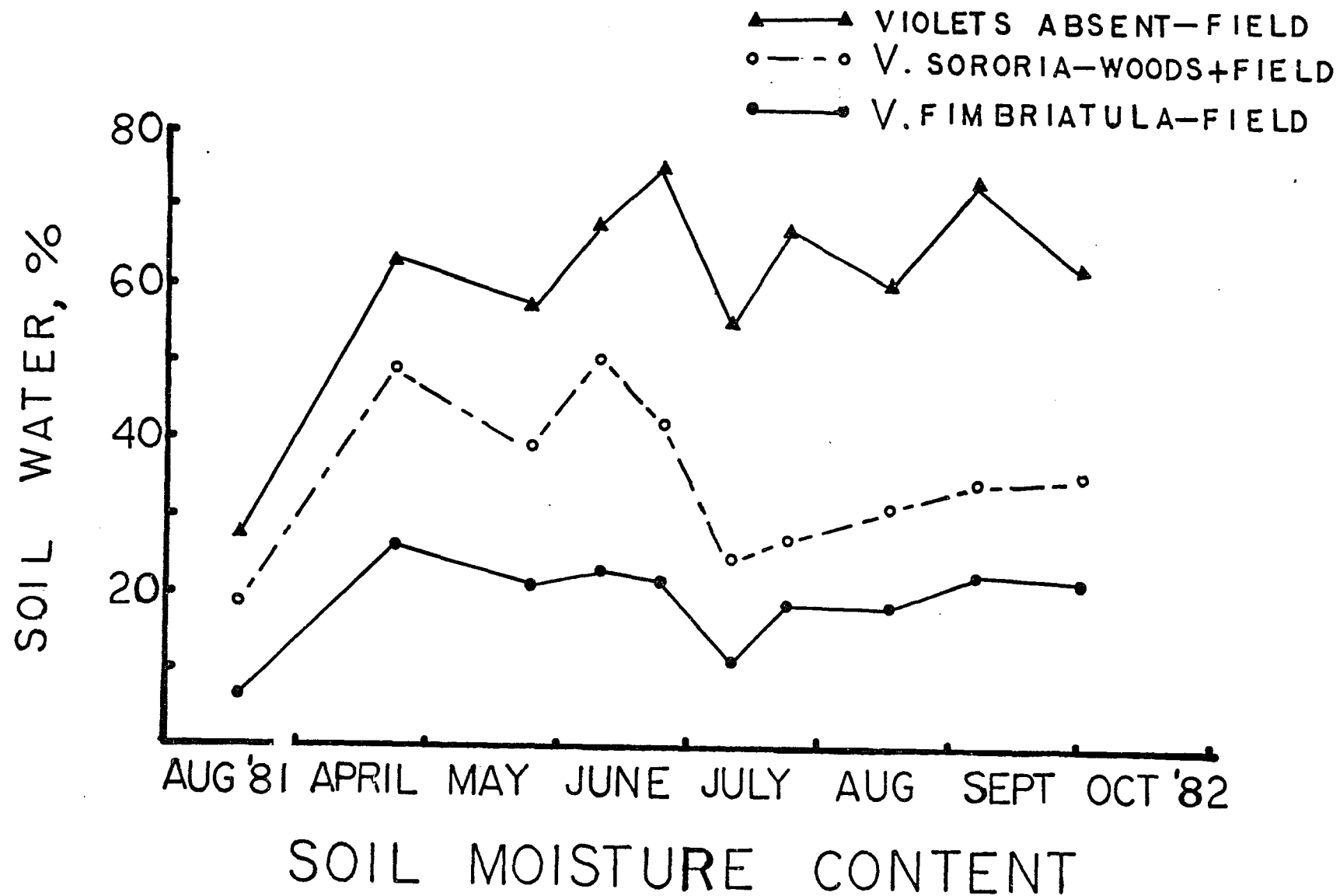


FIGURE 7. SOIL PARTICLE SIZE.

Soil particle size, expressed as a percent of the total dry weight of the soil.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

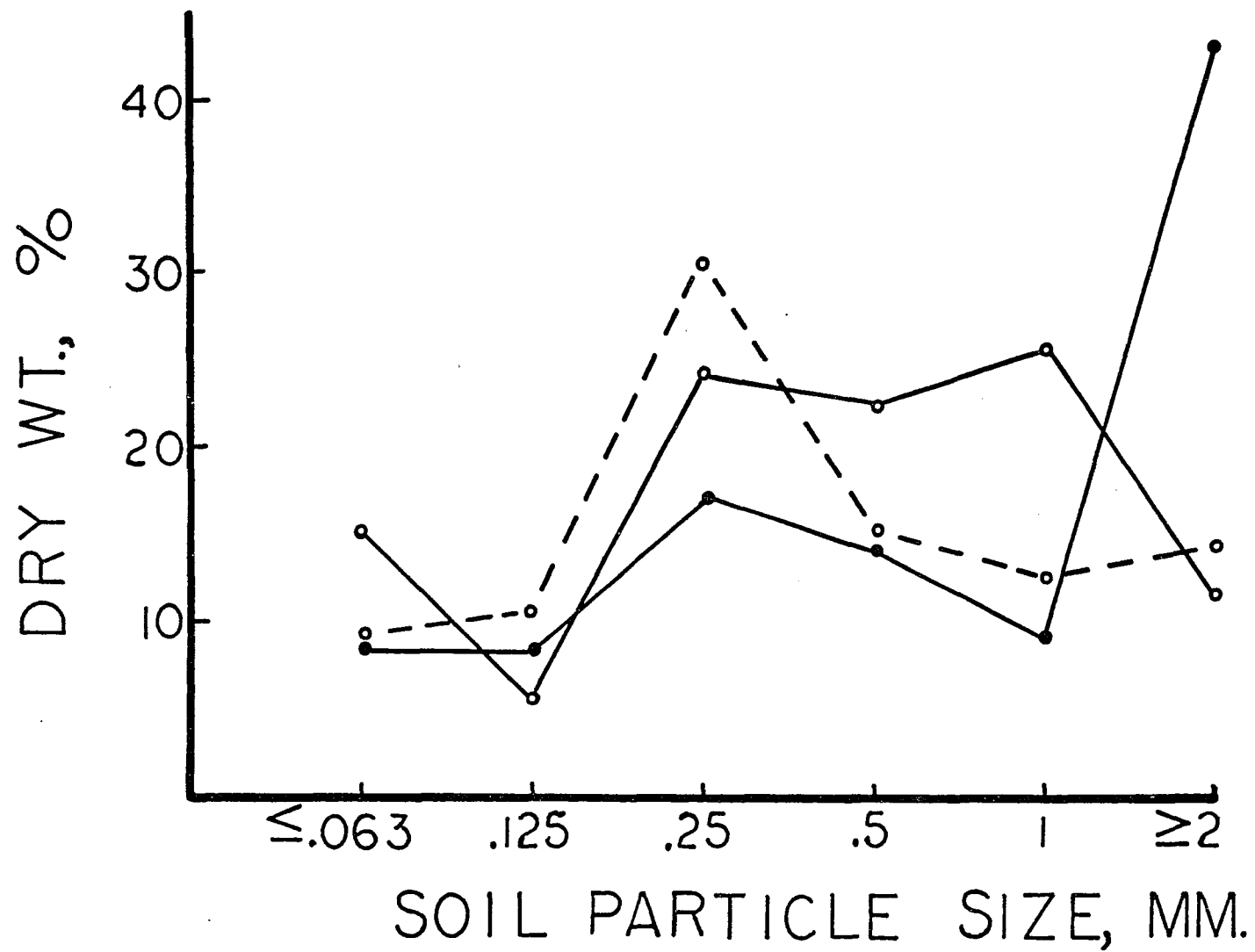


FIGURE 8. SURVIVORSHIP, RECIPROCAL TRANSPLANT #1.

Percent survivorship, reciprocal transplant #1. Plants present from July 1980 (day of transplant) to May 1983.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 8, Figure 9.

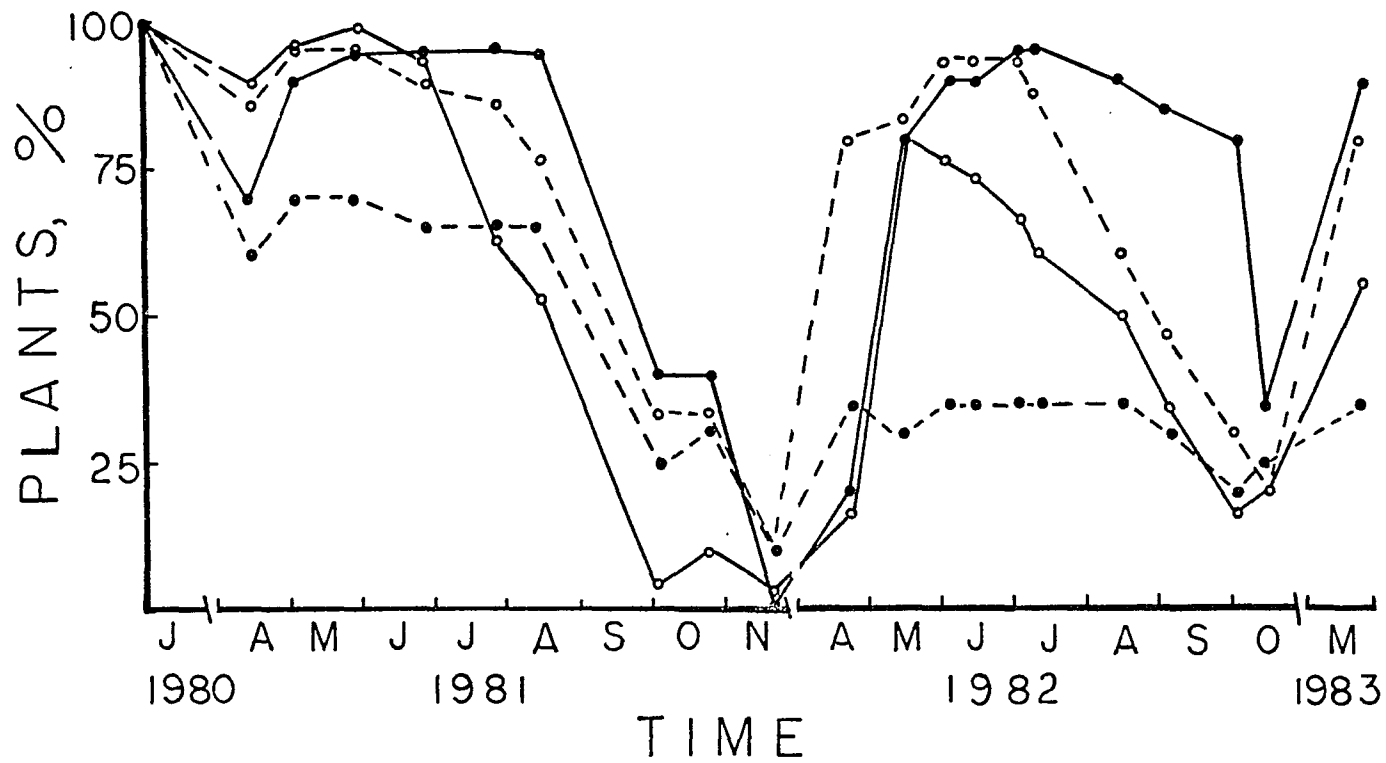


FIGURE 9. SURVIVORSHIP, RECIPROCAL TRANSPLANT #1, 7/11/82.

Percent survivorship, reciprocal transplant #1. Plants present on July 11, 1982, two years from the date of transplant.

See Figure 8.

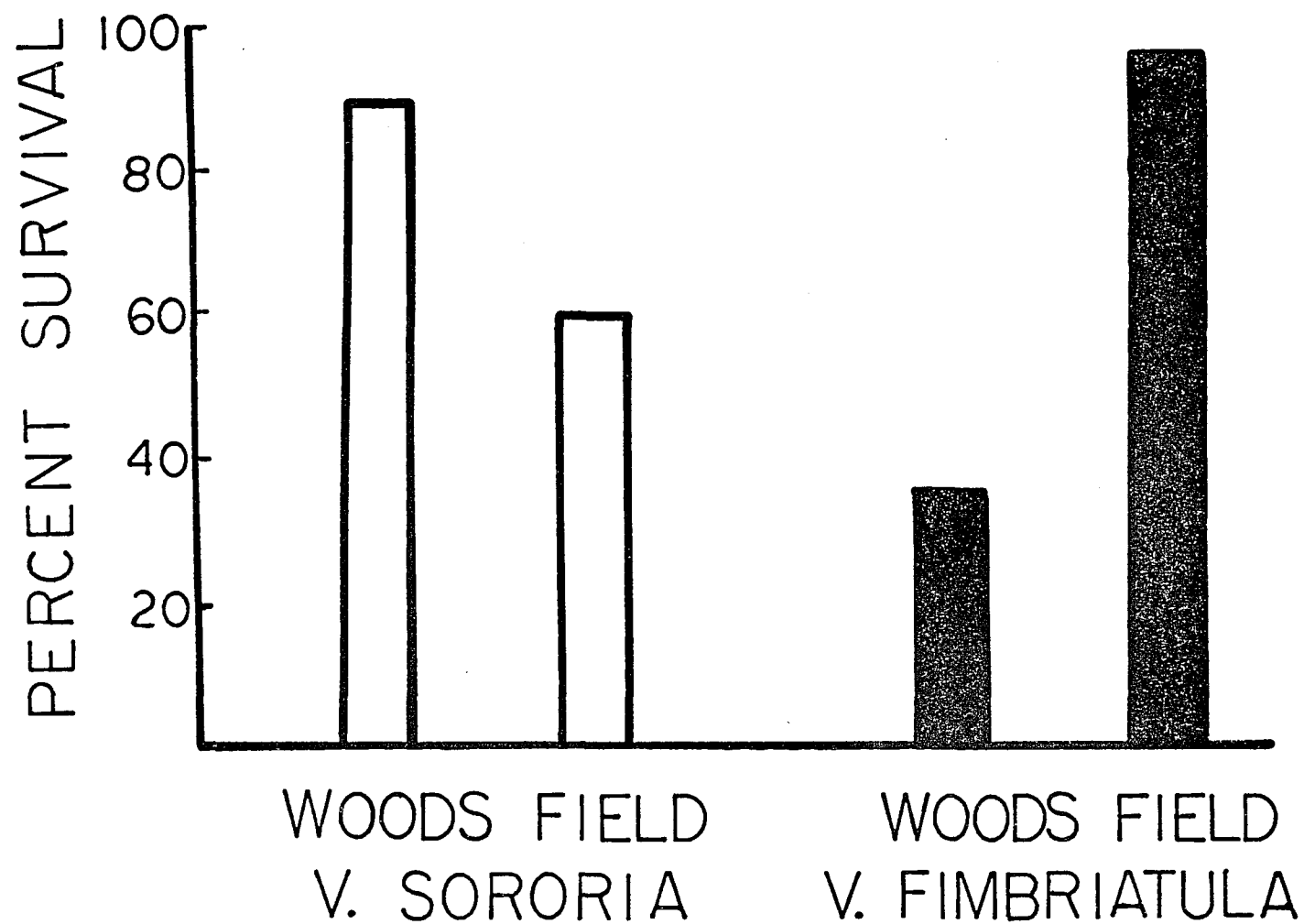


FIGURE 10. SURVIVORSHIP, RECIPROCAL TRANSPLANT #2.

Percent survivorship, reciprocal transplant #2. Plants present from September 22, 1982 (day of transplant) to May 1983.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

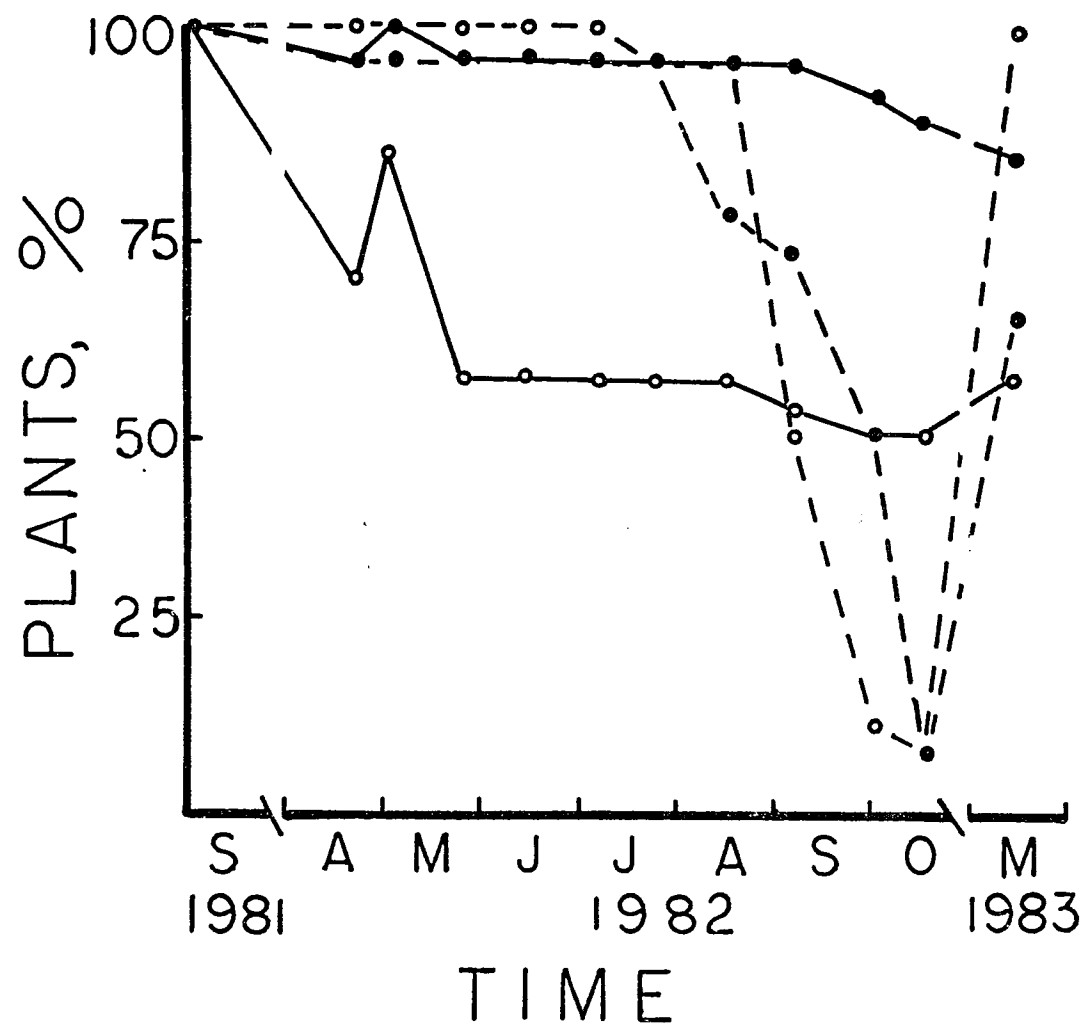


FIGURE 11. # LEAVES PER PLANT, RECIPROCAL TRANSPLANT #1.

Average number of leaves per plant, reciprocal transplant #1, from September 1980 to October 1982 (not including bare petioles).

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 9 for statistical analysis.

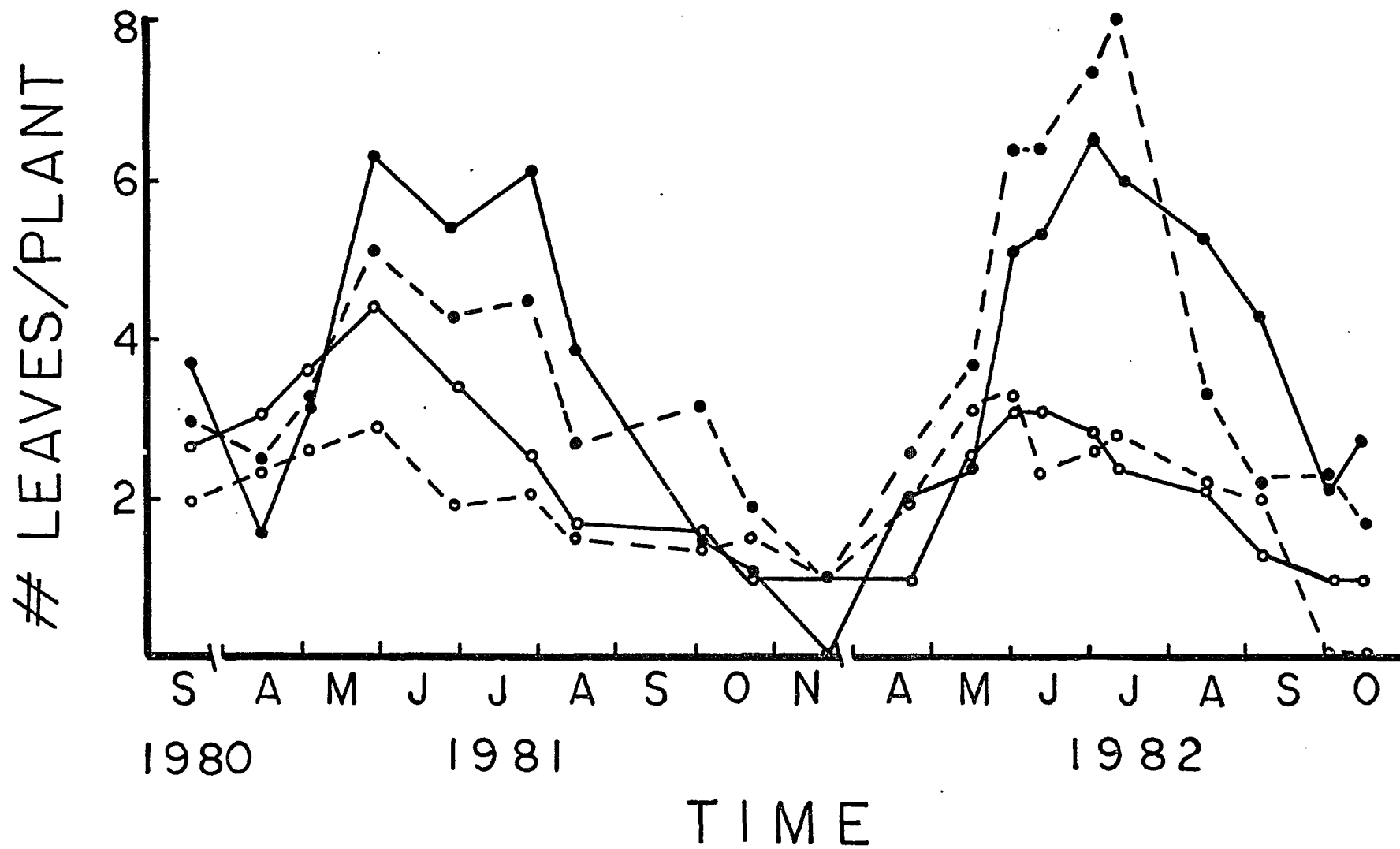


FIGURE 12. # LEAVES PER PLANT, RECIPROCAL TRANSPLANT #2.

Average number of leaves per plant, reciprocal transplant #2, from September 22, 1981 (day of transplant) to October 1982 (not including bare petioles).

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 10 for statistical analysis.

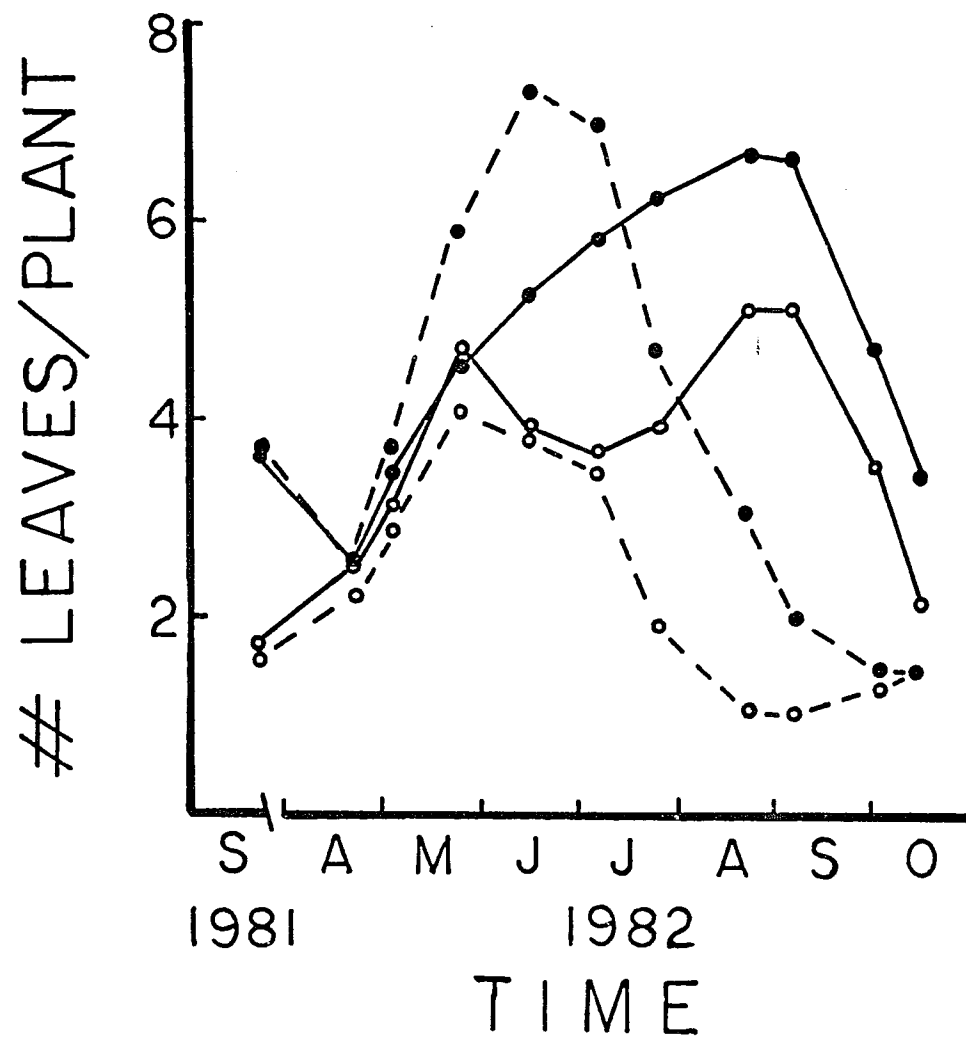


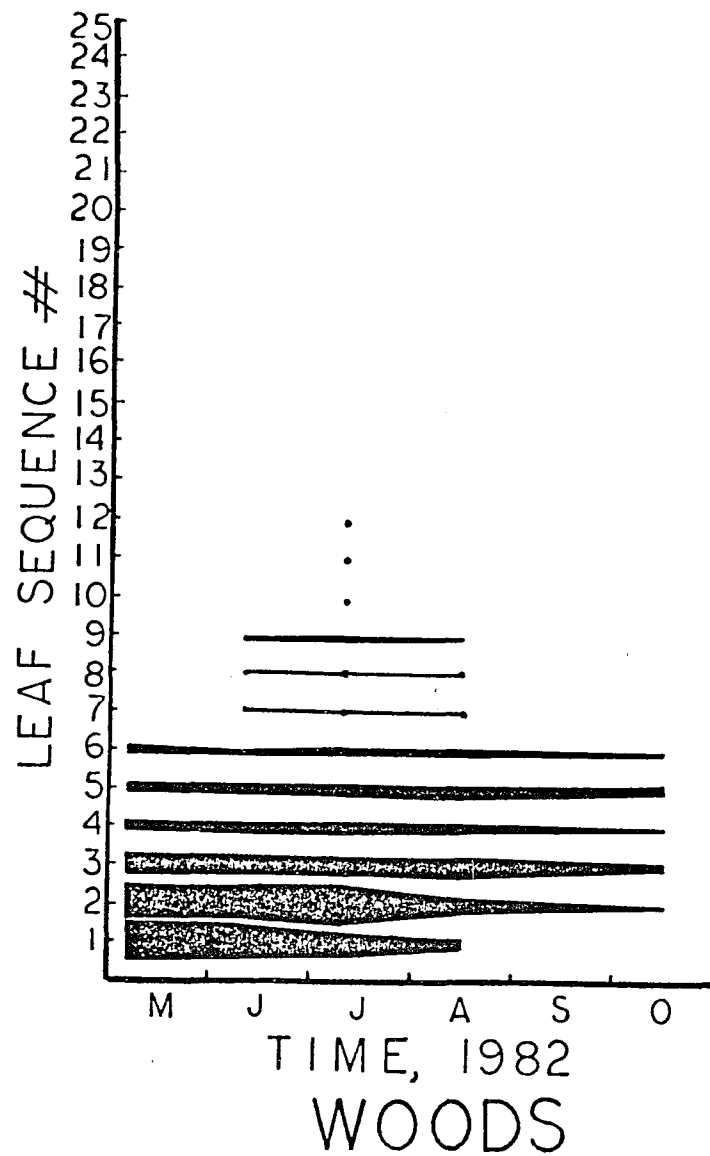
FIGURE 13. LEAF DURATION, V. SORORIA, RECIPROCAL TRANSPLANT #1.

The duration of individual leaves, in order of their sequence of emergence, over one season (May to October, 1982).

Reciprocal transplant #1, V. sororia woods (left), and field (right).

The width of the lines represents the number of leaves of a particular sequence number.

Figures 13-14 go together.



25 LVS

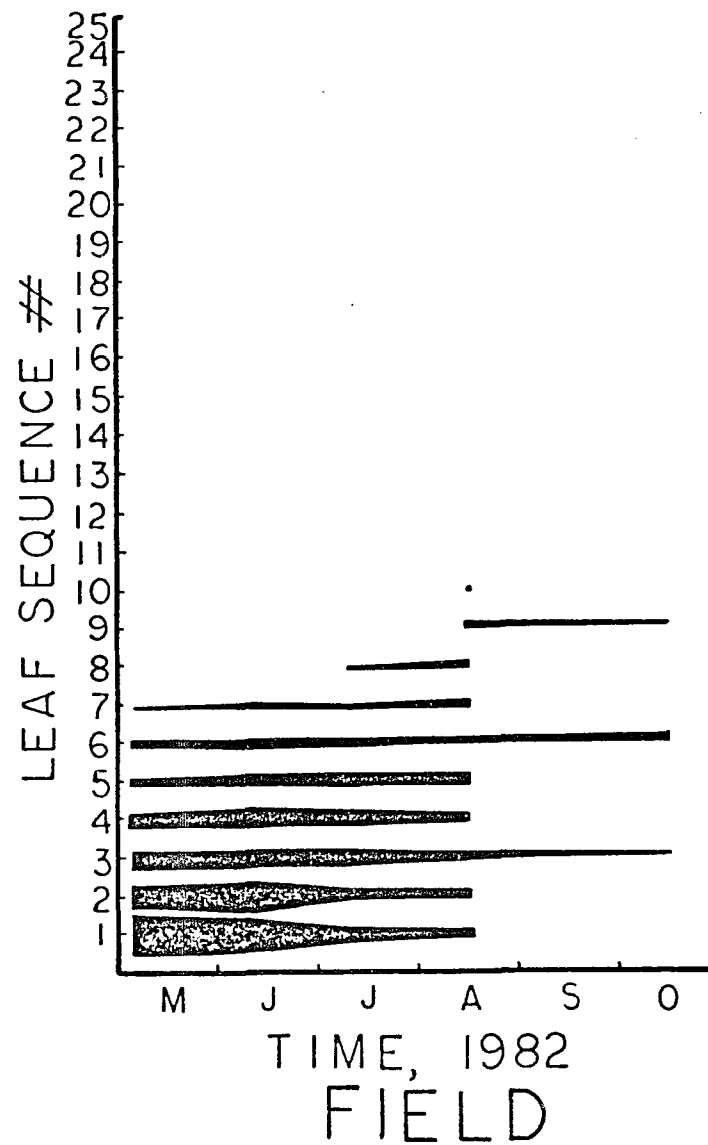


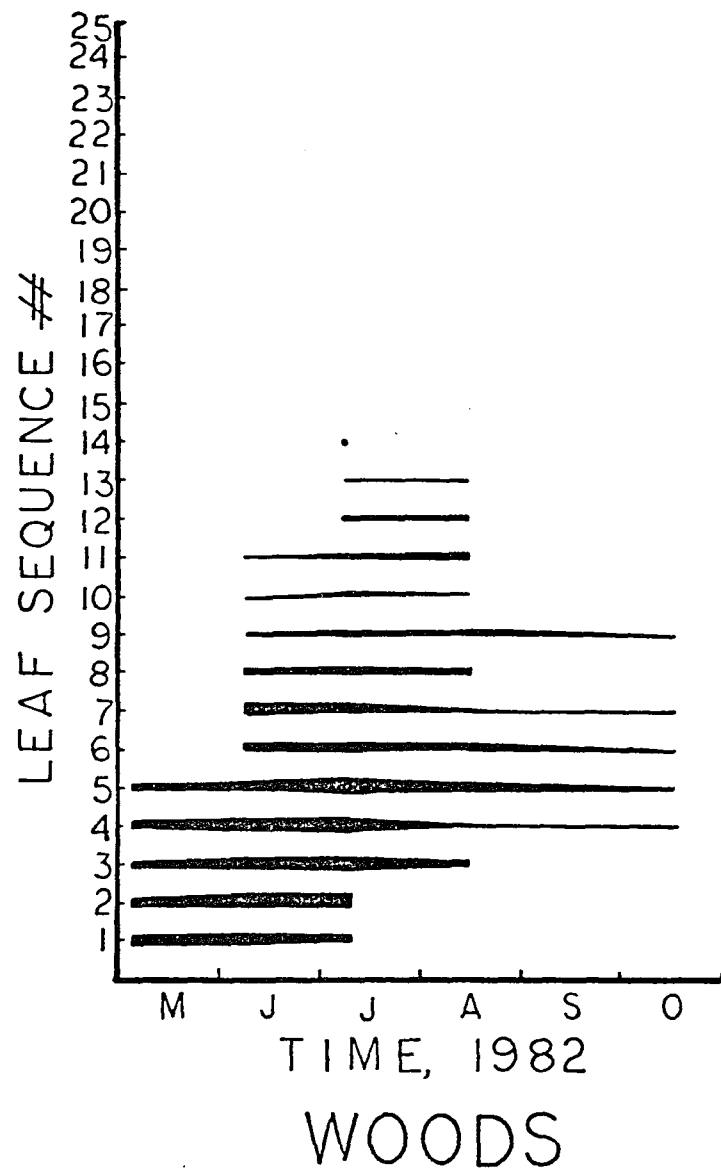
FIGURE 14. LEAF DURATION, V. FIMBRIATULA, RECIP. TRANSP. #1.

The duration of individual leaves, in order of their sequence of emergence, over one season (May to October, 1982).

Reciprocal transplant #1, V. fimbriatula woods (left), and field (right).

The width of the lines represents the number of leaves of a particular sequence number.

Figures 13-14 go together.



25 LVS

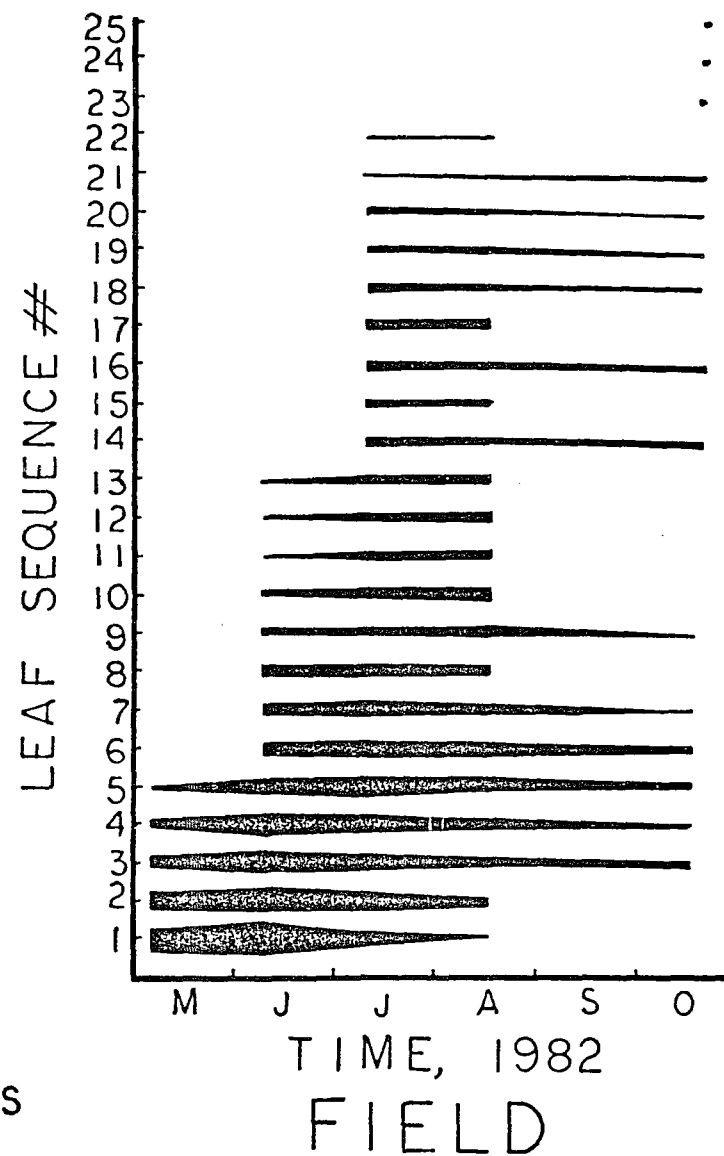


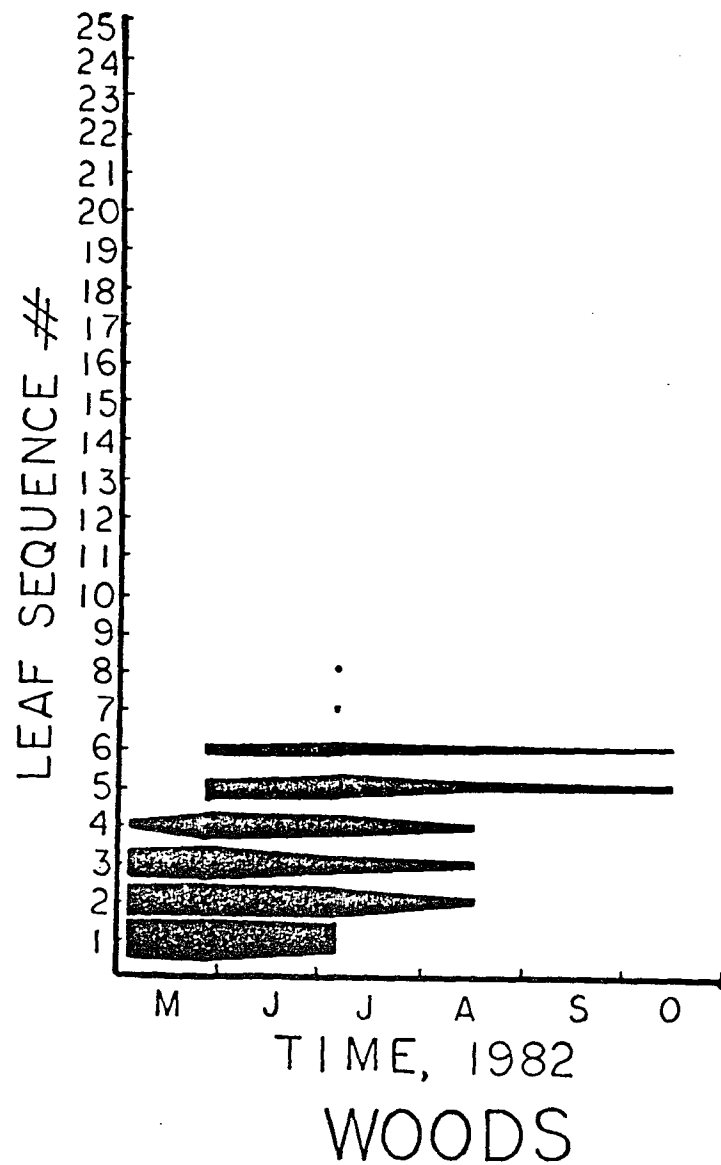
FIGURE 15. LEAF DURATION, V. SORORIA, RECIP. TRANSP. #2.

The duration of individual leaves, in order of their sequence of emergence, over one season (May to October, 1982).

Reciprocal transplant #2, V. sororia woods (left), and field (right).

The width of the lines represents the number of leaves of a particular sequence number.

Figures 15-16 go together.



25 LVS

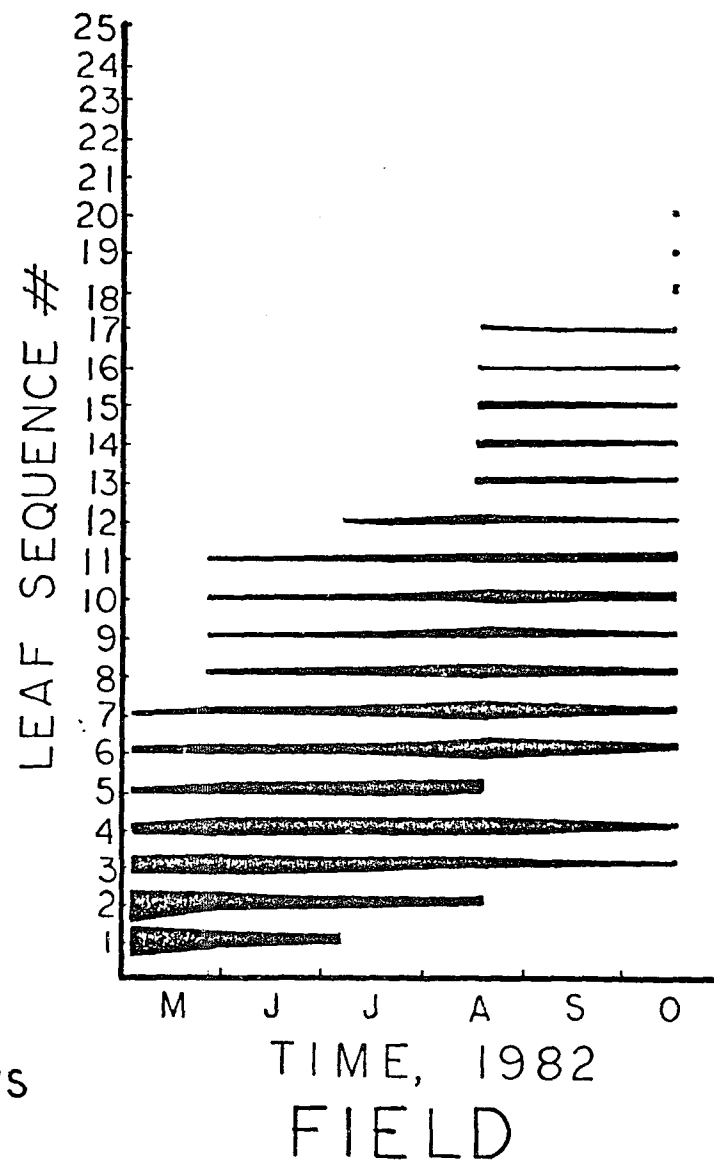


FIGURE 16. LEAF DURATION, V. FIMBRIATULA, RECIP. TRANSP. #2.

The duration of individual leaves, in order of their sequence of emergence, over one season (May to October, 1982).

Reciprocal transplant #2, V. fimbriatula woods (left), and field (right).

The width of the lines represents the number of leaves of a particular sequence number.

Figures 15-16 go together.

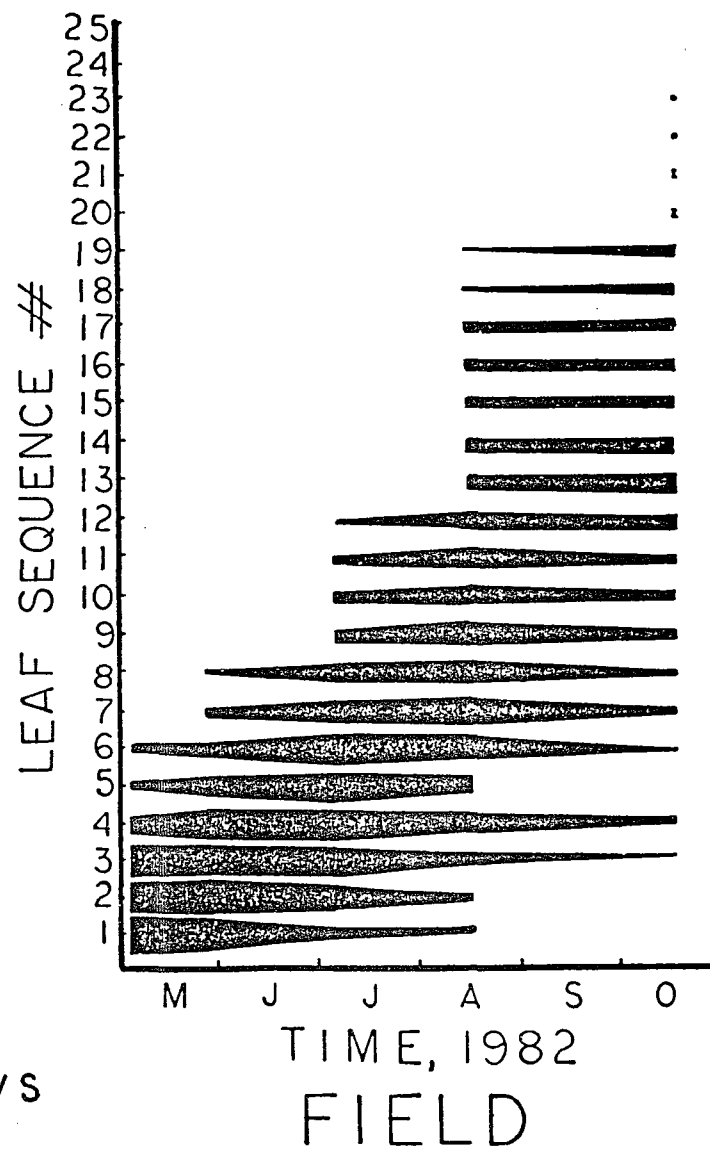
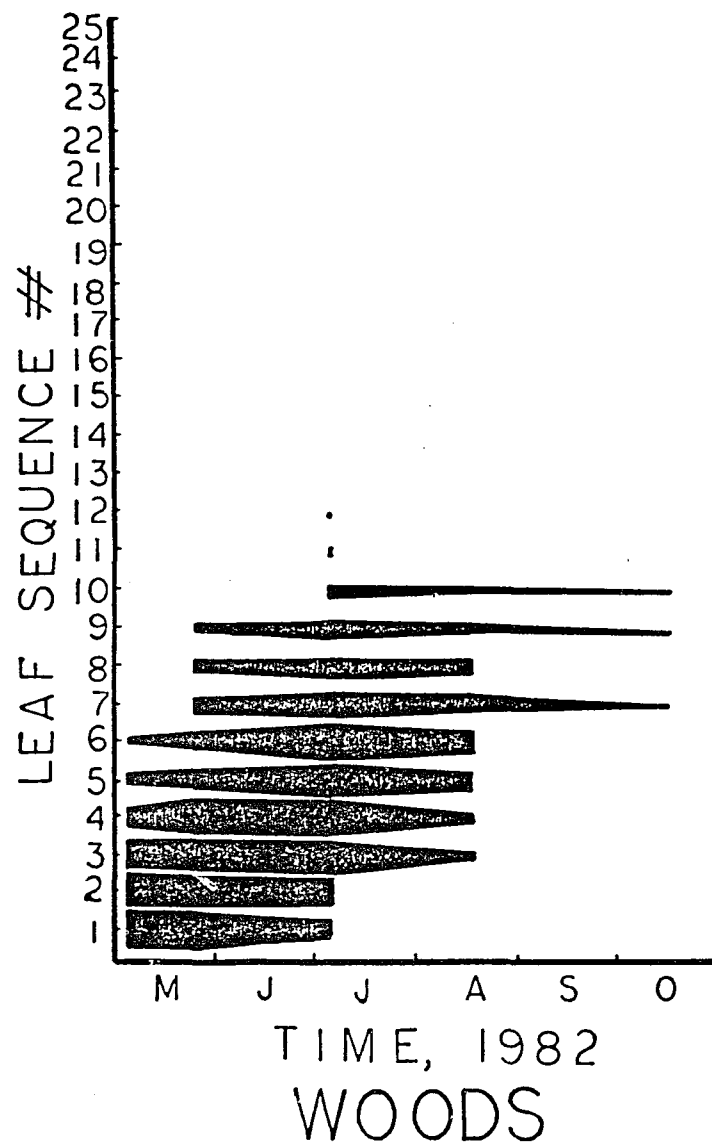


FIGURE 17. LEAF BLADE LENGTH, RECIPROCAL TRANSPLANT #1.

Average length of the leaf blade, reciprocal transplant #1, July 1981 to October 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 9 for statistical analysis. Figures 17-20 go together.

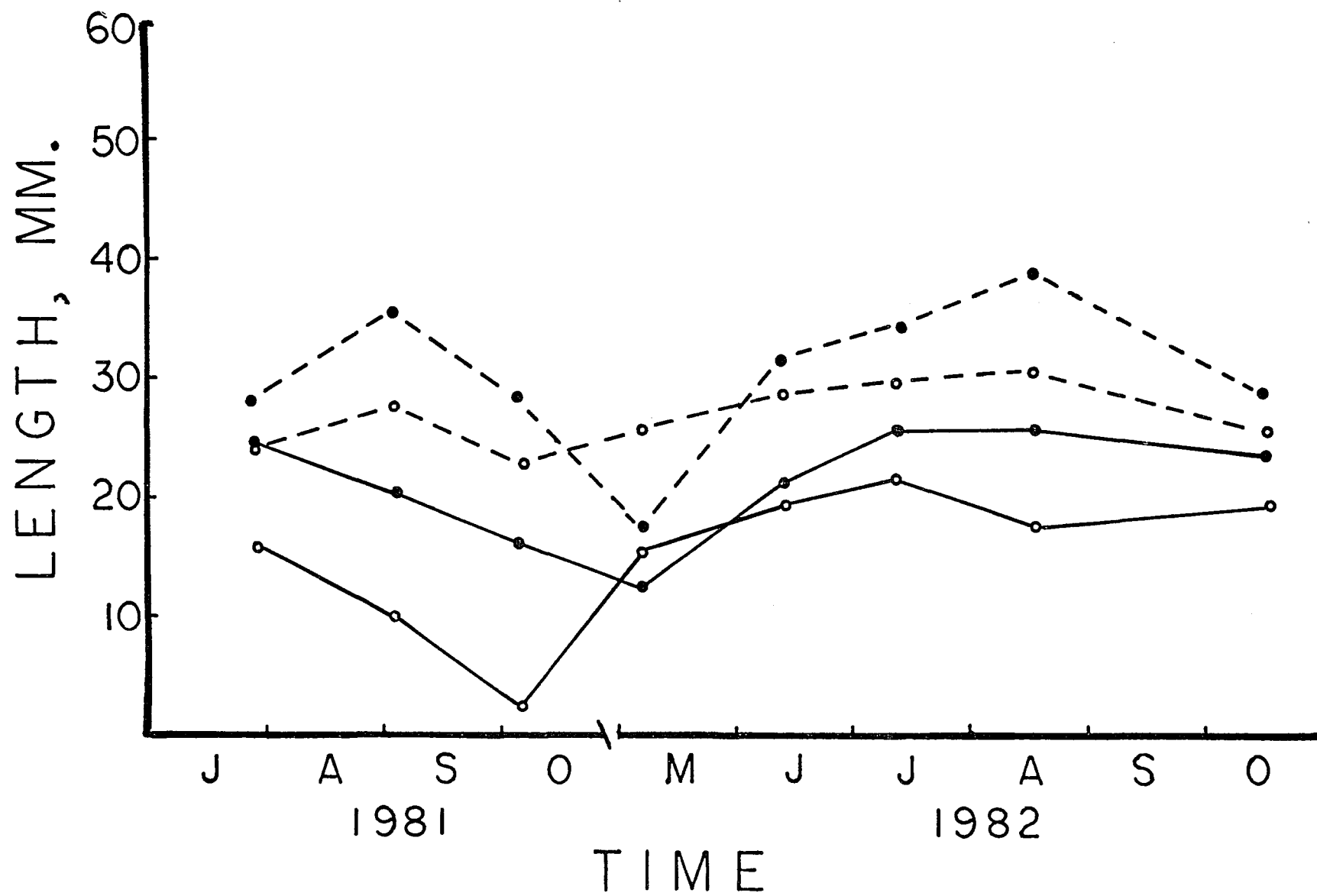


FIGURE 18. LEAF BLADE WIDTH, RECIPROCAL TRANSPLANT #1.

Average width of the leaf blade, reciprocal transplant #1, July 1981 to October 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 9 for statistical analysis. Figures 17-20 go together.

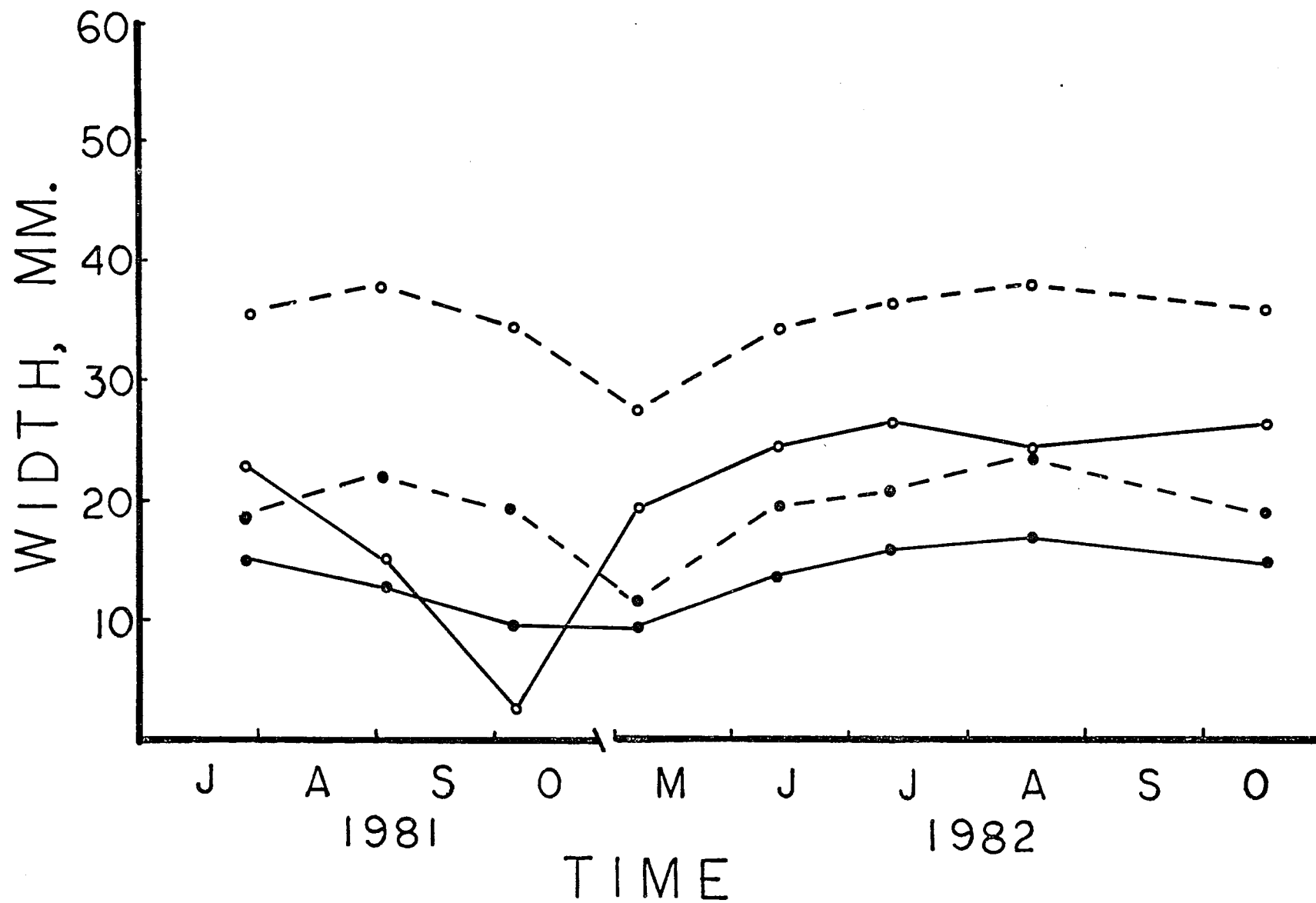


FIGURE 19. LEAF PETIOLE, RECIPROCAL TRANSPLANT #1.

Average leaf petiole length, reciprocal transplant #1, July 1981 to October 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 9 for statistical analysis. Figures 17-20 go together.

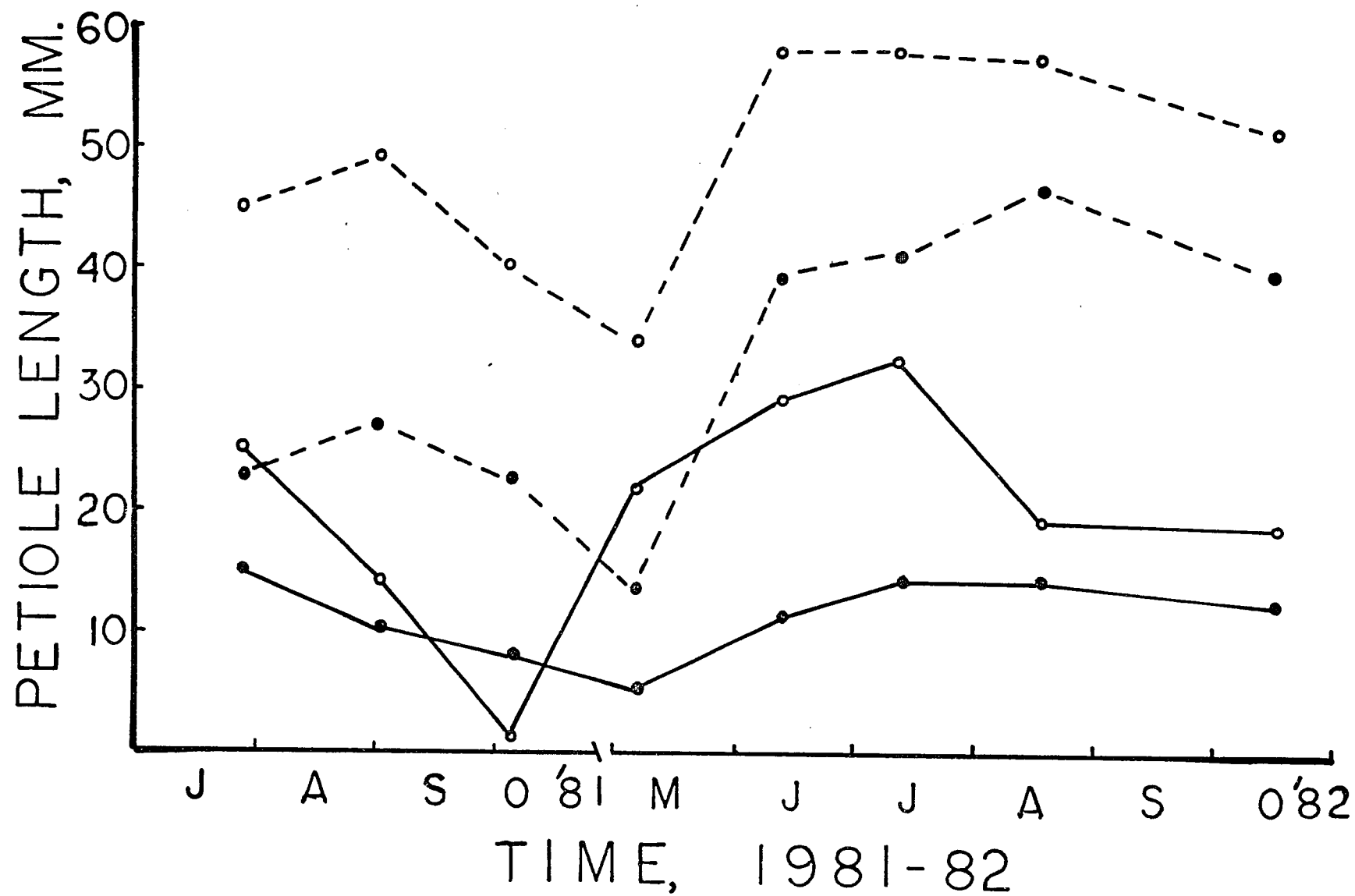
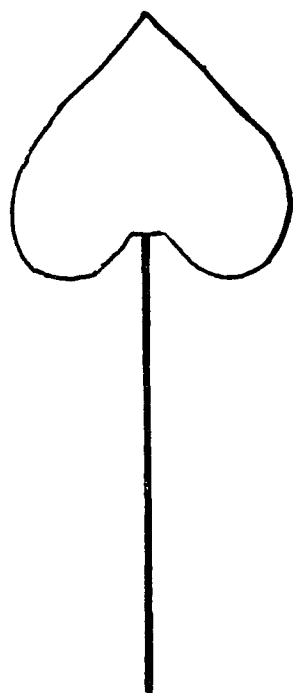


FIGURE 20. AVERAGE LEAF DIMENSIONS, RECIP. TRANSP. #1.

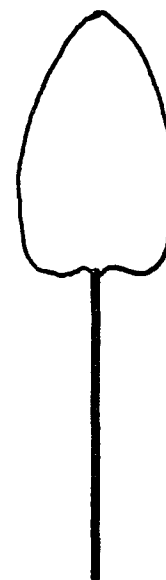
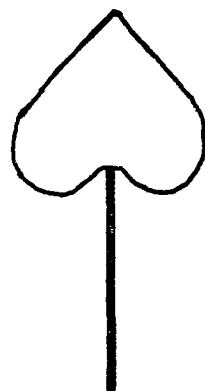
Average leaf dimensions, hand-drawn to scale for length and width of blades, and length of petioles, reciprocal transplant #1.

Leaves measured on 6/12/82, approximately two years after the transplants were made. Figures 17-20 go together.

LENGTH, WIDTH, PETIOLE
CM.



WOODS FIELD
V. SORORIA



WOODS FIELD
V. FIMBRIATULA

FIGURE 21. LEAF BLADE LENGTH, RECIPROCAL TRANSPLANT #2.

Average length of the leaf blade, reciprocal transplant #2, from September 22, 1981 (day of transplant) to October 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 10 for statistical analysis. Figures 21-23 go together.

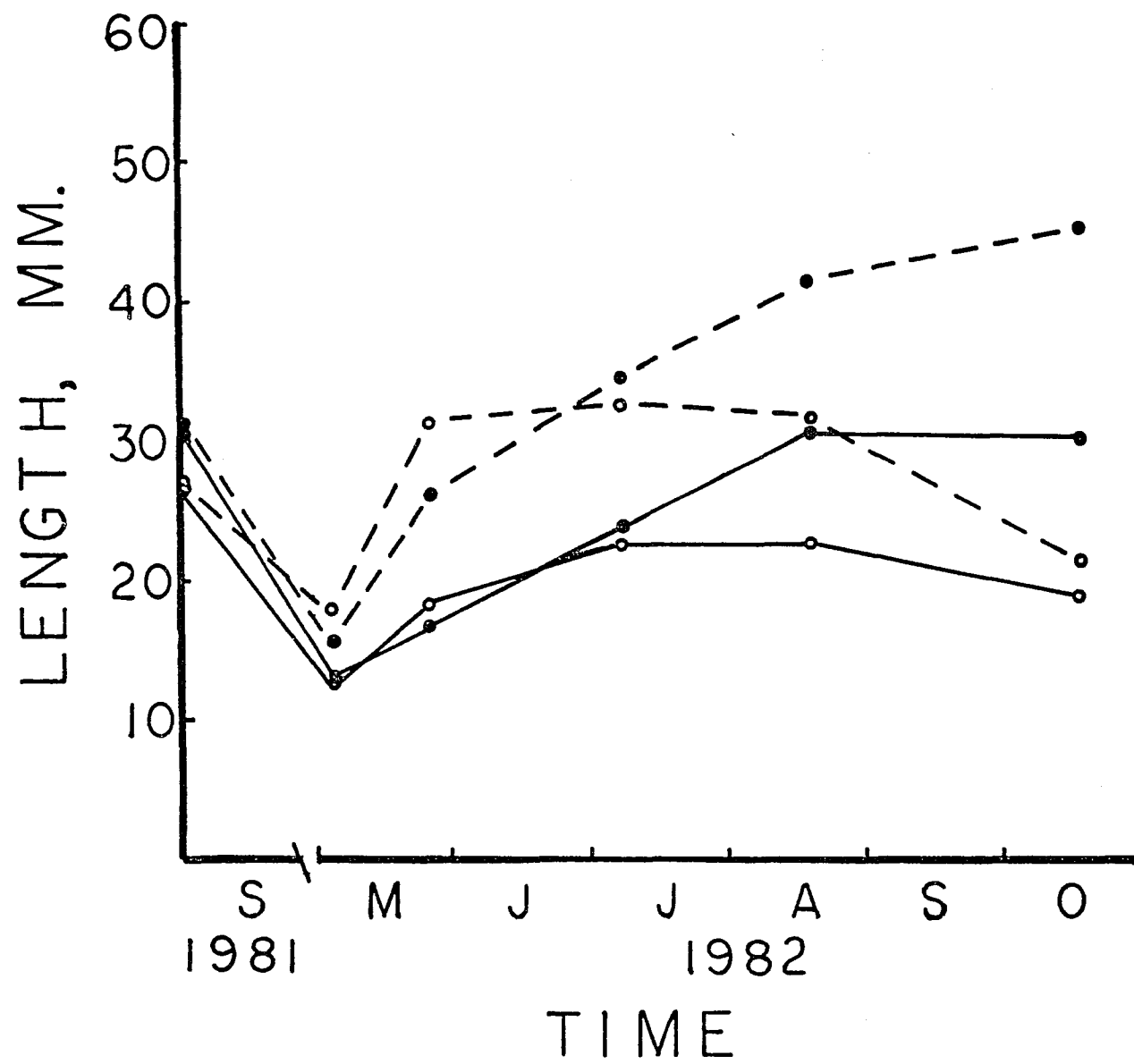


FIGURE 22. LEAF BLADE WIDTH, RECIPROCAL TRANSPLANT #2.

Average width of the leaf blade, reciprocal transplant #2, from September 22, 1981 (day of transplant) to October 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 10 for statistical analysis. Figures 21-23 go together.

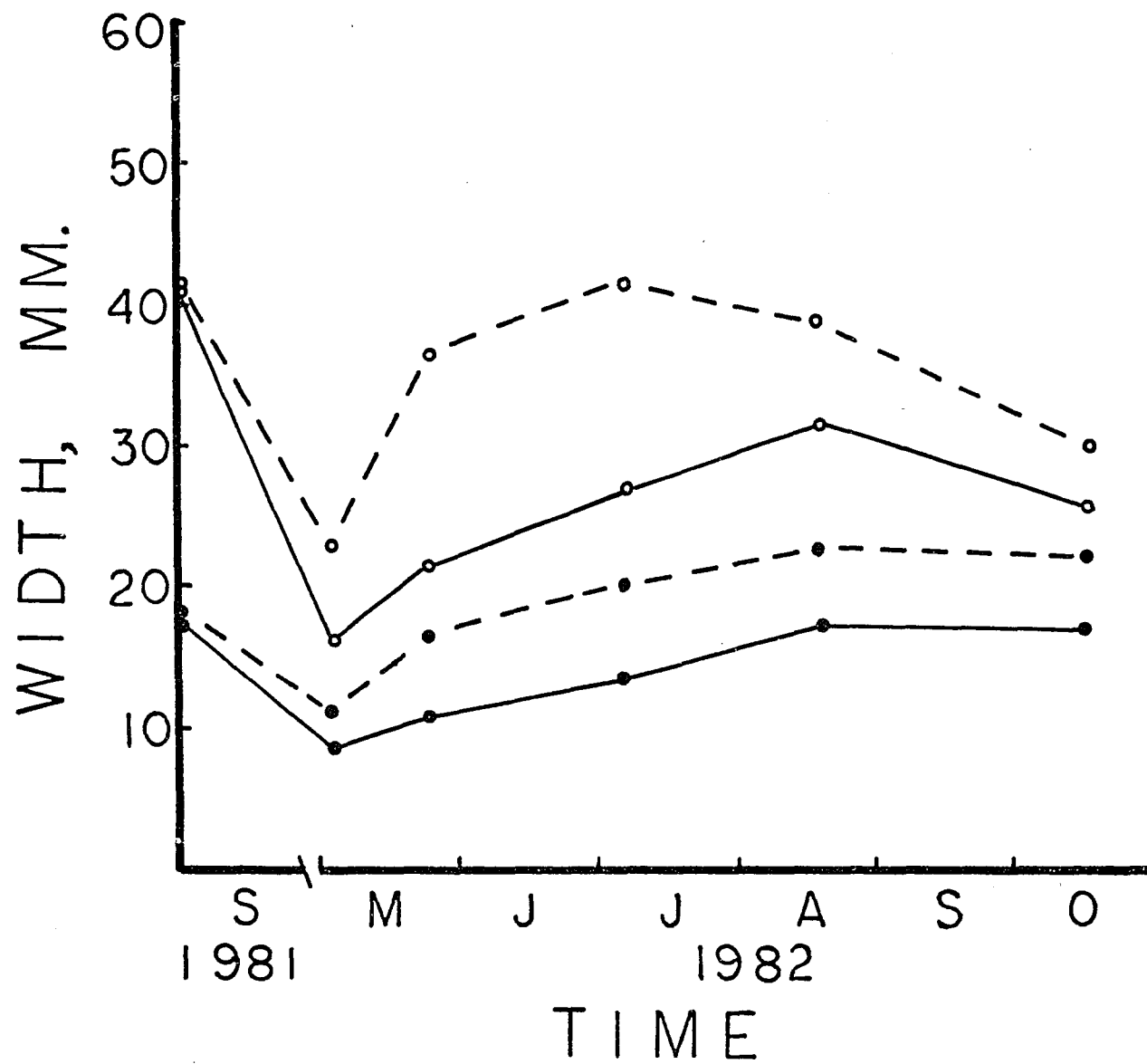


FIGURE 23. LEAF PETIOLE, RECIPROCAL TRANSPLANT #2.

Average leaf petiole length, reciprocal transplant #2, from
September 22, 1981 (day of transplant) to October 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and
solid lines = field, and the dashes = woods.

See Table 10 for statistical analysis. Figures 21-23 go together.

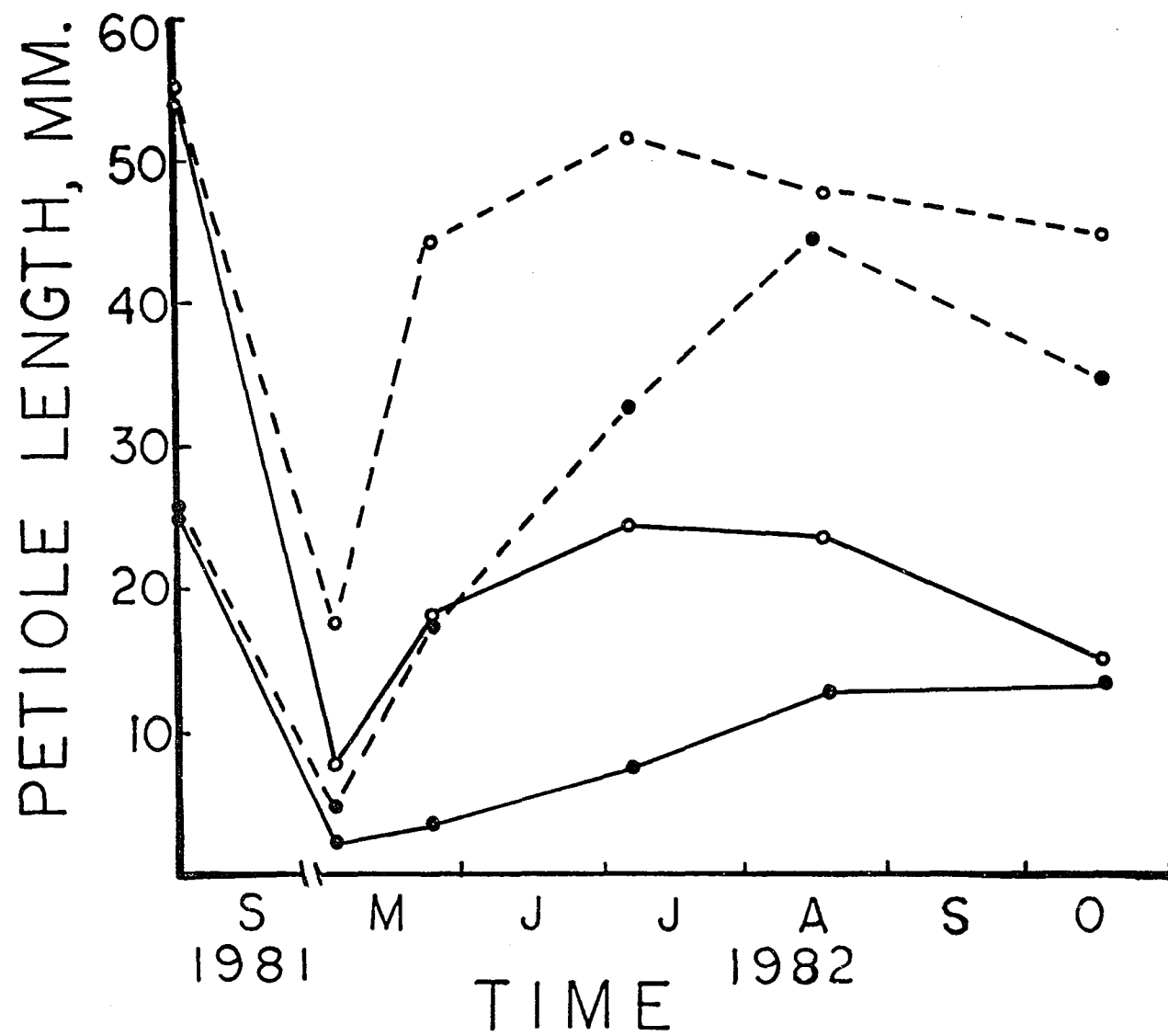


FIGURE 24. # REPRODUCTIVES PER PLANT, RECIPROCAL TRANSPLANT #1.

Average number of reproductives per plant, reciprocal transplant #1, from September 1980 to October 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 9 for statistical analysis.

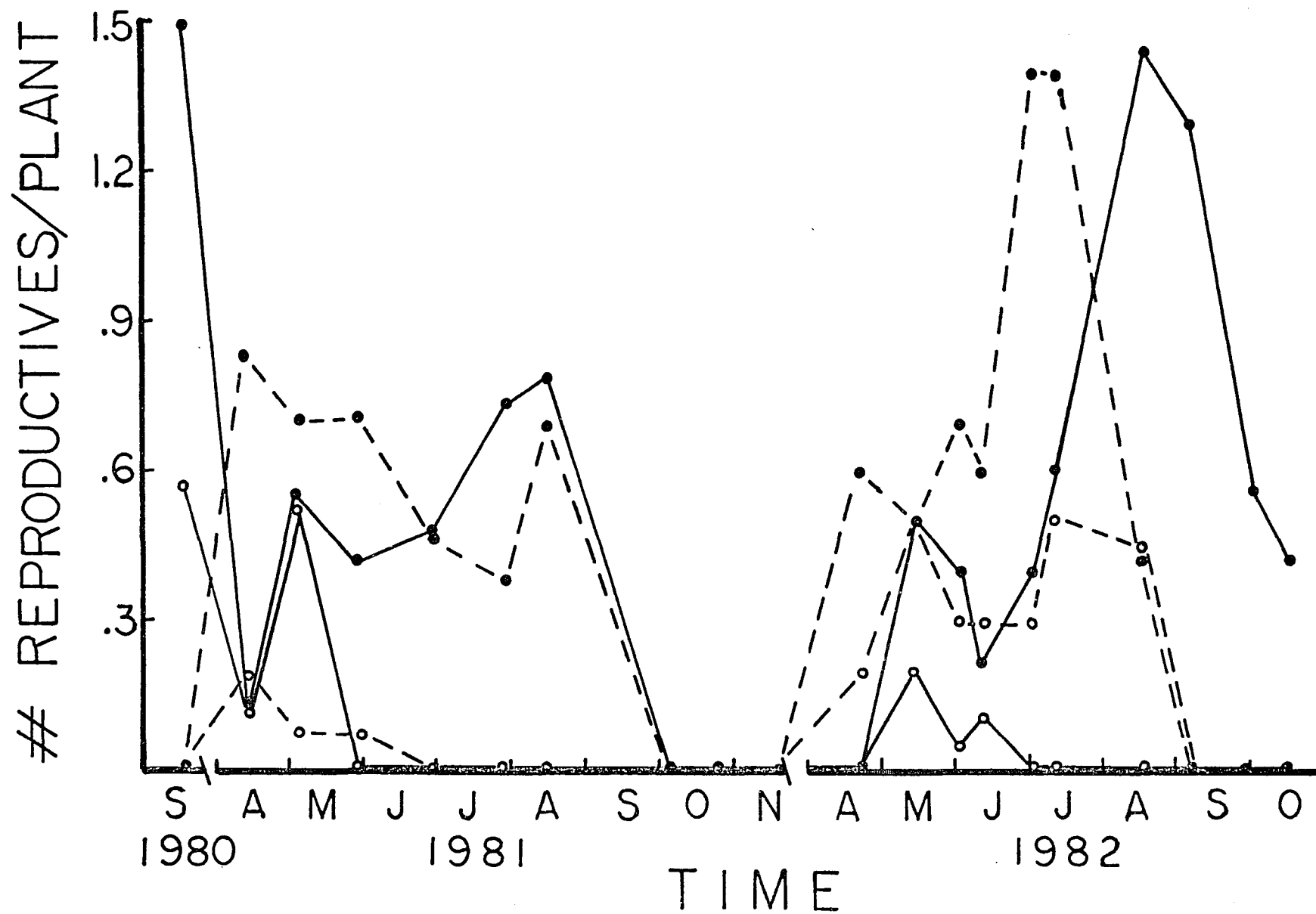


FIGURE 25. # REPRODUCTIVES PER PLANT, RECIPROCAL TRANSPLANT #2.

Average number of reproductives per plant, reciprocal transplant #2, from September 22, 1981 (day of transplant) to October 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 10 for statistical analysis.

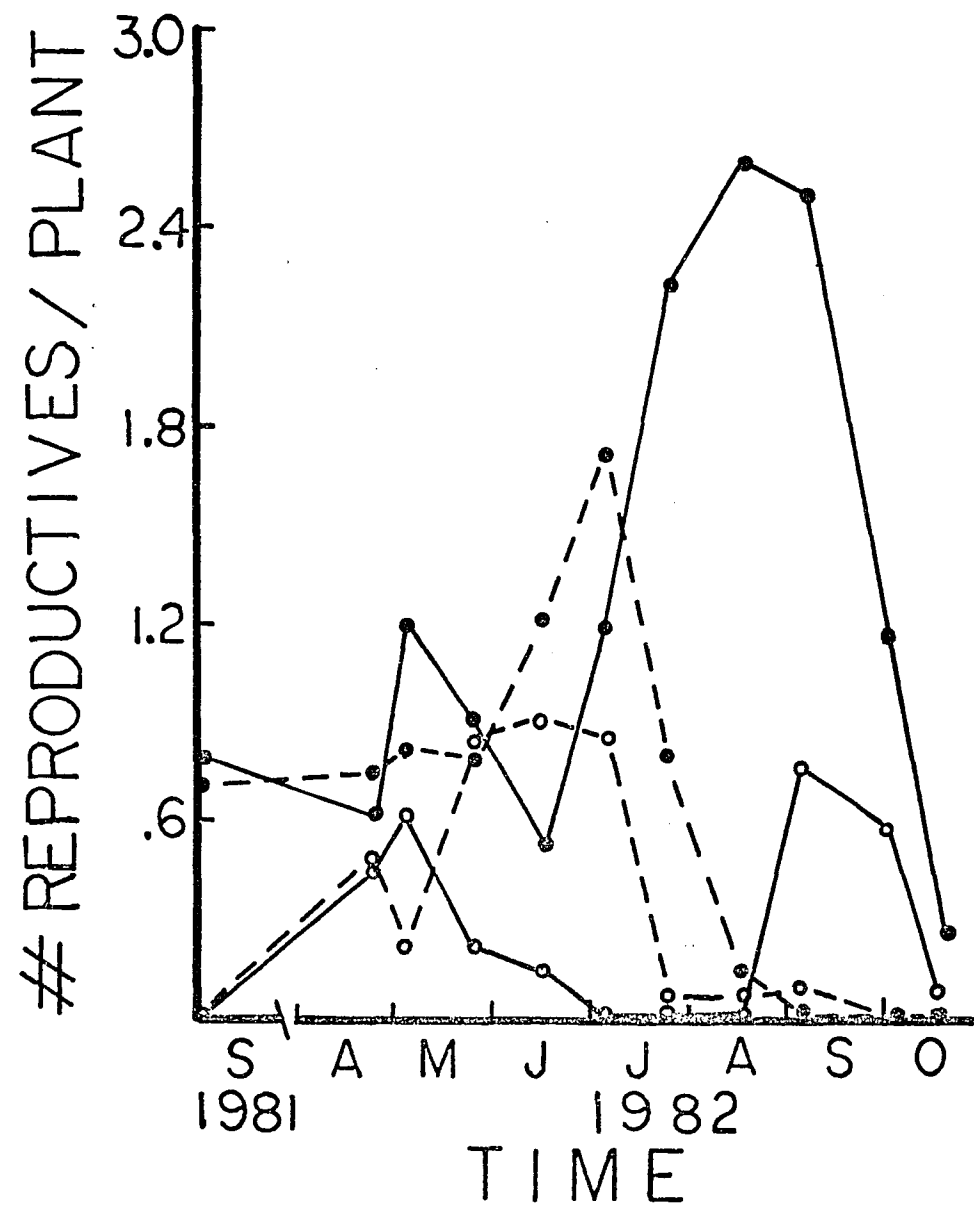


FIGURE 26. REPRODUCTIVE TYPES, V. SORORIA-WOODS, RECIP. TR. #1

Average number of each type of reproductive per plant,
Viola sororia in the woods, reciprocal transplant #1, from
September 1980 to October 1982.

Symbols: open bar = chasmogamous flowers, spotted bar =
chasmogamous fruits, striped bar = cleistogamous flowers, black
bar = cleistogamous fruits.

Figures 26-29 go together.

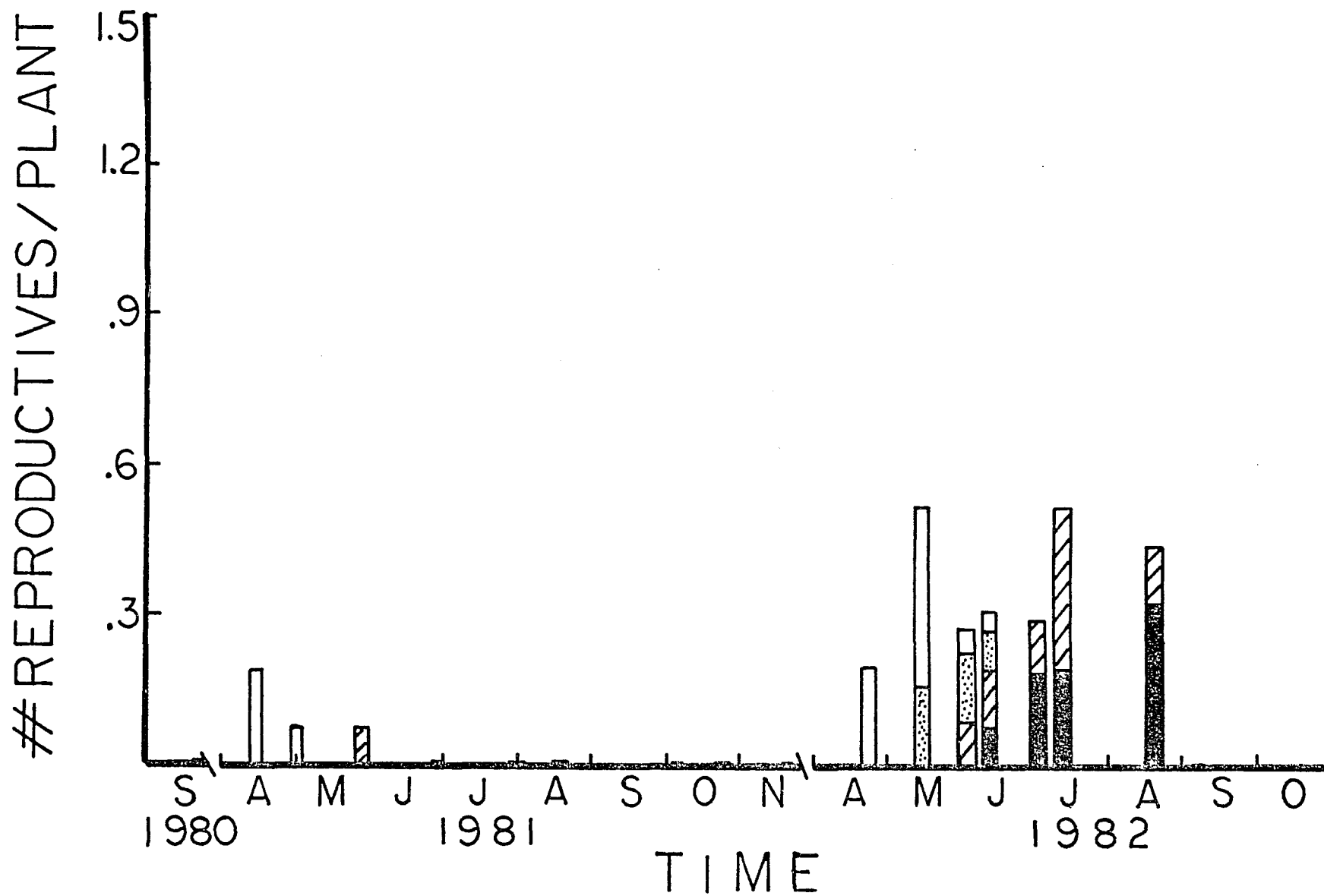


FIGURE 27. REPRODUCTIVE TYPES, V. SORORIA-FIELD, RECIP. TR. #1.

Average number of each type of reproductive per plant,

Viola sororia in the field, reciprocal transplant #1.

Symbols: open bar = chasmogamous flowers, spotted bar =
chasmogamous fruits, striped bar = cleistogamous flowers, black
bar = cleistogamous fruits.

Figures 26-29 go together.

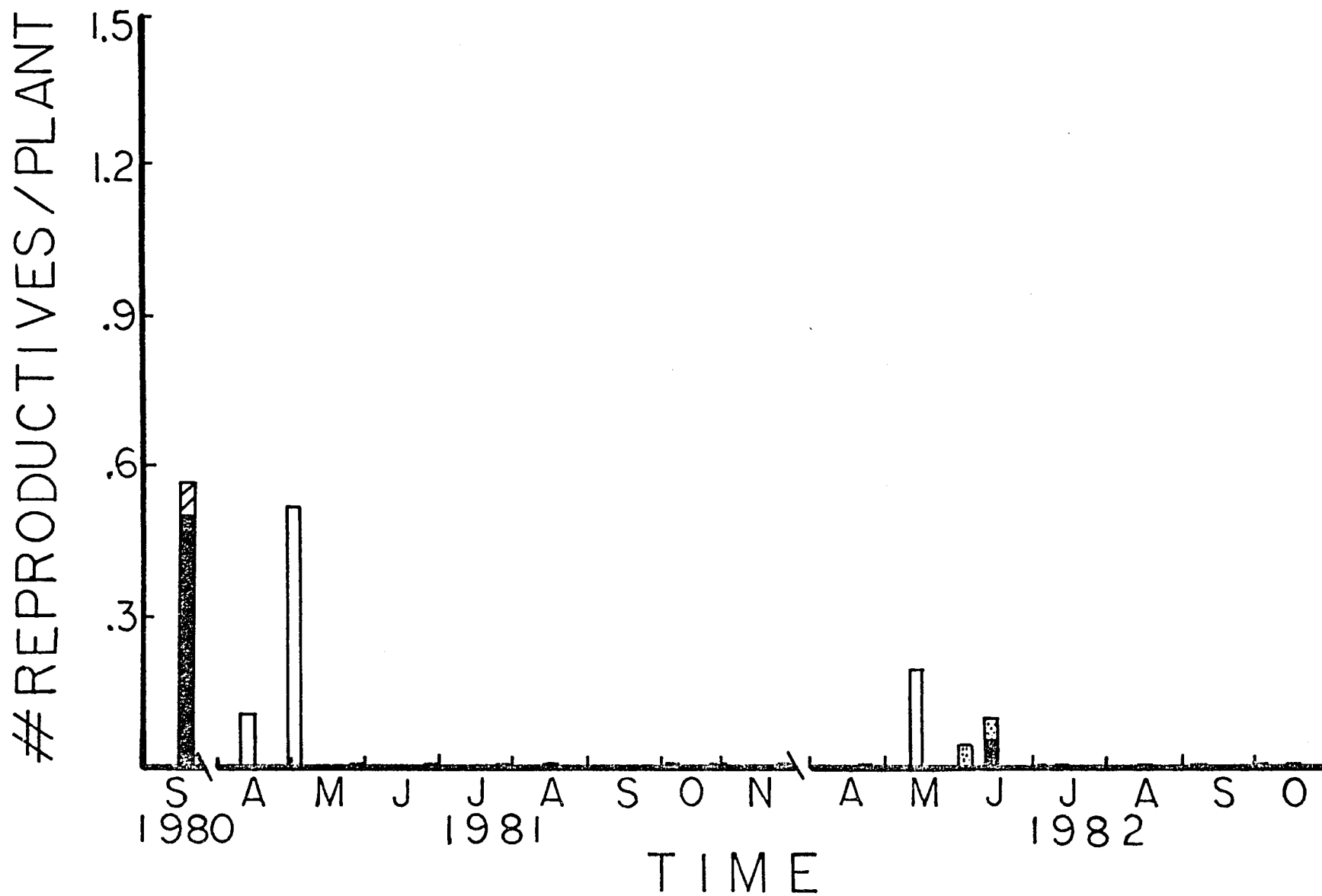


FIGURE 28. REPRODUCTIVE TYPES, V. FIMBRIATULA-WOODS, REC. TR.#1.

Average number of each type of reproductive per plant,

Viola fimbriatula in the woods, reciprocal transplant #1.

Symbols: open bar = chasmogamous flowers, spotted bar =
chasmogamous fruits, striped bar = cleistogamous flowers, black
bar = cleistogamous fruits.

Figures 26-29 go together.

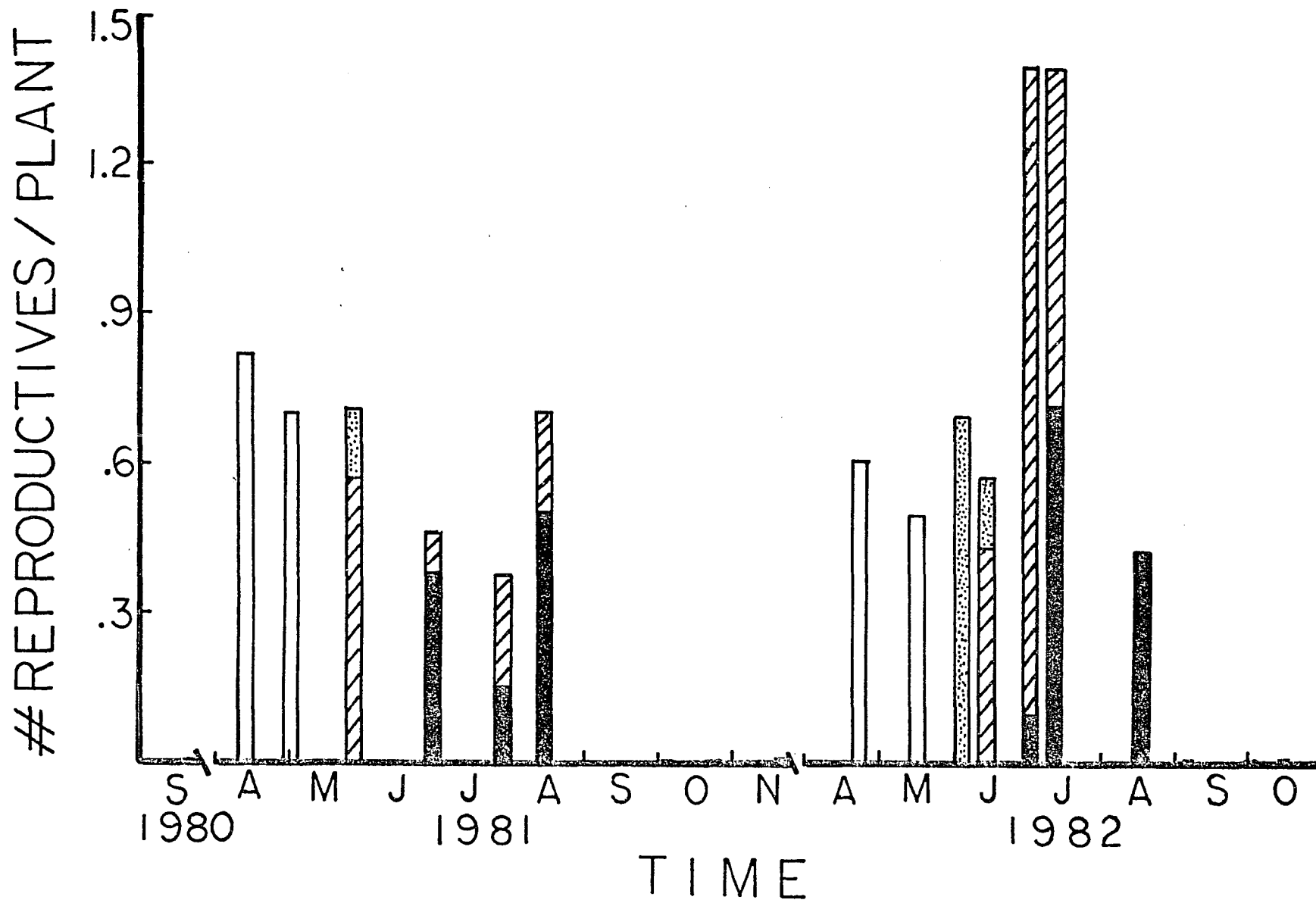


FIGURE 29. REPRODUCTIVE TYPES, V. FIMBRIATULA-FIELD, REC. TR.#1

Average number of each type of reproductive per plant,

Viola fimbriatula in the field, reciprocal transplant #1.

Symbols: open bar = chasmogamous flowers, spotted bar =
chasmogamous fruits, striped bar = cleistogamous flowers, black
bar = cleistogamous fruits.

Figures 26-29 go together.

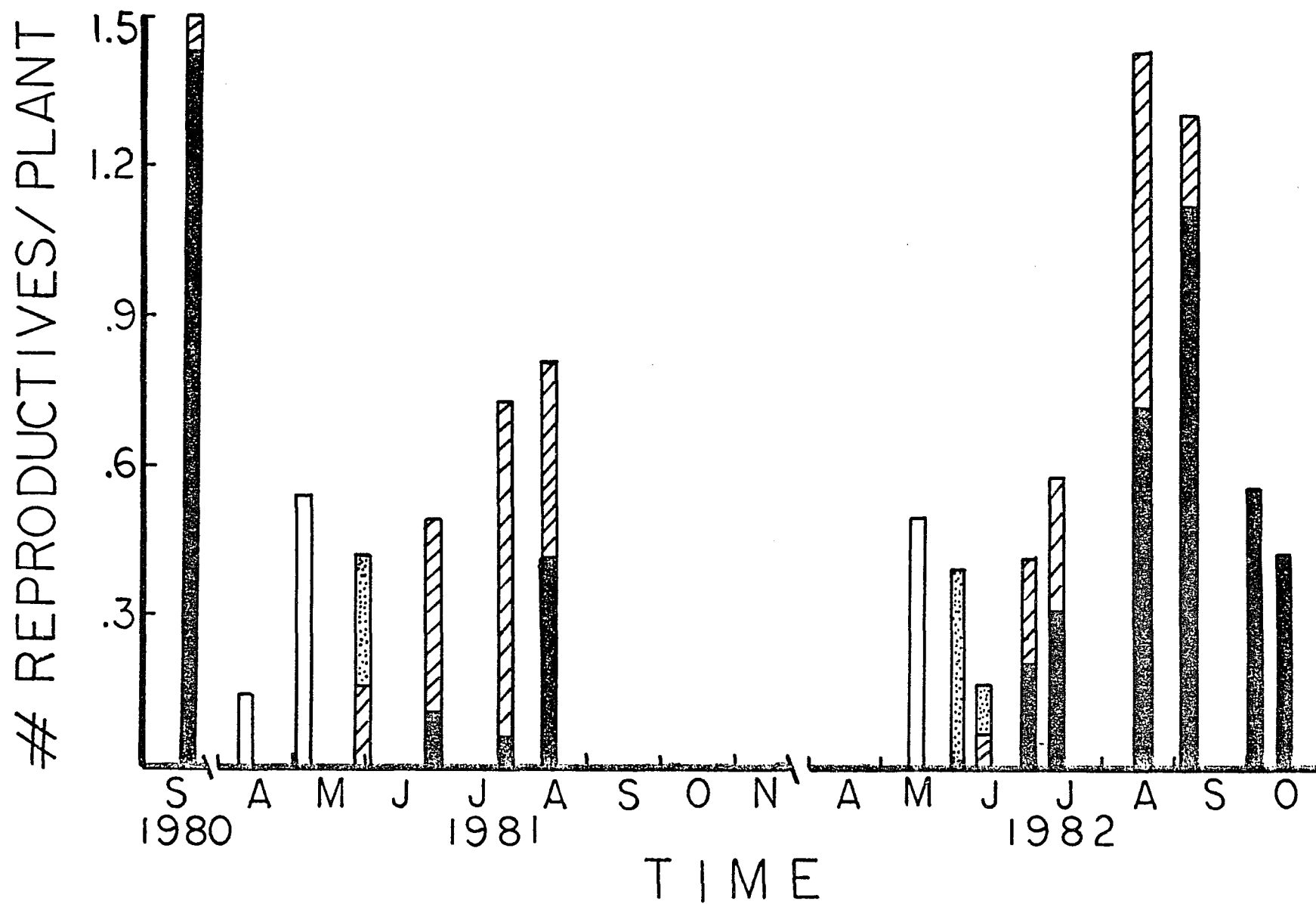


FIGURE 30. REPRODUCTIVE TYPES, V. SORORIA-WOODS, REC. TR. #2.

Average number of each type of reproductive per plant,
Viola sororia in the woods, reciprocal transplant #2, from
September 1981 (day of transplant) to October 1982.

Symbols: open bar = chasmogamous flowers, spotted bar =
chasmogamous fruits, striped bar = cleistogamous flowers, black
bar = cleistogamous fruits.

Figures 30-33 go together.

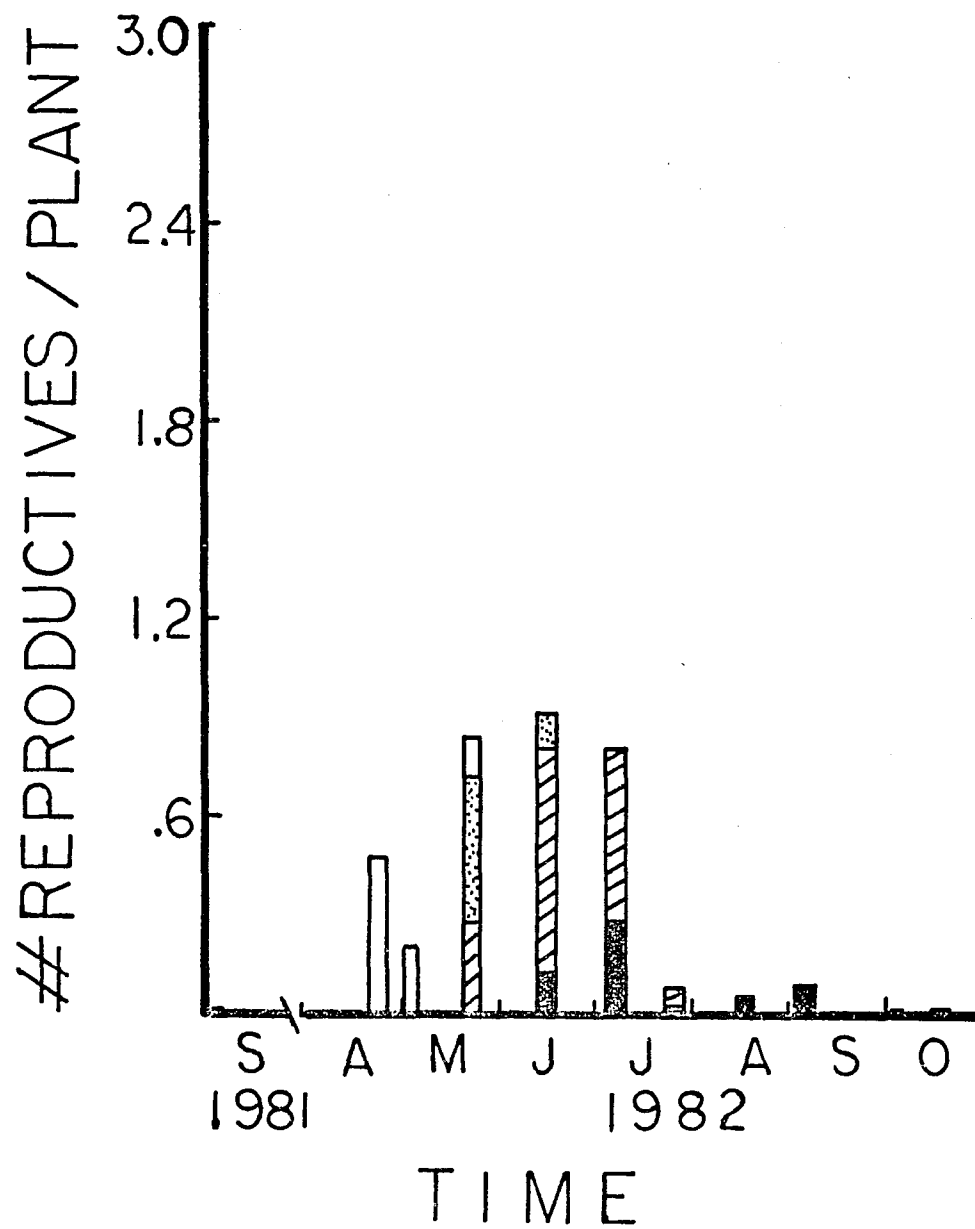


FIGURE 31. REPRODUCTIVE TYPES, V. SORORIA-FIELD, REC. TR. #2.

Average number of each type of reproductive per plant,

Viola sororia in the field, reciprocal transplant #2.

Symbols: open bar = chasmogamous flowers, spotted bar =
chasmogamous fruits, striped bar = cleistogamous flowers, black
bar = cleistogamous fruits.

Figures 30-33 go together.

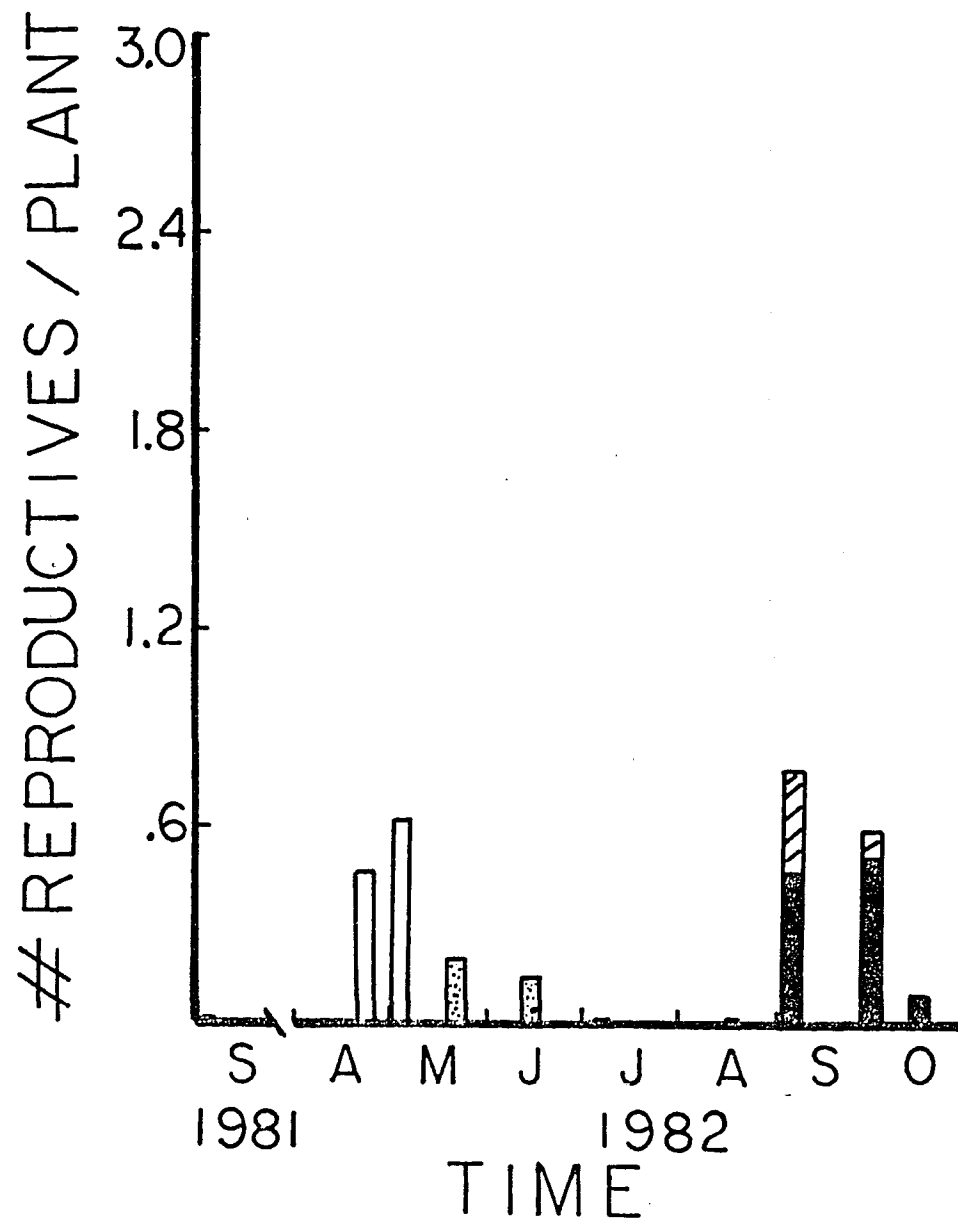


FIGURE 32. REPRODUCTIVE TYPES, V. FIMBRIATULA-WOODS, REC. TR. #2.

Average number of each type of reproductive per plant,

Viola fimbriatula in the woods, reciprocal transplant #2.

Symbols: open bar = chasmogamous flowers, spotted bar =
chasmogamous fruits, striped bar = cleistogamous flowers, black
bar = cleistogamous fruits.

Figures 30-33 go together.

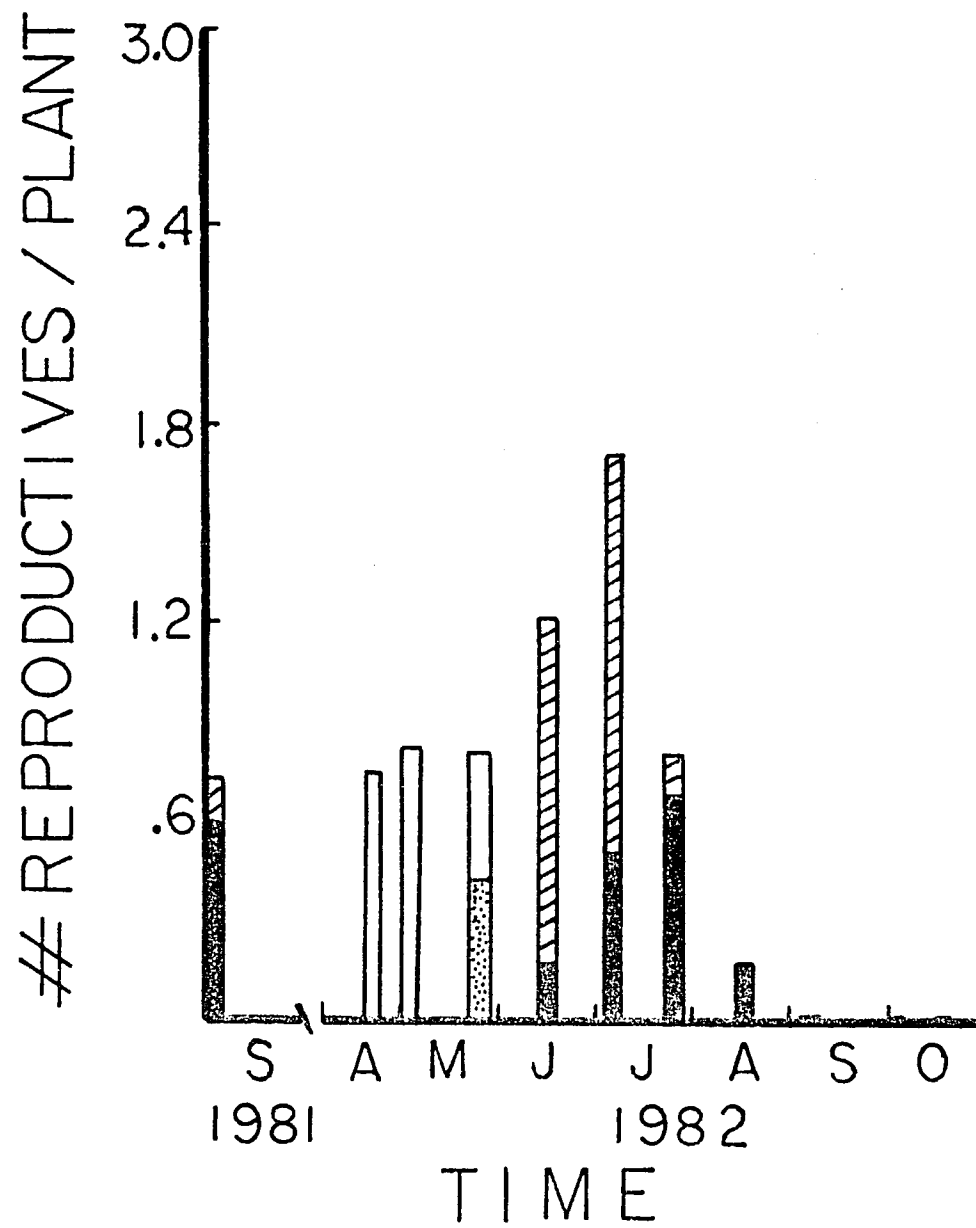


FIGURE 33. REPRODUCTIVE TYPES, V. FIMBRIATULA-FIELD, REC. TR. #2.

Average number of each type of reproductive per plant,

Viola fimbriatula in the field, reciprocal transplant #2.

Symbols: open bar = chasmogamous flowers, spotted bar =
chasmogamous fruits, striped bar = cleistogamous flowers, black
bar = cleistogamous fruits.

Figures 30-33 go together.

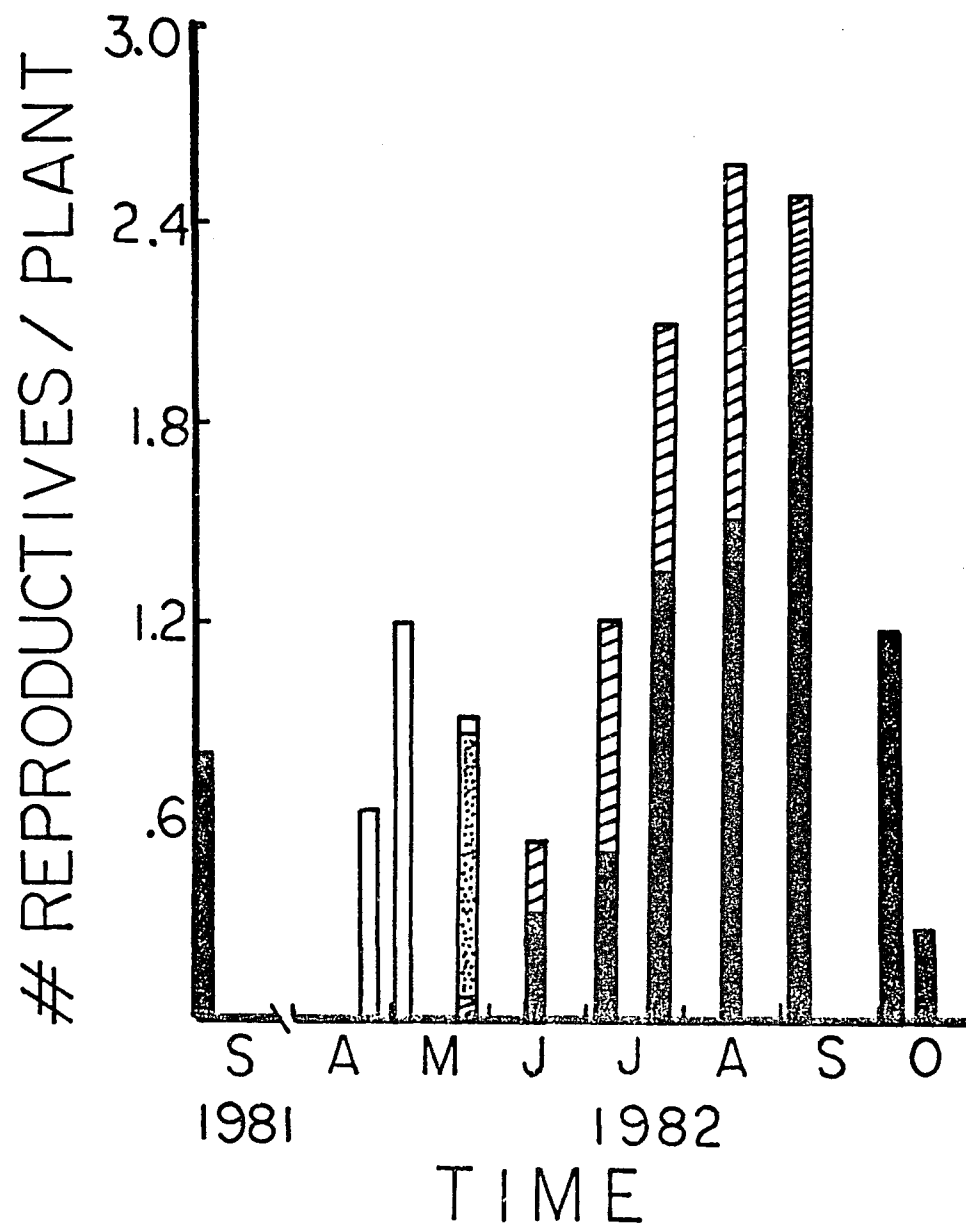


FIGURE 34. PREDATION, RECIPROCAL TRANSPLANT #1.

Percent predation (average percent of total leaf area eaten),
reciprocal transplant #1, from September 1980 to October 1982.
Open circles = V. sororia, closed circles = V. fimbriatula; and
solid lines = field, and the dashes = woods.
See Table 11 for statistical analysis.

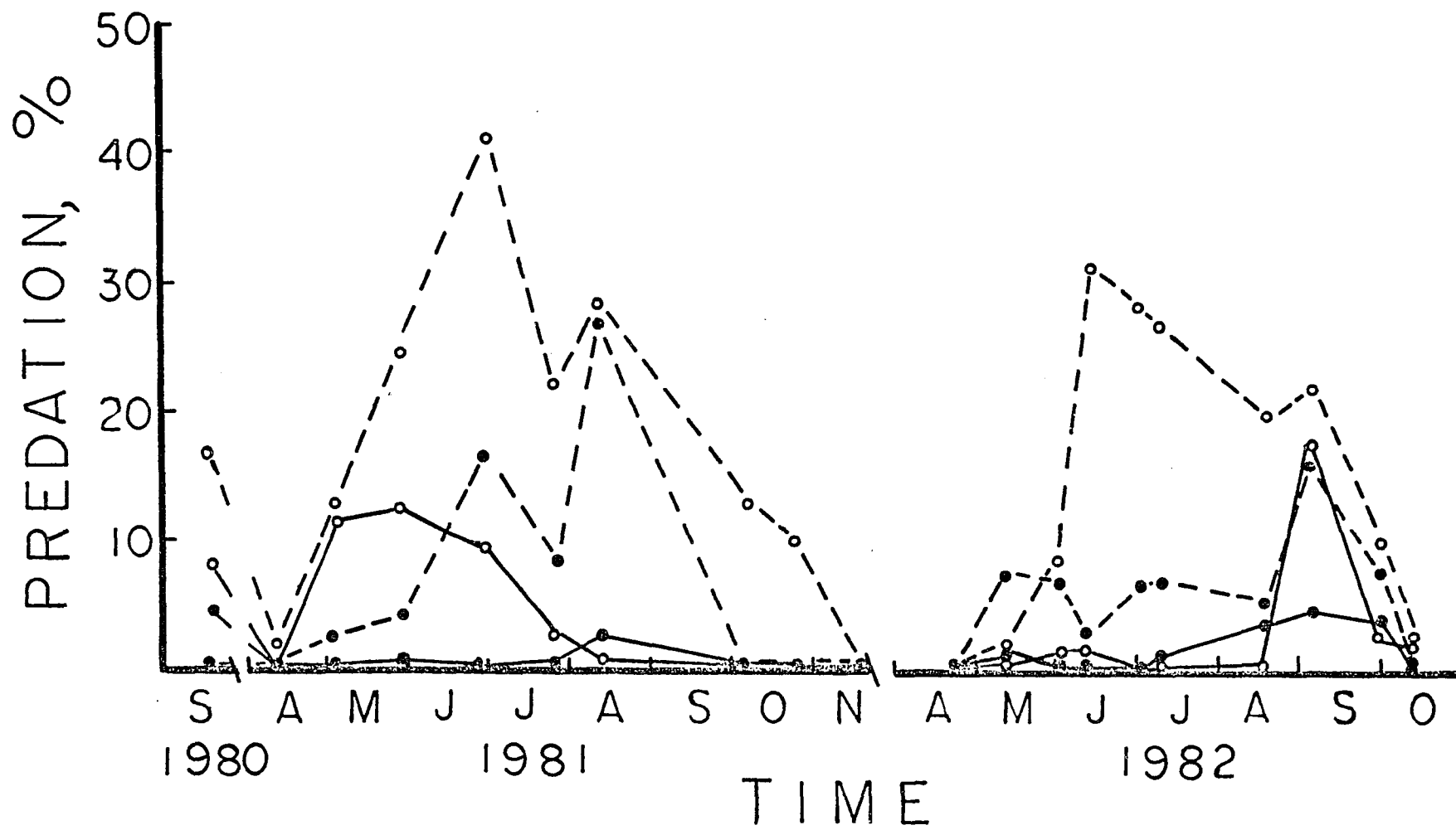


FIGURE 35. PREDATION, RECIPROCAL TRANSPLANT #2.

Percent predation (average percent of total leaf area eaten),
reciprocal transplant #2, from April to October 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and
solid lines = field, and the dashes = woods.

See Table 12 for statistical analysis.

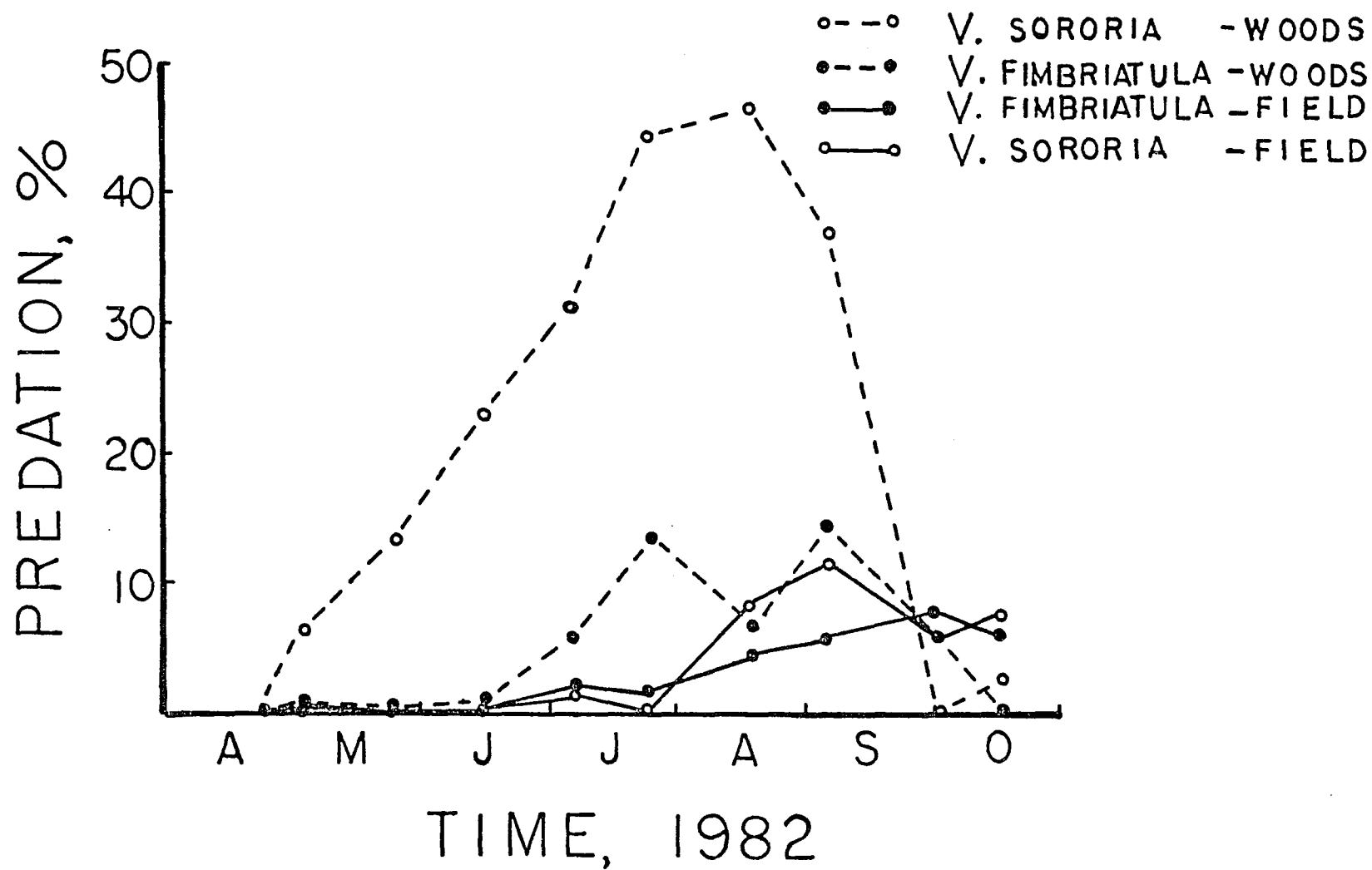


FIGURE 36. SURVIVORSHIP, SEED PLOT #1.

Survivorship (number of plants per plot), seed plot #1, from May 1981 to September 1982.

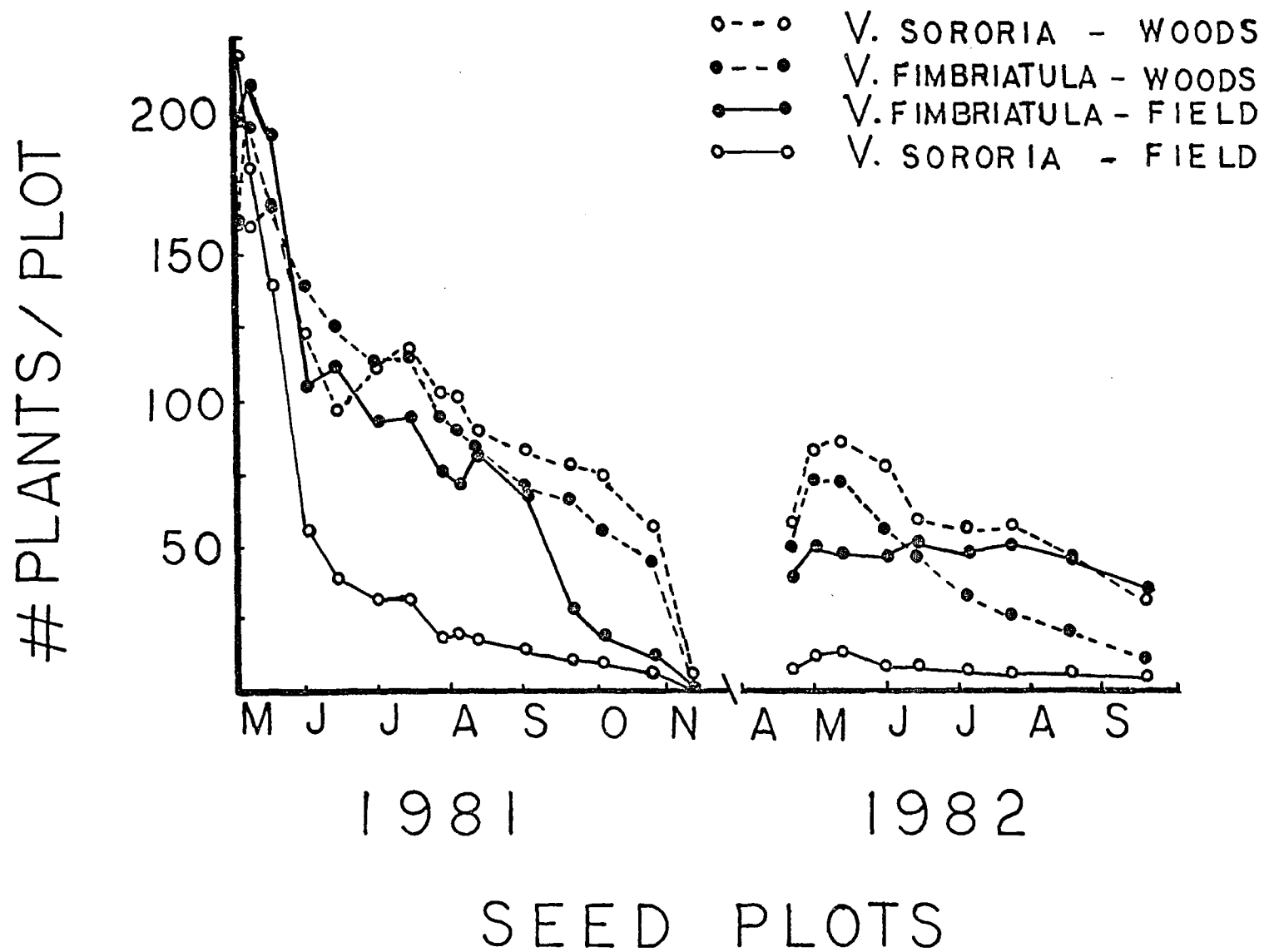


FIGURE 37. SURVIVORSHIP, DISTURBED SEED PLOT #2.

Percent survivorship, disturbed seed plot #2, from April to September 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

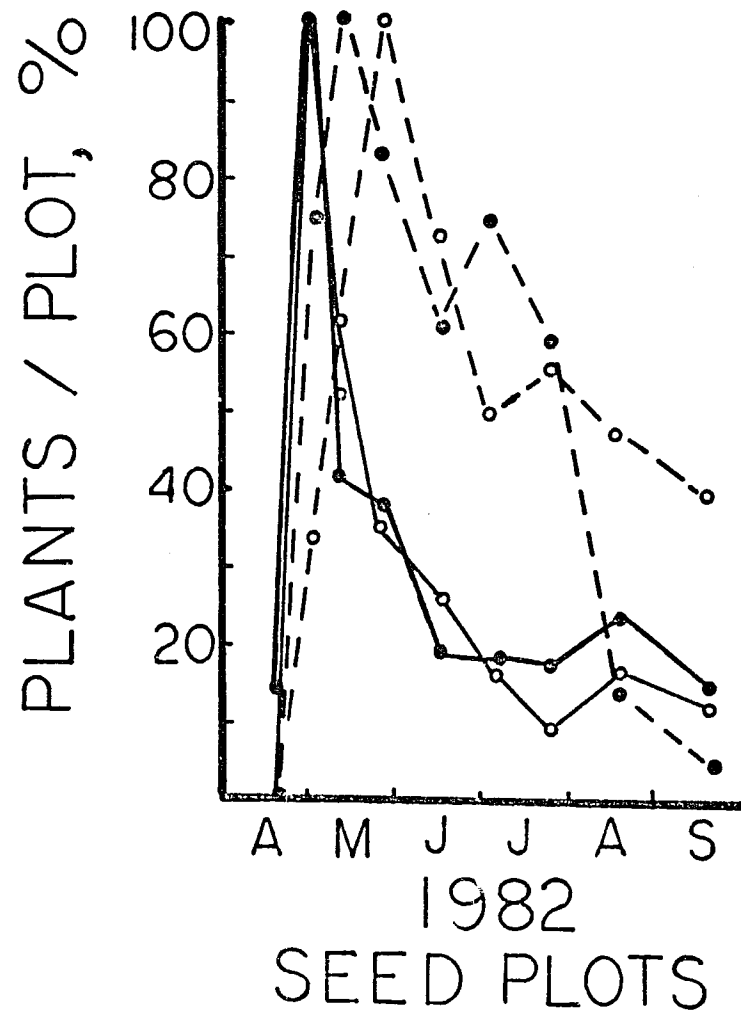


FIGURE 38. SURVIVORSHIP, UNDISTURBED SEED PLOT #2.

Percent survivorship, undisturbed seed plot #2, from April to September 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

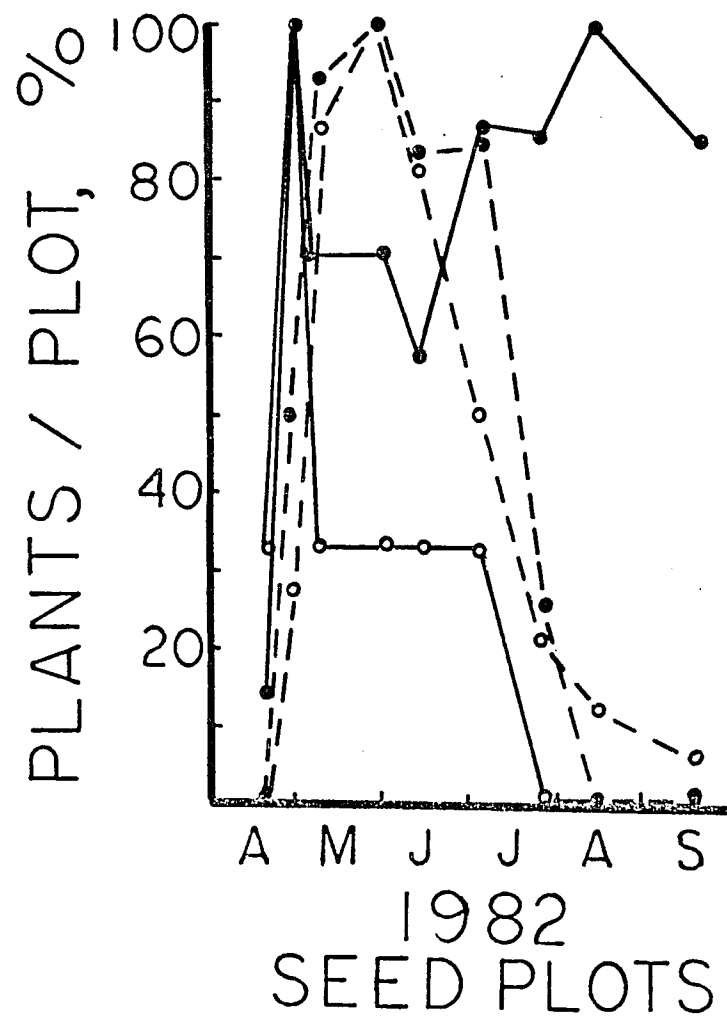


FIGURE 39. PRECIPITATION, WEST POINT, N.Y.

Precipitation in centimeters (actual and normal), for West Point, New York, from September 1980 to May 1983. Data from National Oceanographic and Atmospheric Administration (NOAA).

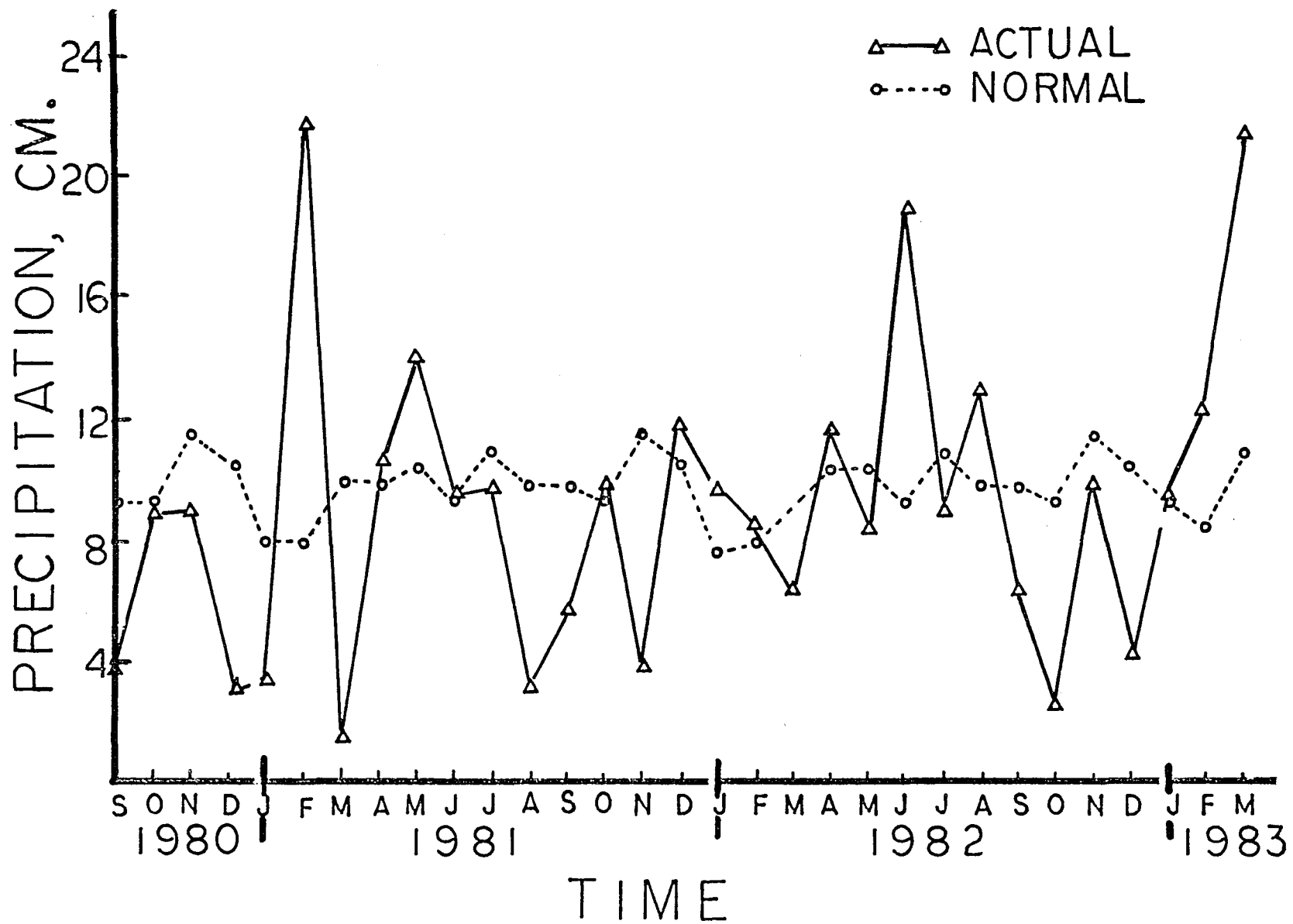


FIGURE 40. # LEAVES PER PLANT, SEED PLOT #1.

Average number of leaves per plant, seed plot #1, from June 1981 to August 1982.

Open circles = V. sororia, closed circles = V. fimbriatula; and solid lines = field, and the dashes = woods.

See Table 15. Figures 40-43 go together.

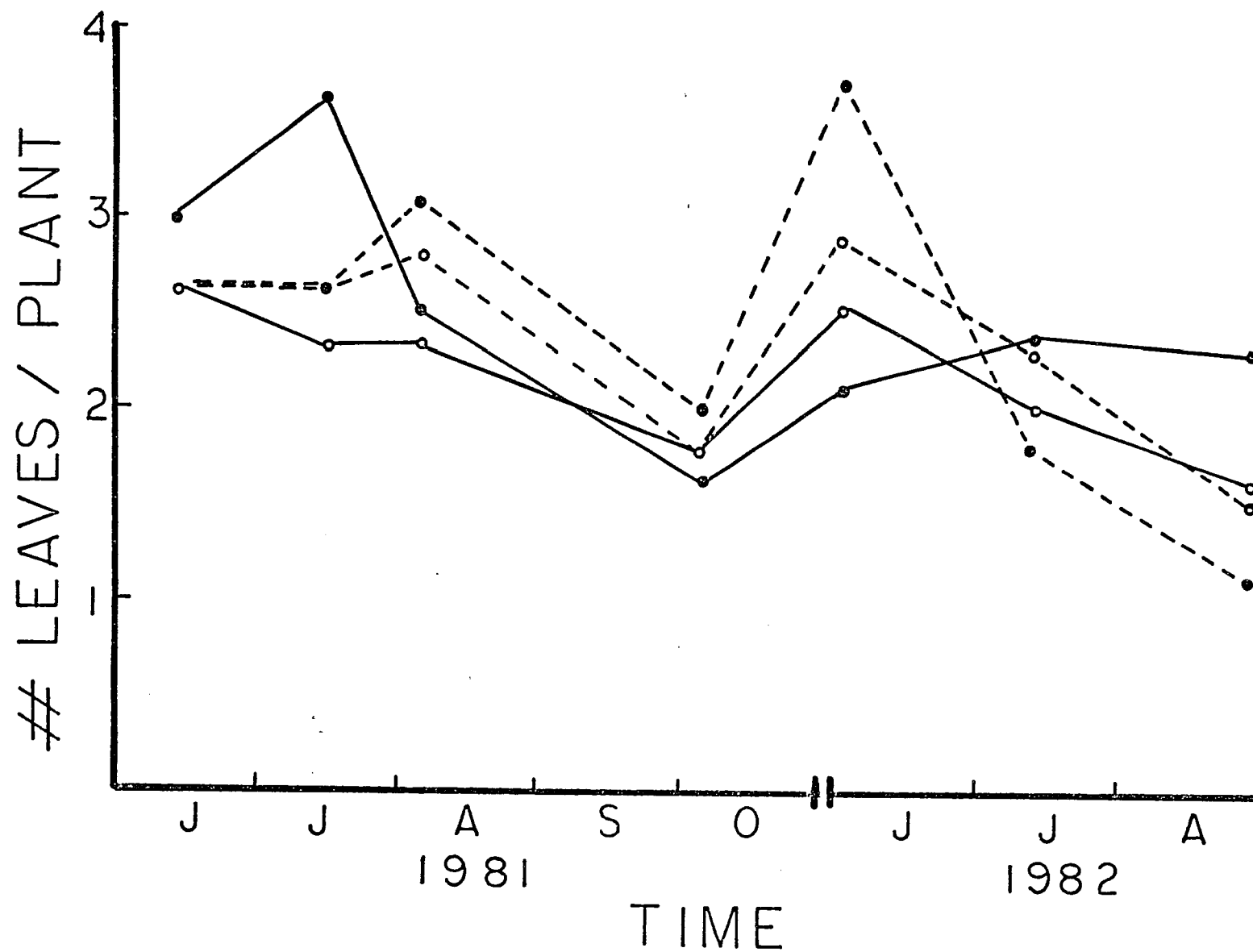


FIGURE 41. LEAF BLADE LENGTH, SEED PLOT #1.

Average length of the leaf blade.

Open circles = V. sororia, closed circles = V. fimbriatula; and
solid lines = field, and the dashes = woods.

See Table 15. Figures 40-43 go together.

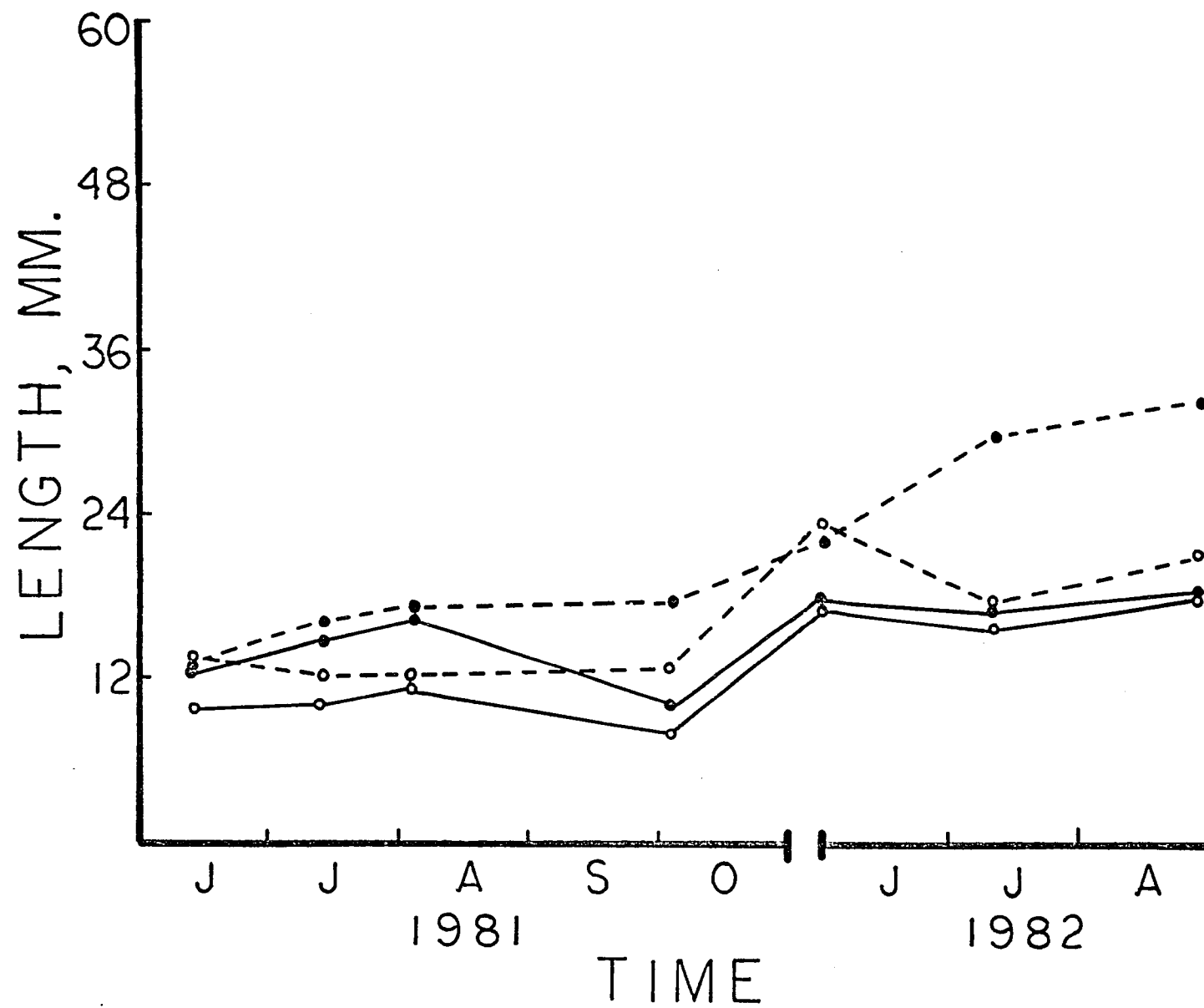


FIGURE 42. LEAF BLADE WIDTH, SEED PLOT #1.

Average width of the leaf blade.

Open circles = V. sororia, closed circles = V. fimbriatula; and
solid lines = field, and the dashes = woods.

See Table 15. Figures 40-43 go together.

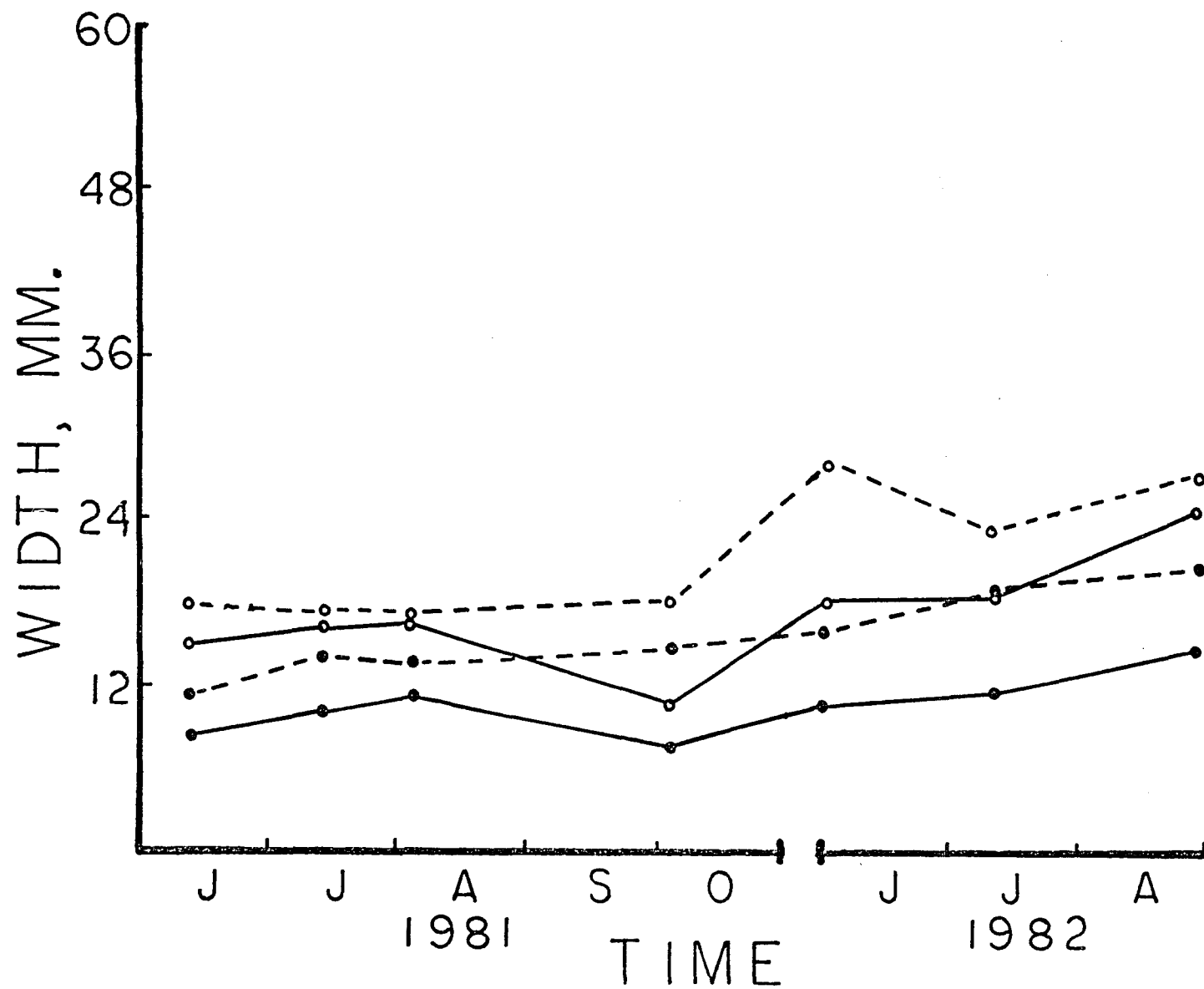


FIGURE 43. LEAF PETIOLE, SEED PLOT #1.

Average leaf petiole length.

Open circles = V. sororia, closed circles = V. fimbriatula; and
solid lines = field, and the dashes = woods.

See Table 15. Figures 40-43 go together.

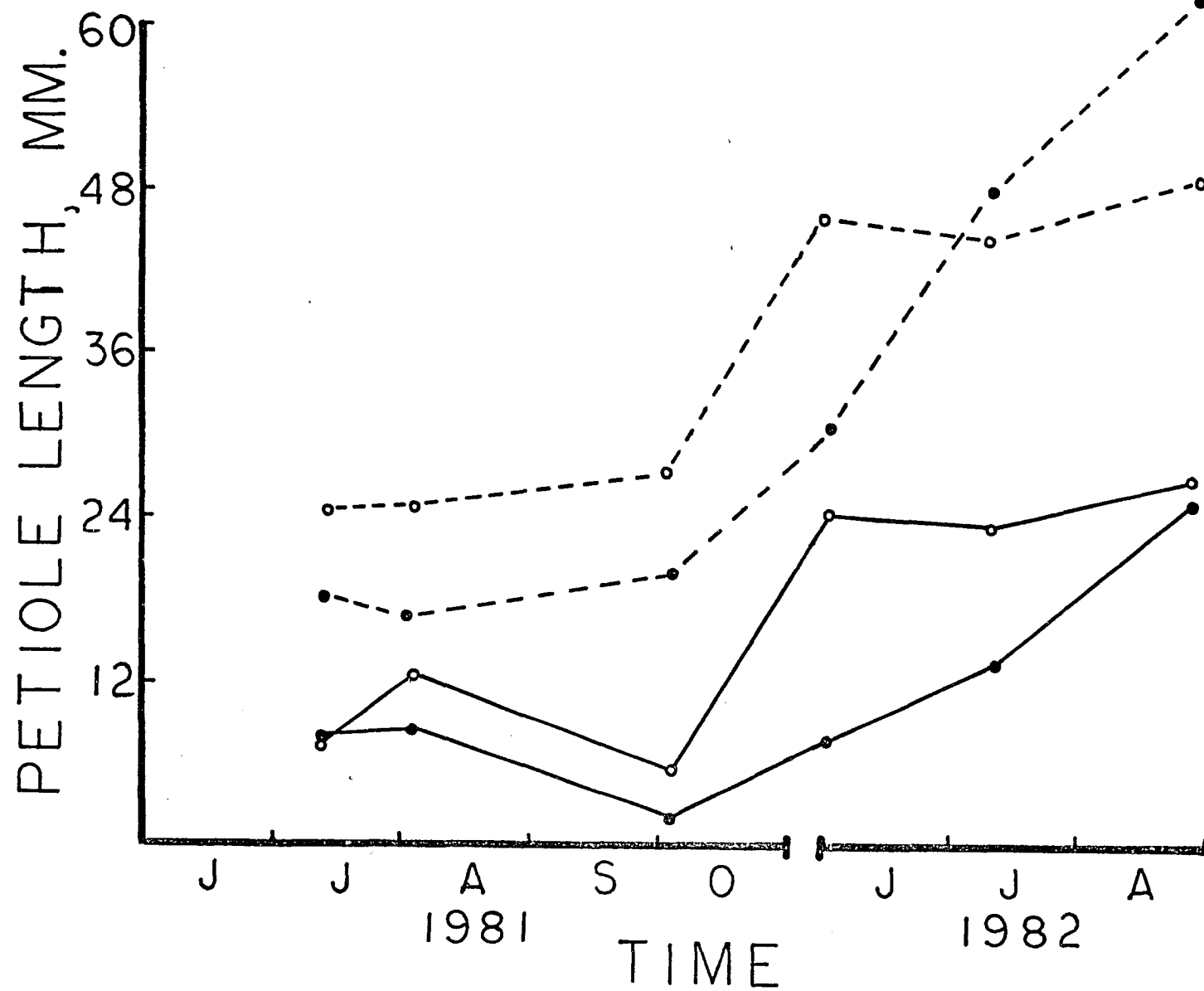


FIGURE 44. PLANT DRY WEIGHTS, PLANTS COLLECTED IN FIELD AND WOODS

Average dry weights (grams) of plant parts and whole plants, for 12 plants of V. sororia and 11 plants of V. fimbriatula collected in each habitat (woods and field), on 8/30/82.

Blad. = leaf blades, Pet. = leaf petioles, Rhiz. = rhizomes, Root = roots, Repr. = reproductives.

See Table 17, 18 for statistical analysis. See Figure 45.

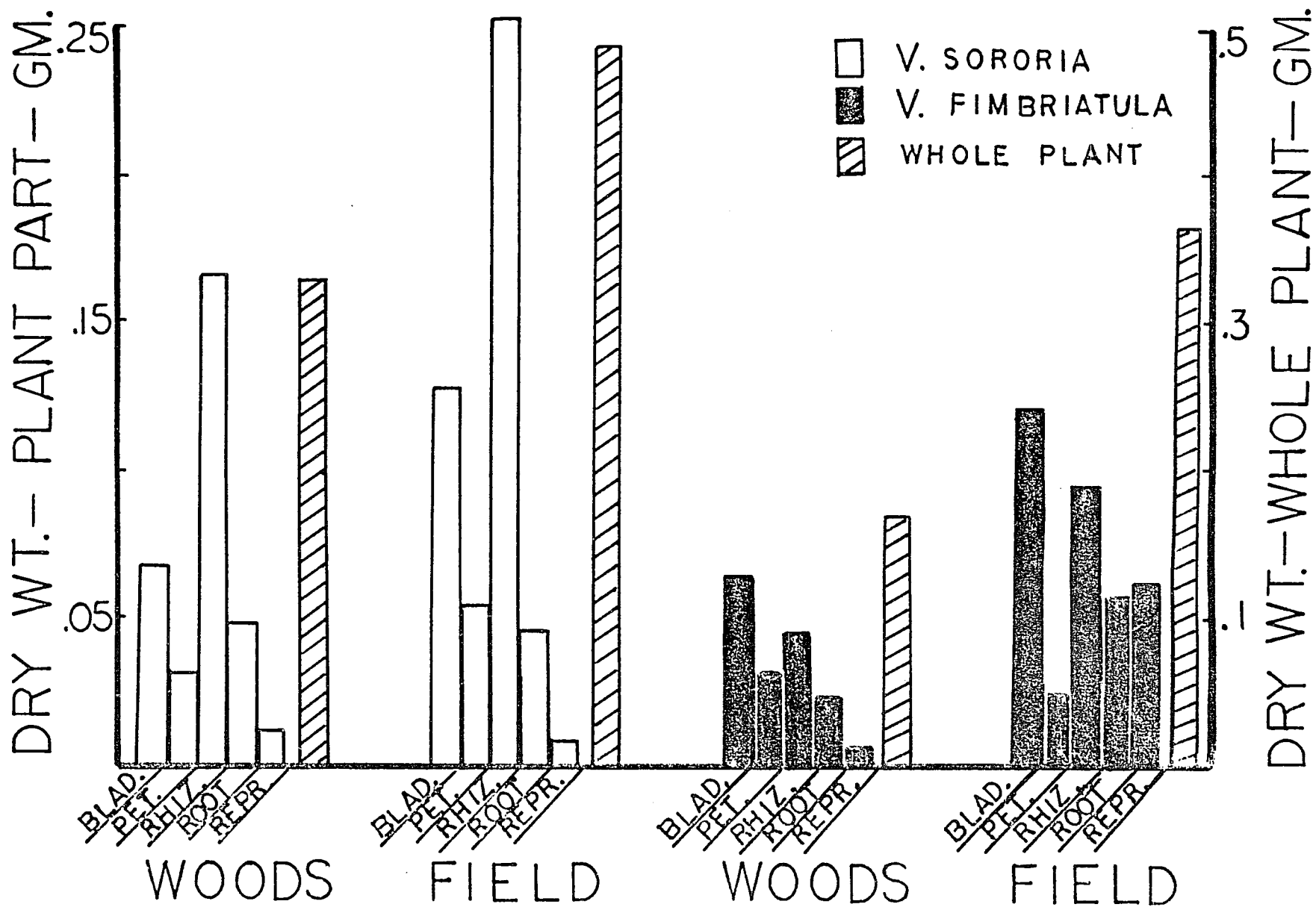


FIGURE 45. CARBON ALLOCATION, PLANTS COLLECTED IN FIELD AND WOODS

Percent carbon allocation, of plant parts and whole plants, for 12 plants of V. sororia and 11 plants of V. fimbriatula collected in each habitat (woods and field), on 8/30/82.

Blad. = leaf blades, Pet. = leaf petioles, Rhiz. = rhizomes, Root = roots, Repr. = reproductives.

See Table 17, 18 for statistical analysis. See Figure 44.

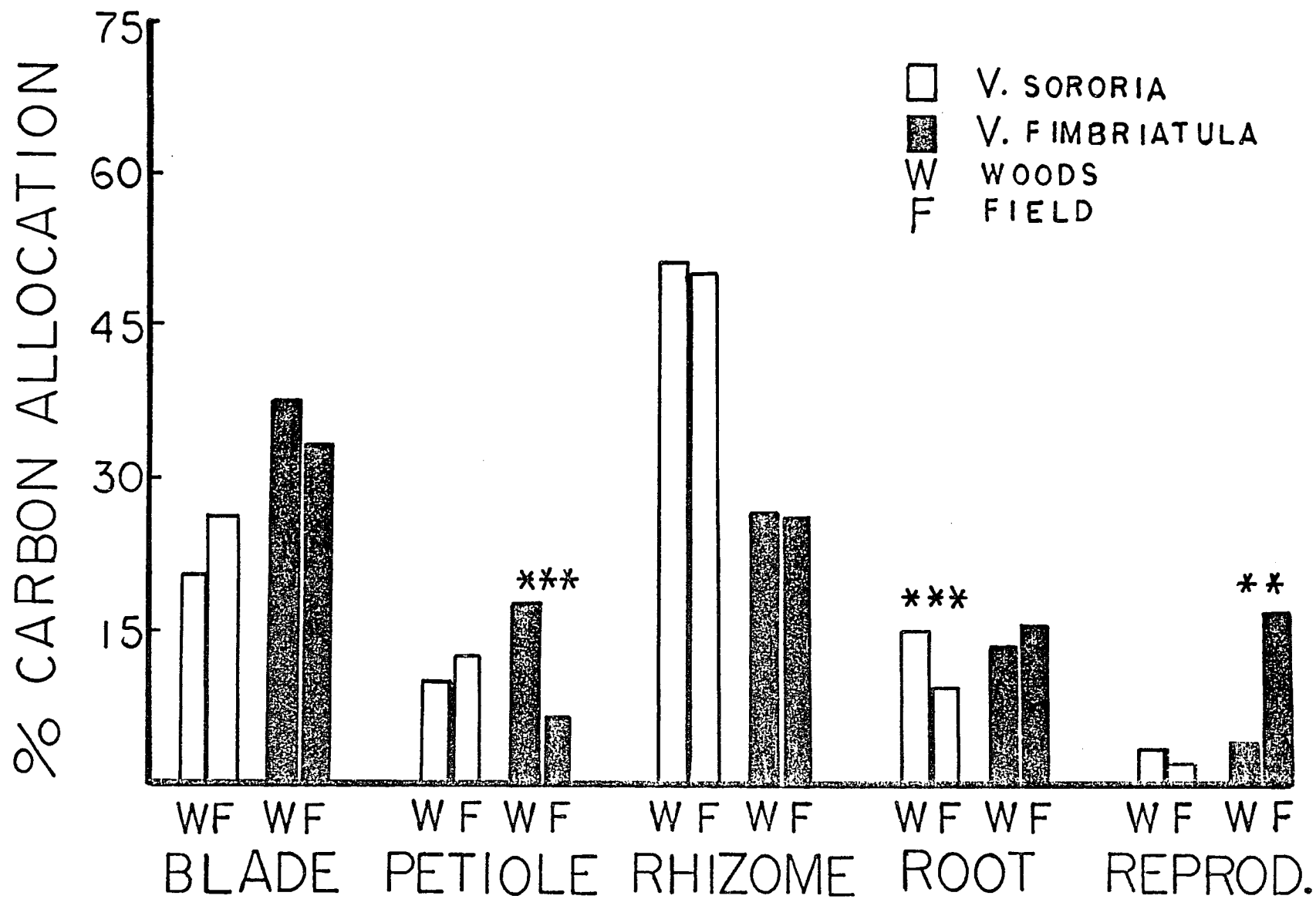
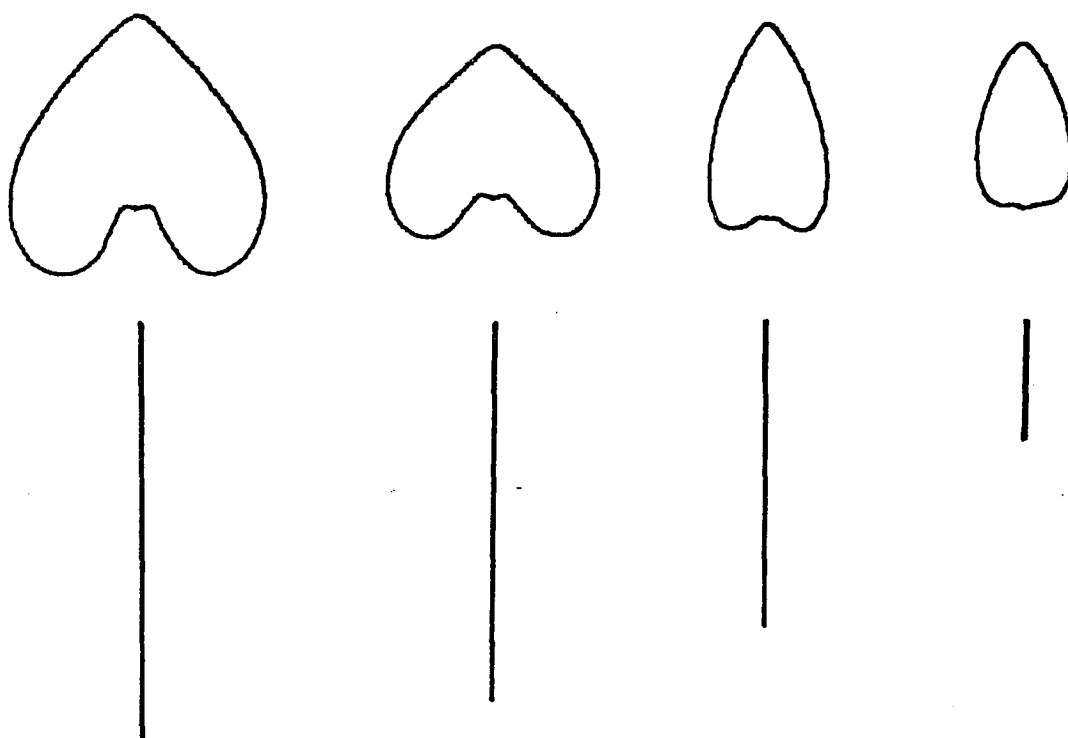


FIGURE 46. AVERAGE LEAF SHAPES, COMPUTER-GENERATED.

Average leaf shapes and sizes for 27 leaves of V. sororia in the woods, 42 leaves of V. sororia in the field, 43 leaves of V. fimbriatula in the woods, and 65 leaves of V. fimbriatula in the field, for plants described in Figures 44, 45 and Tables 17, 18. Leaf shapes were computer-generated using the leaf boundary method, and Fourier analysis.



WOODS

FIELD

WOODS

FIELD

V. SORORIA

V. FIMBRIATULA


2 CM

FIGURE 47. LEAF DIFFUSION RESISTANCE, V. SORORIA.

Diurnal leaf diffusion resistance (sec/cm), for the upper and lower surfaces of one leaf of V. sororia in the field, on 9/19/80.

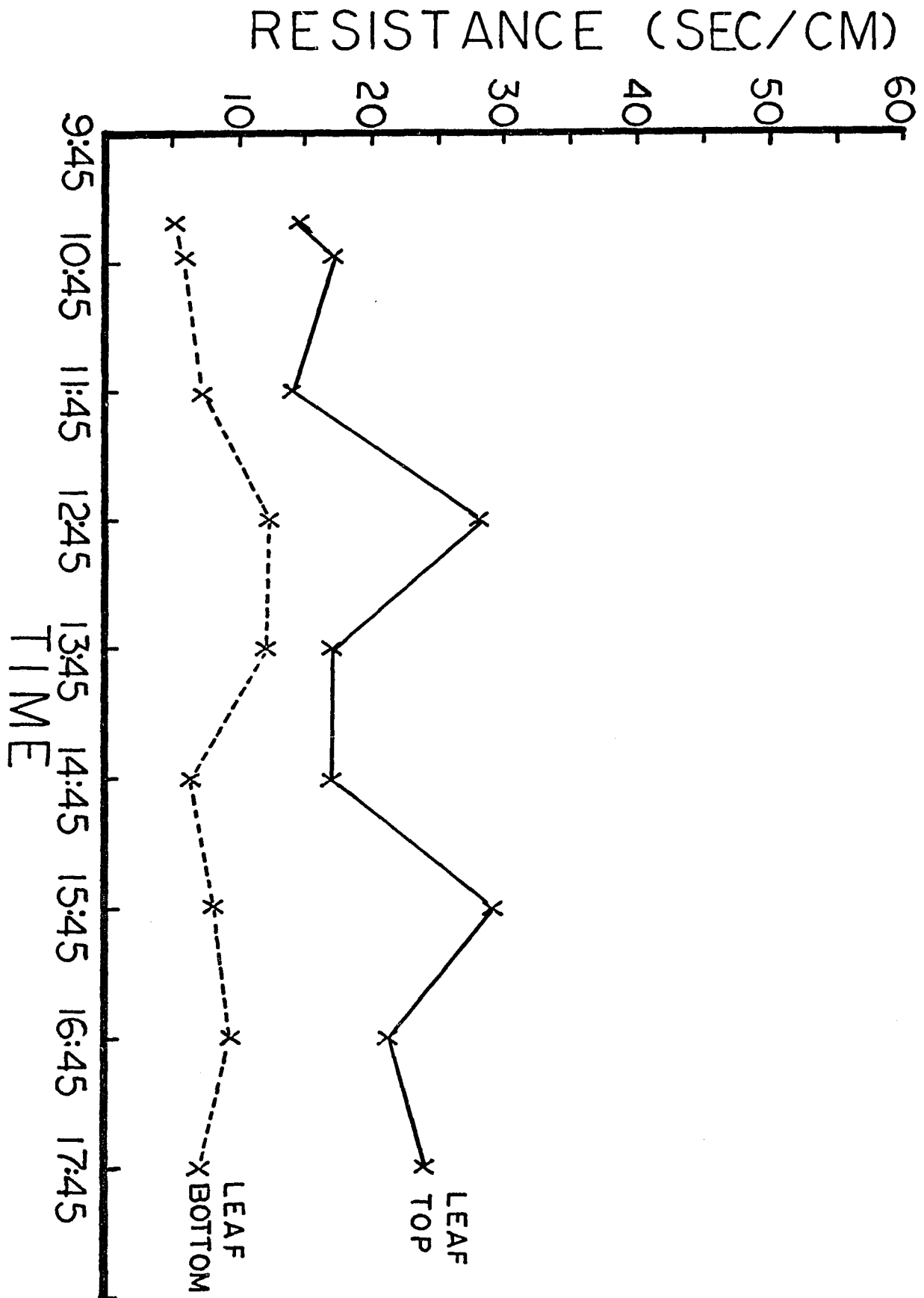


FIGURE 48. LEAF DIFFUSION RESISTANCE, V. FIMBRIATULA.

Diurnal leaf diffusion resistance (sec/cm), for the upper and lower surfaces of two leaves of V. fimbriatula in the field, on 9/19/80.

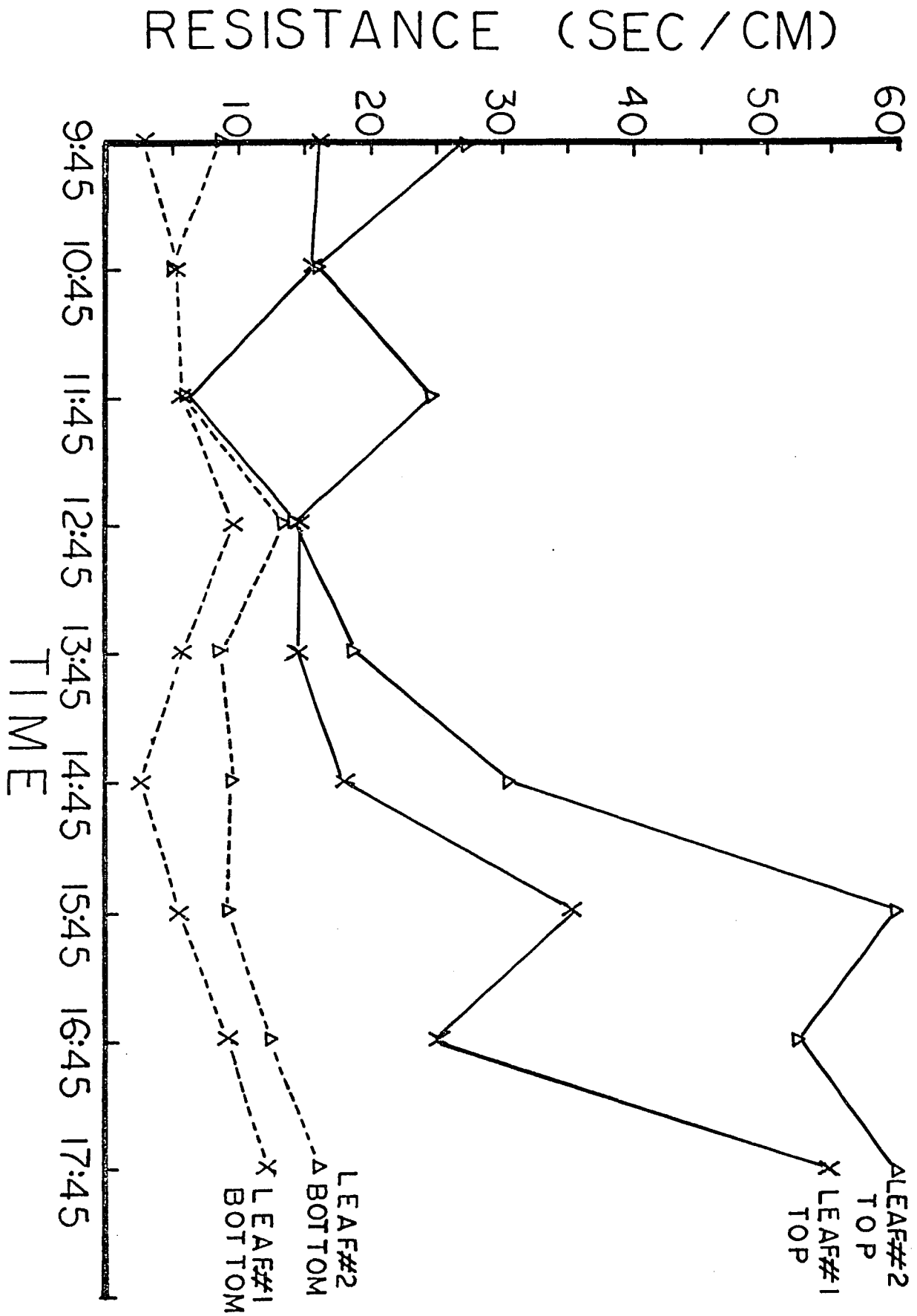


FIGURE 49. DIURNAL LIGHT, AIR TEMPERATURE, RELATIVE HUMIDITY.

Diurnal measurements of light (watts/square meter), air temperature, and relative humidity (%), 2.5 cm above the ground (violet height), in both field and woods, on 9/19/80.

