PATTERNS OF GERMINATION AND ESTABLISHMENT FOR STRIPED MAPLE (*ACER PENSYLVANICUM* L.)

by

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ABSTRACT

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In 1984 and 1986 the patterns of striped maple seedling germination, establishment, and growth were studied at Mt. Misery in the New York Hudson Highlands. Seedlings were tagged in four 10x10m quadrats as well as in a $14m^2$ portion of another 10x10m quadrat. An almost 100% increase in the number of germinated seedlings in 1986 as compared to 1984, and the absence of a seed supply in 1985 and 1986, suggests that the 1986 seedling population is from buried seed from 1984 or before.

Spatial distribution patterns of the surviving 1984 and 1986 seedlings indicate that light is the primary limiting factor for striped maple seedlings. Mean understory photosynthetically active radiation (PAR, 400-700nm) represented an 11.8% to 90.2% reduction from gap-center PAR, and an 84.6% to 98.6% reduction from pre-canopy closure PAR. Seedling growth was not inhibited by herbaceous growth nor by the increased light in canopy gaps. Water was also not a limiting factor for seedling growth, although soil moisture was greater in the lower Mt. Misery sites than at the top of the mountain, where overall seedling survival and size were greater. Significant differences in leaf area, leaf specific weight (LSW), chlorophyll content, shoot and root length and weight, and seedling height and stem diameter indicates that the striped maple population at Mt. Misery is shifting from the lower sites to the upper slope. The recent, first-time logging of the upper slope of the mountain has created a favorable environment, especially with respect to light, for striped maple establishment there: however, the more abundant adult striped maple population growing at the bottom of the mountain in response to several previous loggings has altered what once was a favorable site for establishment, so that the microenvironmental conditions necessary for the continued increase and maintenance of the population are no longer available.

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INTRODUCTION

Life histories of understory woody species are not well known (Ehrenfield, 1980), despite their important position in forest communities. In particular, little is known of the regeneration patterns of many understory species within and outside of forest canopy gaps. The knowledge of recruitment in trees that does exist has come primarily from reconstruction of historical data (Henry and Swan, 1974; Yarrington and Yarrington, 1975) and from silvicultural studies of economically important trees (Smith, 1951).

The seedling dynamics of dominant species have been the subject of various studies. Hett and Loucks (1971) followed seedling mortality of Acer saccharum, Marsh. in 3 sites with differing climatic factors and found none of the environmental stresses that they examined to be influential in sugar maple seedling survival. Weber et al. (1985), in field and laboratory studies, analyzed gas exchange in sugar maple seedlings. Experiments with laboratory-grown seedlings of 5 species selected from a variety of moisture regimes showed differences among species in gas exchange resistance (Wuenscher and Kozlowski, 1971). Variation in stomatal response as related to leaf area, leaf anatomy, light intensity, and humidity was studied in laboratory experiments with seedlings of 5 tree species by Davies and Kozlowski (1974). Harley (1939) performed an extensive study on beech (Fagus sylvatica) seedlings in the field and in the laboratory, measuring growth and nitrogen content of seedlings growing in different soil types. The relationship of herb cover and tree seedling establishment and survival has also been studied (Hough, 1937; Hough and Forbes, 1943; Gysel, 1951; Maguire and Formann, 1983).

As a gap-phase replacement species, Acer pensylvanicum L. is an ecologically important understory component of the northern hardwood forest of the eastern U.S. and Canada (Sargent, 1933), although it is regarded as a nuisance by foresters and silviculturists (Wilson and Fisher, 1977; Horsley and Bjorkborn, 1983). Individuals can persist in the understory for up to 40 years (Hibbs, 1979) growing as little as 0.01m/yr (Kelley and Kincaid, 1986) and reaching an average height of 1.0m (Hibbs et al., 1980). These suppressed trees can grow rapidly into canopy gaps and often form dense stands of understory trees (Wilson and Fischer, 1977; Hibbs et al., 1980). Hibbs et al., (1980) reported an average growth rate of 0.20m/yr in those trees released after logging, and Kelley and Kincaid (1986) found that the mean internode length of released trees was 0.22m.

Although it is known that the first year is one of high mortality for this species (Hibbs, 1979), no quantitative data exists for the seedling dynamics of this period in its life history. Throughout the life history of this species, several factors could contribute to its failure to reach, and, perhaps, more importantly, to maintain a position in the canopy or even subcanopy layer: the inability of shade tolerants to compete with shade intolerant species in canopy gaps because of lateral growth of the already dominant individuals and faster vertical growth by tolerant species which eventually attain canopy dominance is well documented (Canham, 1985; Hicks and Chabot, 1985); suppressed individuals that are not released at some time during their first 35 years usually die (Hibbs et al., 1980); in particular, the bark, buds, and leaves of A. pensylvanicum provide forage for deer, moose, and porcupines, thus severely limiting the trees' growth (Hosier, 1974, as cited in Hibbs et al., 1980; Wilson and Fischer, 1977; Roze, 1985; Kelley, personal observation); seedlings, especially those growing in dense shade, are subject to herbivory and fungal attack (Smith, 1951; Vaartaja, 1962); often, growth of seedlings in canopy gaps is inhibited by a dense herbaceous cover (Hough, 1937; Hough and Forbes, 1943; Gysel, 1951); and Cook (1979) believes that lack of soil moisture and herbivory are the main causes of seedling mortality.

Quantification of the patterns of regeneration and of the biotic and abiotic factors present at the time of seedling germination and establishment provides valuable insight into the mechanisms of the success and maintenance of the present and future adult populations (Daubenmire, 1968; Sagar and Harper, 1961; Harper, 1977; Sarukhan, 1980), and might, perhaps, lead to more effective forest management.

The purpose of this project was to determine if spatial and temporal patterns of germination, establishment, and mortality exist for A. pensylvanicum seedlings in a selectively logged forest in the New York Hudson Highlands, and, if any do exist, the relationship of these patterns to biotic and abiotic factors.

Species Description

Acer pensylvanicum L. (striped maple, moosewood) is a common understory tree of the eastern U.S. and Canada. It has been found as far west as Minnesota and at higher elevations in Georgia, although the largest individuals are found in the Smoky Mountains of Tennessee and the Blue Ridge Mountains of North and South Carolina (Sargent, 1933). Evidence of its being a more dominant element of the forest canopy appears in fossil records from the southeast U.S. (Delcourt et al., 1984).

Striped maple occurs in many forest types, but grows best at higher elevations on northern slopes and on mesic sites (Hibbs et al., 1980). The bark is bright green with white waxy stripes, but becomes darker with age. It can reproduce sexually and vegetatively and may change modes depending upon environmental stresses (Hibbs and Fischer, 1979). Striped maple blooms from late April through June before full leaf development, and produces yellow-green flowers in elongate inflorescences (Fernald, 1950). Male and female flowers occur separately, and pollination is accomplished most often by bees in the genus Andrena (Sullivan, 1983). Seed are normally held on the trees throughout the growing season and dropped in the fall and winter months. Embryo dormancy as well as 'testa-imposed' dormancy have been demonstrated in this species (Wilson et al., 1979).

Striped maple has indeterminant growth. Buds normally contain a pair of preformed early leaves as well as a pair of primordia that may abort, as is common in suppressed individuals, or develop into a second leaf pair (Wilson and Fischer, 1977). Depending upon light intensity, subsequent leaf pairs may develop during the growing season. Two basic forms exist in populations of striped maple: the suppressed seedling and the larger tree found in canopy gaps (Hibbs, 1979). Mortality is highest during two periods, year 1 and years 16-40 (Hibbs, 1979). Open-grown individuals are normally multistemmed as contrasted with the single stem specimens found in a forest understory (Hibbs et al., 1980).

The closest ecological relative of striped maple is *A. spicatum* Lam., the range of which extends further north and west. It and *A. rubrum*, *Betula lutea*, and *Fraxinus americana* are also considered intermediately shade-tolerant species (Bormann and Likens, 1979).

Site Description

The study site is located on the northeast slope of Mt. Misery (elevation 386m) in the Harvard Black Rock Forest in the New York Hudson Highlands (N41°22'30", W74°00'; Fig. 1). In August 1974, 37.17ha on the NE, E, and SE slopes of Mt. Misery were the site of a sawtimber harvest (Jack Karnig, personal communication). At that time, the area consisted of trees in the 90 to 110 year age classes. Slow growth was attributed to the generally poor quality of the sites (thin soil, rocky terrain, steep slope). The upper slopes of this area had previously not been logged due to inaccessibility, but some downhill portions had been lightly cut in the 1930's (Jack Karnig, personal communication). In 1974, heavy cutting occurred in some small patches of trees with a dbh greater than 0.41m. In areas that had only a few trees in this size class, cutting was light to moderate.

In 1982-1984 thirty-one (21 down-slope and 10 on the ridgetop) 10x10m quadrats were established at Mt. Misery, and in these, 873 genets of striped maple were tagged. Two 10x10m quadrats located just to the east of the lower 21 quadrats, were cleared of striped maple, one in 1983 and the other early in 1984. Of these two, one (D2) was enclosed to protect it from browsing in order to follow the regeneration of striped maple by basal sprouting. I selected four 10x10m quadrats (2 at the top of Mt. Misery and 2 down-slope) as representative for a study of striped maple seedling germination and survival. A 14m^2 portion of plot D2 was also included in this study.

The study plots are different in canopy cover, slope, and herbaceous cover. All plots have a NNE aspect dominance. Plot 4, located on the lower slope of Mt. Misery, has a slope of 0 degrees and contains 8 genets (9 ramets) of striped maple (mean dbh= 51.2mm). The east side of the plot has a large canopy opening (Fig. 2). Hay-scented fern (Dennstaedtia punctilobula (Michx.) Moore) grows to a maximum height of 0.8m in this gap and, thus, provides a more immediate canopy for some of the striped maple seedlings than do the adult trees in that plot. The west side of the plot has a rather dense canopy with a very small gap on the western border. Other adult tree species present in this plot include Acer rubrum L. and Hamamelis virginiana L.. Branches of Fagus grandifolia Ehrh. extend into the NW corner of the plot. Several branches from cut and fallen trees lie in the SE corner.

The slope of the mountain increases immediately beyond the southern edge of this plot and litter accumulates there to a maximum depth of 0.07m, especially around the fallen branches.

Plot 17 lies to the SW of Plot 4 and has a dense canopy cover consisting almost exclusively of mature striped maples (37 genets (46 ramets); mean dbh= 45.7mm). A single A. saccharum and 2 H. virginiana also grow in this plot. The only herbaceous growth in this plot consists of 1 Hepatica acutiloba, 2 small Thelypteris noveboracensis (L.) Nieuwl. (New York fern), and 1 Polystichum acrostichoides (Michx.) Schott. (Christmas fern). Plot 17 has only 2 small canopy gaps (Fig. 3), which are being closed by the lateral growth of the adult trees. Rocks cover a large portion of this plot, and a fallen log and 2 stumps are also present. Heavy litter covers most of this plot, which has a slope of 10 degrees.

The two upper plots, T3 and T10, have a slope of 17 and 15 degrees, respectively. They both have a northeastern exposure and have a less dense and higher canopy cover than do plots 4 and 17. Plot T3 has 5 A. pensylvanicum genets (12 ramets) with a mean dbh of 29.4mm, as well as mature Quercus rubra L., Q. alba L., and Ostrya virginiana (Mill.) K. Koch. The plot is essentially divided in half in an E-W direction by a fallen log. The lower portion of the plot has some patches of Polytrichum commune Hedw. and Carex sp. as well as areas with only a thin layer of litter. The upper section of plot T3, where there is a large canopy opening (Fig. 4), is dominated by Dennstaedtia punctilobula and Vaccinium vacillans Torr. with thick patches of P. commune.

Plot T10 has a single striped maple genet (2 ramets) with a dbh of 21.5mm located in the extreme SE corner. The central portion of the plot is almost bare with only a very thin layer of litter. The extreme upper portion of the plot has a thick grassy covering, while the lower end of the plot has a few patches of P. commune Hedw., P. ohiense Ren. and Card., Dicranum fulvum Hook., and Leucobryum glaucum (Hedw.) Schimp., which grows with the D. fulvum. In some places, litter accummulates to a maximum depth of 0.1m. Other mature trees growing in this plot are O. virginiana and Q. rubra. There is a canopy opening in the lower portion of the plot (Fig. 5).

Plot D2 is located on the lower slope of Mt. Misery southeast of plots 4 and 17, and has a slope of 21 degrees, the steepest of the 5 plots. Since the cutting in 1984 of the adult striped maples in this plot, some basal sprouting has occurred providing a canopy cover for some of the seedlings. Other mature trees in the plot are A. rubrum, H. virginiana, and Cornus florida L. Since the opening of the canopy in 1984 (Fig. 6), the plot has been nearly overgrown with Dennstaedtia punctilobula, a common invader of forest clearings (Horsley, 1977b). The large number of rocks often make it diffucult to traverse the plot.

Deer and chipmunks are common throughout the Mt. Misery area.

MATERIALS AND METHODS

In May and June of 1984, 2031 first year seedlings in the 5 plots were tagged with numbered 0.13m plastic swizzle sticks and followed over the growing season. The demographic data collected for the 1984 seedling population were seedling establishment and survival and initial leaf and/or cotyledon predation. Following a halt in data collection during 1985, work resumed in March 1986, when a census was taken of the 1984 seedlings. At that time, many seedlings and/or tags were not apparent because of deep litter and absence of leaves on the plants themselves, so no tags were removed from the plots.

Beginning in early May 1986, newly germinated seedlings (n= 4006) in the same 5 plots were tagged with 0.11m white plastic stakes numbered with oil-based paint. Hay-scented fern was already 0.05m tall when the striped maple seeds began germinating, and by late May, the fern had grown to a maximum height of 0.80m in plots 4, D2, and T3. A census of the seedlings was done approximately every two weeks during both the 1984 and 1986 growing seasons. The same demographic data were collected for the 1986 population as for the 1984 population.

Since this species is known to be able to respond to canopy gaps, quantification of the light regime in the gaps, as well as in the understory, was desired. Measurements of photosynthetically active radiation (PAR, 400-700nm) were made in each plot at solar noon with a hand held quantum sensor (LI-190SB, Li-Cor, Lincoln, Nebraska). The sensor was held horizontally at seedling height, approximately 30-50mm above ground level. On 3 days during the growing season, dawn-to-dusk readings of PAR were recorded at one minute intervals using an 8-channel datalogger (Campbell Scientific Model CR-21). Two quantum sensors (LI-190SB), attached to the datalogger, were positioned in plot 4, one at the gap center and one at the NW gap edge. Data were stored on a cassette recorder and transferred in the lab to an

Apple II series computer. Maximum and minimum air temperatures at the height of the seedlings were recorded on each visit with Taylor thermometers shielded in white A-frame shelters and placed at the lower and upper study sites.

In March 1986, the height of the 1984 seedlings was measured. The position of terminal bud-scale scars was used to determine the growth for both the 1984 and 1985 growing seasons. No seedlings were measured in plot 17 at that time since none were visible, and I wanted to keep disturbance to the site at a minimum. At the end of the 1986 growing season (early October), the height and stem diameter of the surviving seedlings of both the 1984 and 1986 populations were measured.

On 27 June 1986, first year seedlings were collected from areas adjacent to the study plots. Shoot and root lengths and diameters were measured in the field. Shoots and roots were separated and put into labelled glass vials, which were put in a convection oven at 60 degrees for 5 days, after which dry weights were measured. Discs from each plant leaf were dried, weighed, and used to calculate leaf specific weight (LSW, dry weight/ surface area).

For the determination of chlorophyll content, discs were punched from each of the leaves of seedlings collected from areas adjacent to each plot, stored in glass vials, and their fresh weight measured in the laboratory. Five ml of absolute methanol were added to each vial, which was then placed in a convection oven at 60°C for 2 hours. The MeOH-chlorophyll supernatant was removed and centrifuged for 5 min. Using a MacPherson spectrophotometer, absorbance was determined at 650, 665, 720nm.

From these data, total chlorophyll content was calculated using a standard set of equations.

On 27 June, seedling leaves were collected and returned to the lab to obtain preliminary data on stomatal density. Casts were made of adaxial and abaxial surfaces by applying 2 layers of a silicone-based flexible sealant (Silicone II, General Electric Co., N.Y.) to the surfaces. After drying, the silicone layer was peeled off, and a thin layer of colorless nail polish was applied to the silicone peels. Nail polish peels were subsequently taken from the silicone casts. Stomate densities were determined at 100X from the nail polish peels using an Olympus HBT microscope.

Toward the end of the growing season (20 August 1986), leaf length (from the tip to the point of petiole attachment) and width (at the widest point) were measured on all of the remaining seedlings that had retained their leaves (n= 1084). By this time, the leaves on some plants had already abscised, and some leaves had been damaged so badly that no measurement could be taken. Several leaves, measured in the same way, were brought into the lab and traced using a digitizing surface compatible with the Apple II series microcomputer in order to determine exact leaf area (Kincaid and Schneider, 1983). Analysis showed a high coefficient of determination (r^2 =.97) between LxW as measured in the field and actual leaf area. Length and width data were then used in a regression model to compare leaf areas between plots.

On 4 days during the growing season, xylem water potential was measured at solar noon using a Scholander-type (Scholander et al., 1965) pressure chamber (Plant Water Status Console, Soil Moisture Corp., Santa Barbara, CA). Xylem water potential was also measured at dawn to provide a measurement of soil water potential in the different study areas. Since this was a destructive procedure for the striped maple seedlings, the plants were collected from areas adjacent to the study plots. Seedlings were also transplanted and brought into the greenhouse for the determination of permanent wilting point (PWP).

In early October 1986, a final, complete census was taken in each plot, and the height and diameter of each surviving 1984 and 1986 seedling were measured.

Data were analyzed using the methods from Sokal and Rohlf (1981). Nomenclature follows Gleason and Cronquist (1963).

RESULTS

Demography- 1984 population

All striped maple seedlings in the study plots germinated by late June 1984. In all plots except one (17), no new recruits appeared after 15 May 1984. The total number of seedlings tagged in the 5 plots was 2031. Table 1 gives a 3 year summary of the 1984 seedling population flux. Original seedling density in all 5 populations in 1984 ranged from $0.21 m^{-2}$ (T10) to $12.29 m^{-2}$ (D2). Mortality over 3 growing seasons ranged from 33.33% (T10) to 99.76% (17). Figures 7a and 7b show the total number of living plants for each plot over the 1984 and 1986 growing seasons, respectively. The mortality rate between plots was highly significantly different (overall ANOVA, $p<.001$).

Herbivore damage to the seedling leaves themselves at the time of tagging ranged from 2.56% (T3) to 32.56% (D2). Initial mortality was highest in plot 17, which has the densest canopy cover. This same plot experienced the highest mortality after both the initial 1984 growing season (85.71%) and after 3 growing seasons (99.76%). Survival was highest in plot T3 (92.30%) at the end of the 1984 growing season; however, more seedlings in plot T10 (66.67%) survived over the 3 growing seasons.

Figure 8a-e shows the distribution pattern in each study plot of the 1984 seedling population present at the end of the 1986 growing season. Seedlings in the 2 upper plots had a random spatial distribution; those in plots 4 and D2 were non-randomly distributed (Kolmogorov-Smirnov (K-S) goodness-of-fit; p<.01). Too few seedlings survived in Plot 17 for statistical spatial distribution analysis; however, the remaining live seedlings appeared to be randomly distributed.

1986 population

Tagging of the new striped maple seedlings began on 5 May 1986. Newly germinated seedlings appeared as late as 30 July in plots 4, T3, and T10, but a very small number of new seedlings germinated in plots 17 and D2 after the initial tagging in May. Again, plots T3 and T10 had the highest number of survivors after one growing season (Table 2). Herbivore damage at the time of initial tagging ranged from 3.90% in plot D2 to 7.06% in plot T10, overall much less than what was experienced in 1984. The total number of new seedlings in the 5 plots was 4006, almost 100% more than in 1984. Density ranged from $3.45m^{-2}$ in plot T10 to $15.00m^{-2}$ in plot 4. The spatial distribution of germinated seedlings and of first season survivors in plots 4, T3, T10, and D2 was non-random (K-S goodness-of-fit; $p< .01$), while that in plot 17 was random (Figures 9-13).

Figures 14-18 show the recruitment, mortality, and total number of living seedlings over the 1986 growing season for each plot. Recruitment between the 5 plots was not significantly different on a m^2 basis; however, the total number of seedlings alive at any one time between plots over the growing season was significantly different ($p<.001$). The scatter plots of Figure 19a-e show a high correlation between the number of 1986 seedlings that germinated with the number that survived in Plots T3 and T10 ($r^2= .90$): however, in both of the lower Mt. Misery plots (4 and 17), the correlation was low ($r^2= .53$ and .17, respectively). Seedling survival in Plot D2 as correlated with germination was more similar to that in the 2 upper plots ($r^2= .79$) than the 2 lower study areas.

Cohorts of early, mid-, and late-season recruits exhibited varying distributions and mortality rates within plots. Figure 20a-e shows the mortality rates of each cohort in the individual plots. In each case, the pattern of decline was significantly linear with a negative slope($p<.01$; Table 3). For the early-season cohorts, there was a delineation between the upper and lower Mt. Misery sites; i.e., those on the upper slope of the mountain had a significantly lower mortality rate($p<.01$). Seedlings that germinated in June in plots 4, T3, and D2 had similar mortality rates, but all were higher than that in plot

T10. Seedlings in plot 17 experienced the highest initial mortality rate.

In all plots, more late-season recruits survived than either the early or mid-season recruits. Of the original 1500 seedlings tagged on 5 May in plot 4, only 315 (21.0%) survived. Only 37.5% of the June recruits survived, and 60% of the seedlings that germinated in July in plot 4 survived to the end of the growing season. The early and mid-season recruits in plot 4 had a non-random spatial distribution(K-S goodness-of-fit; $p<.01$), whereas those that germinated later in the growing season were randomly distributed. Seedlings in each cohort that survived to the end of the growing season were randomly distributed. Seedlings from each cohort germinated under the hay-scented fern in plot 4. Total survival in the fern area was 26%, whereas that for the seedlings in the adjacent gap area was 34%; however, the rate of mortality of these essentially 'sun and shade' seedling cohorts was not significantly different.

In plot 17, only 1.45% of the original 895 seedlings survived, and none of the June and July recruits survived. All of the germinated seedlings in this plot were randomly distributed, as were the survivors.

Seedlings that germinated early in plot T10 had a 73.62% survivorship, while 80.77% of the early June recruits survived and 87.50% of the July seedlings lived. Germination patterns in plot T10 were non-random ($p<.01$), as were the spatial distribution patterns of the survivors of the early and mid-season cohorts ($p<.01$). The survivors of the late-season cohort, though, were randomly distributed.

Almost 3/4 (71.43%) of the seedlings in the early cohort in plot T3 survived over the growing season; 70.41% of the mid-season cohort survived; and 93.10% of the late-season cohort survived. Early and mid-season cohorts were non-randomly distributed ($p<.01$), but the seedlings in the late-season cohort were randomly distributed just as the mid- and late-season cohort survivors were. Again, the early cohort survivors were non-randomly distributed ($p<.01$).

Only 27.97% of the original seedlings survived in plot D2, while 12.5% of the June recruits survived, and 66.67% of the July recruits survived. The spatial distribution patterns of germination and survival of the early recruits in plot D2 were non-random($p<.001$), whereas those of the late-season cohort were random.

Photosynthetically Active Radiation

Mean midday photosynthetically active radiation (PAR, 400-700nm) measured prior to canopy closure and in gap centers and the understory after full canopy development is presented in Table 4a. Average pre-canopy PAR was between 220 $\mu Em^{-2}s^{-1}$ and 673 $\mu Em^{-2}s^{-1}$. There was no significant difference between plots in pre-canopy PAR nor in gap-center PAR after full canopy development. After canopy development more than 92% of all PAR readings in gap centers were below 200 $\mu Em^{-2}s^{-1}$, and, in the understory, almost 96% of the readings were below 100 $\mu Em^{-2}s^{-1}$ (Table 4b). Average midday PAR in the understory was between 8

$\mu Em^{-2}s^{-1}$ (plot 17) and 75 $\mu Em^{-2}s^{-1}$ (plot T10). Gap-center PARs compared to understory PARs were least variable and not significantly different in plots T10 and D2, whereas those in plots 4 and T3 were significantly different ($p < .05$). The most significant difference in average midday PAR occurred in plot 17 ($p < .001$), where gap-center PAR (90 $\mu Em^{-2}s^{-1}$) was more than 10 times greater than mean understory PAR (8.4 $\mu Em^{-2}s^{-1}$). PAR in the understory represented a reduction from pre-canopy values of between 84.6% (D2) to 98.6% (17). There was no significant difference in understory PAR in plots T3, T10, and D2. Significant differences did occur between plots 4 and 17 and 4 and T10. For each plot, seasonal variation in midday PAR was not significantly different in the gap centers or in the understory (ANOVA).

Figures 21-23 show the diurnal course of PAR as measured in the gap-center and at the gap edge of plot 4 on 3 days during the growing season. Peaks in PAR are the result of sunflecks. Maximum values recorded during these peaks were between 600 and >1322 $\mu Em^{-2}s^{-1}$ in the gap center, and ranged from <200 to >800 $\mu Em^{-2}s^{-1}$ at the gap edge.

Sunflecks have been shown to provide an important contribution to the total daily net carbon gain for understory seedlings (Chazdon, 1986; Weber et al., 1986; Young and Smith, 1979; Bjorkman et al., 1972). Since plot 17 had the densest canopy cover, and, therefore, the lowest understory PAR values, the contribution of light from sunflecks could be vital to the survival of seedlings there. Sunflecks in plot 17 ranged in size from $640cm^2$ to $7200cm^2$, and in duration from <1min to >16min. Sunfleck PAR was between 30 and 100 $\mu Em^{-2}s^{-1}$, with a mean of 96 $\mu Em^{-2}s^{-1}$.

Figure 24 shows the seasonal maximum and minimum air temperatures for the upper and lower Mount Misery sites. Average minimum temperatures at both locations were similar; however, average maximum temperatures at the upper sites were more than 5 degrees above those at the lower study sites.

Seedling Height and Stem Diameter

1984 population

Seedlings in plot D2 grew the most in each year (Table 5), and were significantly larger ($p< .001$) after 3 growing seasons both in total mean height and stem diameter (Table 6). Growth in height was significantly different ($p< .01$) among plots after the first growing season, as well as at the end of each of the subsequent 2 years ($p< .001$). Comparisons within each plot of height growth over each of the 3 years showed no significant differences (2-way ANOVA).

Plots 17 and T10 had the shortest seedlings (mean= 52.0mm and 60.5mm, respectively) at the end of 3 growing seasons, but the seedlings in plot T10 had the third largest average stem diameter (Table 6). At the end of the first growing season there were no significant differences in height between seedlings found at the lower Mt. Misery study plots and those at the top of Mt. Misery.

After each of the next 2 growing seasons, seedlings at the lower Mt. Misery sites were significantly larger in height (1985: $p< .05$; 1986: $p< .01$) than those in the upper study plots. Mean stem diameter after 3 growing seasons was not significantly between the upper and lower study sites.

1986 population

Table 7 gives the mean height and stem dameter of the 1986 seedlings. Heights between plots were highly significantly different ($p< .001$), and plants growing in plot D2 again were the largest both in mean height and stem diameter. Within plots in 1986, the mean height of the early, mid-, and late-season cohorts was noteworthy only in plot T10, where the mean height of the mid-season cohort was significantly larger ($p< .01$) than that of the early cohort. Although the mean height of the seedlings growing underneath the fern and in the canopy gap of plot 4 was not significantly different, the mean stem diameter of the seedlings growing underneath the fern was significantly larger ($p< .05$).

Contrasting with the 1984 seedling population, 1986 plants growing in the lower Mt. Misery plots were significantly larger in height ($p< .001$; mean= 59.2mm, n= 443) than those growing at the top of the mountain (mean= 52.3mm, n= 702). An overall ANOVA comparing first season growth of the 2 populations showed a significantly larger ($p< .001$) mean height for the 1986 striped maple seedlings (mean= 55.0, n=1145). Within each study plot except T3, there were significant differences in first season height growth between the 1984 and 1986 populations (Table 8). Seedlings growing in the upper Mt. Misery study sites were significantly larger ($p < .01$) in stem diameter than those in the lower plots.

Shoot and Root Data

Preliminary data on root and shoot length and weight are shown in Table 9. Shoot lengths between plots were not significantly different. Seedlings growing in Plot 17 had the longest shoots (mean length= 54.3mm), while those in Plot 4 had the shortest (mean length= 37.3mm). An overall ANOVA showed that root lengths were significantly different between plots ($p < .05$), and were the longest and most well-developed in plots T3 and T10. Plants in plots 4 and 17 had the shortest roots, and those in plot 17 showed no evidence of the development of root hairs. Roots of seedlings growing in the upper two plots were significantly longer ($p < .05; n = 6$) than those in the lower areas ($n = 9$). There was no significant difference in shoot length of seedlings in the upper and lower plots.

Average seedling shoot weight ranged from 0.9734g in Plot 17 to 1.0287g in Plot T10. Shoot weight was significantly different ($p < .01$) between plots, and the mean shoot weight of seedlings growing in the upper plots was greater than that of seedlings in the lower study sites (K-S test: $p < .01$). Mean root weight was between 3.6333E-03g (plot 17) and 0.0316g (plot T10). Seedlings growing the two upper plots had significantly heavier roots (K-S test: $p < .01$) than those in the lower plots.

Leaf Specific Weight

Leaf specific weight (LSW), which is an indicator of leaf thickness and the degree of mesophyll development, was highly significantly different between plots ($p < .001$). Values ranged from $0.0123 gm^{-2}$ in plot 17 to $0.0289 gm^{-2}$ in plot D2 (Table 10). Mean LSW was significantly larger ($p < .01$) in the upper two plots (mean= $0.0241 gm^{-2}$) as compared with that in the lower Mt. Misery study plots (mean= $0.0179 gm^{-2}$).

Chlorophyll Content

Average total chlorophyll content (g/m^2) was highly significantly different ($p < .001$) between the 5 plots, and was highest in plot 17 and in seedlings taken from the open areas of plot 4 (Table 4). There was no significant difference in chlorophyll content between plots T3, T10, and D2. These same plots had the least reduction from gap-center to understory PAR (Table 11). Leaf disks were taken separately from plants growing under the hay-scented fern in plot 4 to determine if the fern 'canopy' affected chlorophyll content. Seedlings growing underneath the hay-scented fern in plot 4 (4F) had significantly less chlorophyll than those in the more open areas of plot 4

($p < .001$) and those in plot 17 ($p < .01$).

Leaf Area

1984 population

A total of 364 node-1 leaves of the 2 year old striped maple seedlings were measured in late August of 1986. At that time many leaves had already abscised. Plants in only plots 4, T3, and D2 made a second leaf pair, and a few seedlings in plot D2 made a third pair of leaves. Table 12 gives the average area in mm^2 of leaves measured in each plot.

Leaf areas of node-1 leaves were highly significantly different ($p < .001$) between plots. Plants in plot D2 had the largest leaves (mean= 4674.65mm^2; n= 75), while those in plot 17 had the smallest (mean= 756mm^2; n= 2). Due to the small sample size, no statistical analyses of leaf areas included data from plot 17. Node-1 leaves of seedlings in the lower Mt. Misery plots (4, 17, D2) were highly significantly larger ($p < .001$) than those of the seedlings in the upper plots (T3 and T10).

1986 population

A total of 1825 node-1 leaves on 1084 plants were measured in late August 1986. By that time between 33.0% (T10) and 98.7% (17) of the seedlings had lost their leaves due to predation, fungal growth, drought stress, or other causes. Plants in plots 4, T3, T10, and D2 had made a second pair of leaves in this first growing season. From observations made earlier in the growing season, no seedlings in plots 17 produced a second leaf pair.

Table 13 gives the average area in mm^2 of node-1 and node-2 leaves measured in each plot. Plants in plot T10 had the largest node-1 leaves ($p< .001$; mean= $685.43 mm^2$; n= 522), while those in plot 17 had the smallest (mean= $414.76 mm^2$; n= 17). Areas of the node-1 leaves were highly significantly different between plots ($p< .001$). Node-1 leaves on plants growing in the upper plots were significantly larger ($p< .001$) than those on plants in the lower Mt. Misery plots.

In 4 plots (4, T3, T10, D2) there were a total of 247 node-2 leaves produced on the 1986 seedlings. Leaf areas (mm^2) of these leaves were significantly different between plots ($p< .001$). Plants in plots T3 and T10 had the largest node-2 leaves ($p< .001$; Table 13), compared with those growing in the lower 2 plots, 4 and D2.

Stomate Density

No stomates were present on the adaxial leaf surfaces. Stomate density on the abaxial surfaces was significantly different (ANOVA, $p<.001$) between the 5 study plots (Table 14). Leaves from the plot with the densest canopy (17) had the highest stomate density (mean= $330.44/mm^2$; n=5), while those in plot D2 had the fewest stomates (mean = 228.57; n=5). There was no significant difference in stomate density between seedlings growing in the upper and lower study plots.

Xylem Water Potential

Table 15 presents mean dawn and midday xylem water potential for striped maple seedlings growing in the upper and lower study sites at Mt. Misery measured during the 1986 growing season. On each day that measurements were obtained, mean midday water potential was not significantly different between plots except in September, when seedlings taken from areas adjacent to the 2 upper quadrats exhibited more stressful conditions ($p<.01$; mean= 1.577 MPa). Across the growing season, seedlings growing at the upper Mt. Misery study sites showed no significant difference in midday xylem water potential from those growing at the lower sites (2-way ANOVA).

On 2 days, dawn xylem water potential, which is a good measure of soil water potential (Nobel, 1983), was measured in the 5 plots. The 2 upper plots (T3 and T10) had significantly drier soils both in early July ($p< .001$) and later in the same month ($p< .05$). In neither case, though, were seedlings near permanent wilting point, which was determined in the greenhouse to be >3.5 MPa for seedlings from both upper and lower sites.

DISCUSSION

Almost 100% more striped maple seeds germinated in 1986 (4006) than in 1984 (2031) in the Mt. Misery study sites. There was early-season drop of striped maple seeds in 1985 and 1986 at Mt. Misery (personal observation) and in other parts of New England (Tim Sipe, personal communication). In both areas, 1984 was a year of heavy seed production for striped maple. As is normal for this species, seeds were held on the trees throughout the growing season and then dispersed during the fall and winter. From this, it appears that the larger population of striped maple seedlings in 1986 must be from stored seeds from 1984 or before. Seed storage for other intermediately shade-tolerant species is commonly 2 to 5 years (Marquis, 1975). Wilson et al. (1979) found that only .03% of sown seeds germinated in the first year and 24.8% germinated the 2nd year; however, Marquis (1975) found that 90% of the striped maple seedlings germinating in the first 2 years did so in the 1st year. Wilson et al. (1979) also found that the stratification requirement for striped maple is at least 5 months, and that most seeds that fall directly on the litter surface require an additional 1 to 2 years of litter cover to obtain the conditions necessary for germination.

Curiously, no _A. pensylvanicum_ exist in an intermediate size class at Mt. Misery. A census of stems in 1983 and 1984 revealed that all stems approximately 1m tall were dead. Therefore, 2 size-classes exist in the quadrats at Mt. Misery- the adult and the young seedling, 1 to 3 years old. There are no suppressed seedlings in the area, yet this is one of the 2 size classes described for this species (Hibbs, 1979). These data suggest a cyclic recruitment pattern for _A_. _pensylvanicum_ at Mt. Misery. This type of recruitment is common for tree species: Henry and Swan (1974) found in SW New Hampshire that beech was recruited on average once every 10 years after 1815.

As for many plant species (Hibbs, 1980; Harper and White, 1974; Harper, 1977; Hamrich and Lee, 1987), the highest levels of mortality in _A_. _pensylvanicum_ occur in the first weeks of seedling germination and establishment. Early- and mid-season cohorts experienced higher mortality overall than did seedlings that germinated later in the growing season. The concept of 'safe sites' (Harper, 1977) implies favorable microsites for both germination and subsequent establishment and growth. High mortality rates for early- and mid-season recruits at Mt. Misery might be due to limited numbers of safe sites available for permanent establishment, or to intraspecific competition for available light, moisture, and mineral nutrients necessary for further growth after germination. Putwain and Harper (1970) reported that "...favorable conditions for seedling establishment may occur for very short periods of time, at infrequent intervals or in locally disturbed microsites."

Survival of striped maple seedlings at Mt. Misery appears primarily related to light, which is controlled by the height and density of the canopy. Overall seedling survival was highest in the 2 upper quadrats, where the canopies, which consist primarily of _Quercus_ sp., were higher and less dense. There are very few striped maple adults growing in the subcanopy on the upper slope of Mt. Misery. On the other hand, the dense canopy of plot 17 consists almost exclusively of adult striped maples. Whereas having a larger number of adults might increase the number of seeds produced (and, therefore, larger numbers of germinated seedlings), this was not an advantage in this case; i.e., a small percentage (0.24% in 1984, and 3.46% in 1986) of the seedlings germinating in plot 17 survived under the canopy of the same species. Curtis (1959, as cited in Hett and Loucks, 1971) found similar results for sugar maple. Hibbs et al. (1980) found that striped maple grows best under thin canopies and in small canopy gaps.

In plot 4, seedling survival was also lowest where the canopy was densest, on the east side of the plot. After 1 and 3 growing seasons, surviving seedlings in this plot were grouped in areas corresponding to canopy gaps. Surviving seedlings of the 1984 and 1986 populations in plot D2 also had a clumped spatial distribution corresponding to the canopy gaps.

Surviving seedlings from the 1984 population in the upper 2 plots were randomly distributed. Canopy structure appeared to have no influence on the germination or survival of the 1984 cohorts in these 2 plots: however, the spatial distribution of survivors of the 1986 population was somewhat governed by the canopy structure, but not in such a drastic way as in the 2 lower plots. Even though there appears to be clumping of seedlings, the canopy did not prove to be as limiting for seedling survival in these plots, as noted by the low mortality rate there.

In all plots, except 17, germinated seedlings were spatially clumped. In plot 17, seedling cohorts were randomly distributed. Mortality there appeared to be due more to low PAR, damping off, and physical disruption to the habitat by chipmunks and from normal water run-off from the upper slopes of Mt. Misery.

Seedling morphology was also influenced by available light. Seedlings growing in plot 17 were the smallest overall in stem dimensions in both the 1984 and the 1986 populations. They ranked 4th in height in first-year growth for 1986. Typically, seedlings growing in dense shade and in deep litter have longer hypocotyls (Hamrich and Lee, 1987). Seedlings taken from areas adjacent to plot 17 did have the longest shoots, but the shortest and least developed roots. Seedlings within the plot produced the smallest leaves and apparently received insufficient light to make enough photosynthate to increase overall plant size. Leaves on these plants were also the thinnest (LSW= $0.0123 gm^{-2}$), a trait common for leaves of mature 'shade' plants as well.

Because tree seedlings are part of the herbaceous layer of the forest understory, they are subject to the same environmental stresses as are the herbaceous plants, as well as the stresses imposed by the herbs themselves. The herb stratum, then, may to come extent control the spatial distribution and density of tree seedlings (Horsley, 1977a, 1977b; Maguire and Formann, 1983). In all plots except 17 at Mt. Misery, overall spatial distribution patterns of seedling germination and survival were non-random. These results are consistent with the findings of others (Spring, 1922; Bray, 1956; Daniels, 1978), who found that the non-random distribution was related to biotic and abiotic factors. Striped maple seedlings were not inhibited by the herbaceous growth in any of the plots, whether it was fern, Vaccinium sp., or moss, whereas in other studies, a negative interaction between herbs and tree seedling establishment was observed (Shirley, 1945; Daniels, 1978), especially in logged forests (Hough, 1937; Hough and Forbes, 1943; Horsley, 1977a, 1977b). On the other hand, Smith (1951) found that seedlings growing in patches of Polytrichum had greater chances of survival than those growing on thin litter or bare patches. In plot 4, PAR under the hay-scented fern was higher than in plot 17, which had no herbaceous growth, so the herbaceous canopy was less limiting for light than the dense canopy of striped maple adults.

Nor was it apparent that any allelopathic inhibition from the ferns affected the seedlings (Horsley, 1977a,b). In other comparisons of seedlings found underneath the fern and those growing in the open in plot 4, there were no significant differences in height, stem diameter, leaf area, or root and shoot biomass, nor in the number of surviving seedlings over the 1986 growing season.

Contrary to the findings of others (Gysel, 1951; Sulser, 1971, as cited in Maguire and Formann, 1983), there was no indication of the inhibition of the germination or establishment of striped maple seedlings in canopy gaps. In plot D2, where a large canopy opening was created early in 1984, seedlings of both the 1984 and 1986 populations were the largest in height, and the 1984 cohort had the largest mean stem diameter. Two-year old seedlings in this same plot also produced the largest leaves compared to seedlings in the other study plots. In fact, in plots 4, 17, and D2 canopy gaps enhanced rather than inhibited seedling growth and survival.

Physical disturbance to the study sites was clearly harmful only in plots 4, 17, and D2. In each case, sections of the established quadrats where litter was the heaviest were the favorite 'playgrounds' for the chipmunk population. Seedlings that fell on litter and subsequently germinated there were more likely than not to have been disturbed by the chipmunks. Deer grazing was minimal in the study areas.

For seedling survival, understory PAR was the primary limiting factor, for only there were there significant differences between and within plots in available light for photosynthesis. Reduction in PAR from gap-center to understory ranged from 11.8% (T10) to 90.2% (17). Shirley (1945), in studies of the effect of light on conifer seedlings, found that growth was poor when light intensity was reduced more than 65%. More than 85% of midday PAR in the understory at the Mt. Misery study sites was $50\mu molm^{-2}s^{-1}$ or below. Chazdon (1986) found that 80% of understory PAR averaged over 5min intervals was less than $10\mu molm^{-2}s^{-1}$. At Mt. Misery PAR measured in the understory rarely exceeded $50 \mu molm^{-2}s^{-1}$, whereas that in gap-centers rarely exceeded $100\mu molm^{-2}s^{-1}$. Therefore, daily carbon gain in gap-centers was potentially 2 times greater than that in the understory.

Shirley (1945) also found that in dry areas, shade improved seedling growth but not survival. Height growth of the 1984 and 1986 seedling populations was limited in plot T10, where soils were drier than those in the lower quadrats: however, stem diameter and weight and root weight for the 1986 seedlings were highest in this plot, and shoot and root length were second highest of all the plots at Mt. Misery. Understory PAR was highest in plots T10 and T3, where seedling survival was highest after 3 years and after 1 growing season. Understory PAR in plot D2 was similar to that measured in the 2 upper quadrats. It is physically similar to the upper quadrats in that it has a higher, thinner canopy, and also has no A. pensylvanicum adults. Although shorter seedlings were found in the upper plots, other morphological features illustrate that more photosynthate was directed to storage areas.

Although they have been shown to provide an important contribution to the total net daily carbon gain for understory seedlings (Bjorkman et al., 1972; Young and Smith, 1979; Chazdon, 1986; Weber et al., 1986), sunflecks did not appear to be sufficient in size, duration, or intensity for seedling survival in Plot 17, which had the densest canopy cover.

Water was not limiting to the striped maple seedlings. At no time during either year of study did the plants appear under stress, nor did water potential measurements approach PWP which was determined in greenhouse experiments. Hibbs (1980) found that striped maple has a negative asscciation with hemlocks; i.e., that more mesic rather than moist habitats are favored by this species. Higher seedling survival in the upper quadrats could be partially attributed to the drier soils there, as determined by dawn stem water potential. No hemlocks grow near the upper quadrats, but they are found in the lower study areas.

It was initially postulated that environmental differences might exist between the upper and lower slopes of Mt. Misery since there are fewer striped maple adults at the top of the mountain. Average maximum temperatures were higher by greater than 5 degrees at the top. Stem diameter of the seedling population of the upper quadrats was larger, suggesting that more photosynthate was directed to stems and roots, which were larger in both length and weight. LSW was greater in leaves taken from the upper plots; i.e., greater mesophyll development, which in turn determines the photosynthetic capacity of a leaf. If more photosynthesis can occur, then greater is the possibility of survival. Node-1 leaf area was also larger on seedlings growing at the top of Mt. Misery, as was the area of the node-2 leaves of the 1986 population: however, leaf area of the 3-year old plants at the bottom of the mountain was greater, as was seedling height. Chlorophyll content was significantly higher ($p< .001$) in leaves taken from plants growing in the lower study sites than in those from the upper quadrats. Chlorophyll content is also normally higher in 'shade' plants.

The striped maple population at Mt. Misery appears to be shifting from the lower Mt. Misery area to the upper portion, if, in fact, the seedling population is a good indicator. The lower portions of Mt. Misery were logged on several occasions prior to the cutting at the top of the mountain simply because of easier accessibility. Striped maple established itself there in response to the opening of the canopy and has now become a dominant member of the canopy. As is common in any plant community, what once was a favorable site for establishment has now been altered by the dominant species itself, so that the necessary microenvironmental conditions for establishment and maintenance of the population are no longer available. On the other hand, the more recent logging of the upper slope of Mt. Misery has created a favorable microclimate, especially with respect to light, for striped maple to regenerate and establish itself there.

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Table 1. Population flux of 1984 striped maple seedlings in 5 plots at Mt. Misery.

	PLOT				
	4	17	T3	T10	D2
a) plants m^{-2}, 15 May 1984	5.67	9.73	.39	.21	12.29
b) plants m^{-2}, 20 June 1984	5.67	12.32	.39	.21	12.29
c) plants m^{-2}, Oct. 1984	3.68	1.76	.36	.17	10.36
d) plants m^{-2}, Oct. 1986	1.32	0.03	.19	.14	4.14
e) c-b	-1.99	-10.56	-.03	-.04	-1.93
f) d-b	-4.35	-12.29	-.20	-.70	-8.15
g) c-b/153 (1 season)	-.01	-.07	-	-	-.01
h) %survival-1984 (c/b*100)	64.90	14.29	92.31	80.95	84.30
i) %survival-1986 (d/b*100)	23.28	0.24	48.72	66.67	33.69
j) %mortality-1986 (100-i)	76.72	99.76	51.28	33.33	66.31
k) %w/herbivore damage-1984	3.17	10.63	2.56	9.52	32.56
l) tags unaccounted-for	89	42	2	1	57

Table 2. Population flux of 1986 striped maple seedlings in 5 plots at Mt. Misery.

	PLOT				
	4	17	T3	T10	D2
a) plants m^{-2}, 5 May 1986	15.00	8.95	3.92	3.45	10.21
b) plants m^{-2}, 27 June 1986	8.09	1.39	4.52	3.89	8.00
c) plants m^{-2}, 5 Oct. 1986	4.18	0.31	3.79	3.34	3.07
d) net change (c-a)	-10.82	-8.64	-0.13	-0.11	-7.14
e) c-a/153 days	-0.071	-.056	-	-	-0.05
f) % survival (c/a*100)	27.87	3.46	96.68	96.81	30.07
g) % mortality (100-f)	72.13	96.54	3.32	3.19	69.93
h) %w/ herbivore damage	4.23	5.56	4.82	7.06	3.90
i) tags unaccounted for	16	18	7	5	0

Table 3. Early, mid-, and late-season cohort mortality rates of striped maple seedlings germinated in 1986 at Mt. Misery.

Plot	4	17	D2	T3	T10
EARLY	$-.0664^{b}$	$-.04377^{b}$	$-.05133^{b}$	$-.00758^{b}$	$-.00618^{b}$
MIDDLE	$-.0027^{b}$	----	$-.00325^{b}$	$-.00219^{b}$	$-.0005^{ns}$
LATE	$-.0007^{a}$	----	$-.0006^{ns}$	----	----

Significance levels of slope: ns= not significant; a= $p < .01$; b= $p < .001$

Table 4. a) Mean midday PAR ($\mu Em^{-2}s^{-1}$) in 5 plots at Mt. Misery, May- Sept., 1986. Numbers in parentheses represent number of readings per plot. Significance levels at the far right refer to the reduction in PAR from gap-center to understory within each study plot.

Plot	pre-canopy	post-canopy	
		gap-center	understory
4	328 (9)	75 (5)	27 (4)*
17	562 (9)	90 (4)	8.4 (25)***
T10	586 (8)	85 (4)	75 (4)^{ns}
T3	673 (8)	135 (4)	60 (4)*
D2	280 (2)	58 (5)	43 (5)^{ns}
	ns	ns	***

b) Percent of readings in different PAR ranges in the gap-centers and in the understory over the 1986 growing season at Mt. Misery.

PAR ($uEm^{-2}s^{-1}$)	% of readings	
	gap-center	understory
20-49	40.8	83.0
50-99	29.6	12.7
100-199	22.2	4.3
200-299	7.4	0

Table 5. Mean growth in height (mm) of 3 growing seasons of the 1984 striped maple seedling population at Mt. Misery. Standard error of the mean (SE) and sample size (n) are indicated.

Plot	1984(n)	SE	1985(n)	SE	1986(n)	SE
4	48.3(127)	1.32	14.4(124)	0.91	23.1(68)	1.97
T3	53.4 (21)	3.58	17.0 (21)	2.66	13.6(11)	3.32
T10	39.2 (12)	2.21	11.3 (12)	3.77	9.2(10)	1.86
D2	54.7 (56)	2.36	42.8 (56)	5.32	35.9(35)	3.58

Table 6. Mean height (mm) and stem diameter (mm) of the 1984 striped maple seedlings measured in Oct. 1986. Standard error of the mean (SE) and sample size (n) are also given.

Plot	Height	SE	Stem diameter	SE	n
4	84.4	1.672	1.25	.0245	134
17	52.0	12.124	1.00	.1528	3
T3	78.1	5.720	1.23	.0405	19
T10	60.5	4.471	1.40	.0602	14
D2	124.7	6.308	2.05	.0574	57

Table 7. Mean height (mm) and stem diameter (mm) of the 1986 striped maple seedlings measured in October 1986. Standard error of the mean (SE) and sample size (n) are also given.

Plot	Height	SE	Stem diameter	SE	n
4	58.4	0.710	0.91	8.7E-03	402
17	55.5	2.159	0.99	0.045	13
T3	54.7	0.756	1.03	8.5E-03	372
T10	49.6	0.828	1.13	9.0E-03	330
D2	67.2	2.745	0.99	0.021	41

Table 8. Mean height growth (mm) after the 1st growing season for the 1984 and 1986 striped maple populations. Sample size (n), standard error of the mean (SE), and statistical significance are also given.

	1984			1986			
Plot	mean	n	SE	mean	n	SE	p
4	48.3	127	1.320	58.3	402	0.710	***+
D2	54.7	56	2.362	67.1	41	2.748	**
T3	53.4	21	2.211	54.7	372	0.756	*
T10	39.2	12	3.575	49.6	330	0.828	ns

+: *** = p< .001; **= p< .01; *= p< .05; ns= not significant

Table 9. Shoot and root length (mm) and weight (g) of first year striped maple seedlings taken from sites adjacent to the 5 study plots at Mt. Misery, as measured in 1986. For each plot, n=3.

	SHOOT		ROOT	
Plot	Length	Weight	Length	Weight
4	37.3	0.986	41.7	0.012
17	54.3	0.973	29.7	3.6E-03
D2	38.7	0.986	58.7	0.014
T3	47.0	1.003	69.0	0.028
T10	52.7	1.029	67.7	0.032

Table 10. Average leaf specific weight (LSW) in g/m^2 of striped maple seedling leaves taken from the 1986 seedling population. Standard error of the mean (SE) and sample size (n) are given.

Plot	LSW (g/m^2)	n	SE
4	0.0148	6	5.0E-04
17	0.0123	6	9.0E-04
D2	0.0289	6	4.0E-03
T3	0.0240	6	3.0E-04
T10	0.0242	6	1.2E-03

Table 11. Mean chlorophyll content (g/m^2) for striped maple seedlings at Mt. Misery in 5 study plots and between quadrats at the top and bottom of the mountain. Also given are sample size (n) and standard error of the mean (SE).

Plot	Mean	n	SE
4	0.2428	6	0.003
4F	0.1930	6	0.010
17	0.2413	6	0.006
D2	0.1537	6	0.018
T3	0.1562	4	0.019
T10	0.1448	6	0.007
	p<.001		
TOP	0.1493	10	8.5E-03
BOTTOM	0.2077	24	9.2E-03
	p<.001		

Table 12. Average leaf area (mm^2) of the the 1984 striped maple seedling population in 5 plots at Mt. Misery. Measurements were made in August 1986.

Plot	node 1	SE	n	node 2	SE	n	node 3	SE	n
4	1838.19*	106.7	238	528.86	78.7	28	----		
17	756.0	399.0	2	----			----		
D2	4674.7^{+}	463.3	75	1449.40	284.6	15	1908.44	246.5	9
T3	1123.3	182.2	34	463.30		3	----		
T10	1050.33	178.2	15	----			----		

*= $p<$ .001

$^{+}$= $p<$ .05

Table 13. Average leaf area (mm^2) of the 1986 striped maple seedling population in 5 plots at Mt. Misery. Measurements were made in August 1986. Sample size (n) and standard error of the mean (SE) are also shown.

Plot	node 1	SE	n	node 2	SE	n
4	495.82	9.237	636	200.26	14.709	74
17	414.77	35.088	17	----		
D2	483.17	32.574	35	268.24	17.800	38
T3	604.96	9.915	615	344.70	18.706	88
T10	685.43	9.622	522	344.66	26.751	47

Table 14. Average abaxial stomate density (mm^{-2}) of striped maple seedlings from the 1986 population. Stomates in 5 fields of view were counted on each leaf.

Plot	Mean	SE
4	248.44	18.84
4F	243.48	17.83
17	330.44	22.43
D2	228.57	26.23
T3	253.42	23.44
T10	268.32	18.67

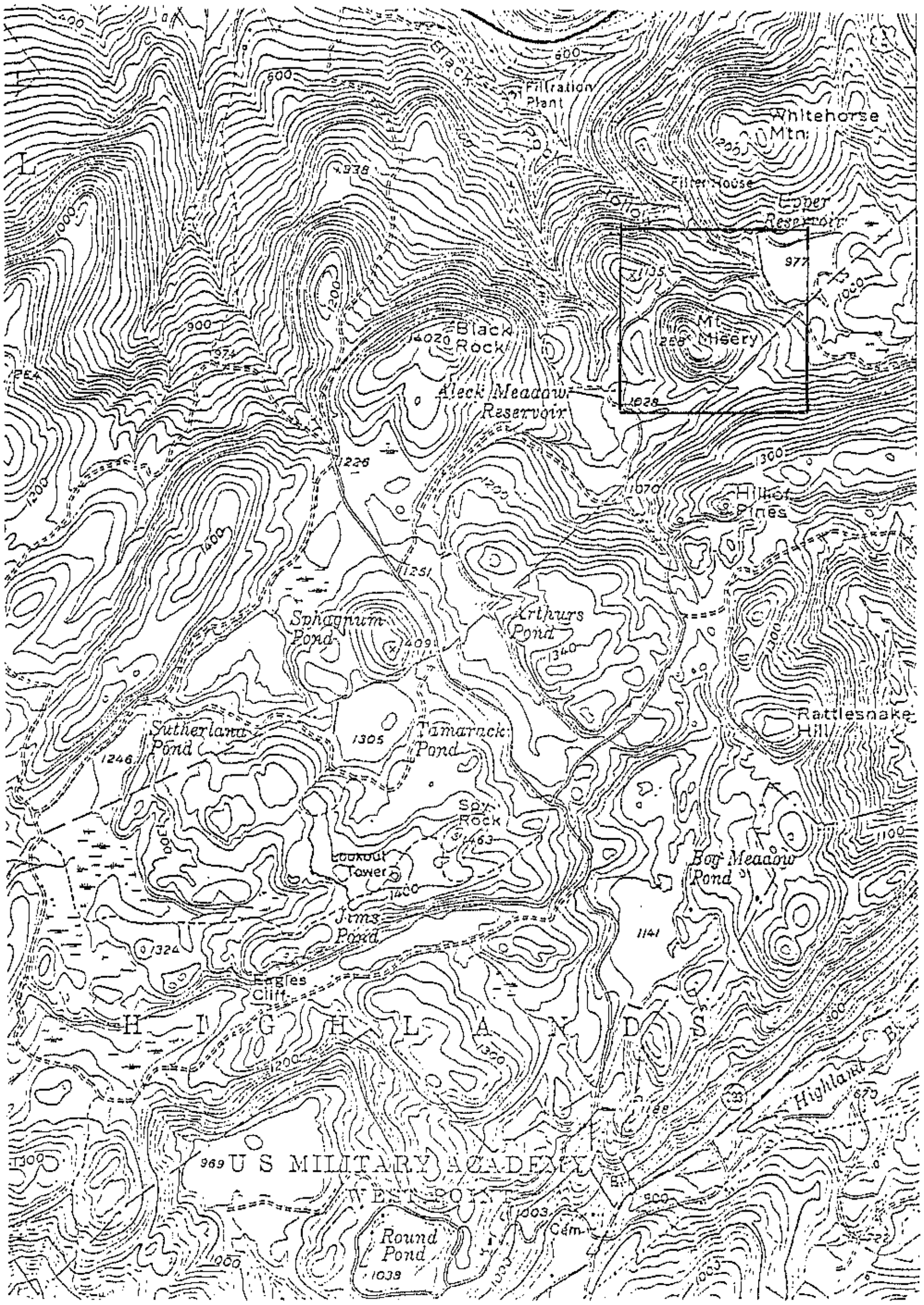
Table 15. Mean dawn and midday xylem water potential (MPa) for striped maple seedlings growing in the upper and lower study sites at Mt. Misery during the 1986 growing season.

		UPPER SITES			LOWER SITES			
	date	mean	SE	n	mean	SE	n	
DAWN	7/11	.391	.0348	9	.158	.0143	19	***[1]
	7/25	.571	.0441	15	.452	.0273	18	*
		ns			ns			
MIDDAY	6/27	.719	.0791	10	.563	.0789	10	ns
	7/11	.883	.1052	12	.719	.0791	18	ns
	7/25	.807	.0666	11	.823	.0795	12	ns
	9/10	1.577	.0833	6	1.220	.0727	18	*
		ns			ns			

---

1) Significance levels: *=p< 0.05; ***=p< .001; ns= not significant

Figure 1. Topographic map of the Harvard Black Rock Forest.
(U.S. Dept. of Interior Geological Survey)


Filtration Plant
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Whitehorse Mtn
Filter House
Upper Reservoir
977
938
Mt Misery
1135
1028
Black Rock
1402
Aleck Meadow Reservoir
900
974
1200
1226
1300
1070
Hilltop Pines
1251
Arthurs Pond
1340
Sphagnum Pond
1409
Sutherland Pond
1246
1305
Tamarack Pond
Rattlesnake Hill
Spy Rock
1463
Lookout Tower
1400
Bog Meadow Pond
1100
Jims Pond
1141
1324
Eagles Cliff
H I G H L A N D S
Highland
969
U S MILITARY ACADEMY
WEST POINT
1003
Cem
Round Pond
1039

Figure 2. Canopy opening on the east side of Plot 4 at Mt. Misery. Photographs were taken from ground level using a Minolta SRT101 camera with a 28mm lens.

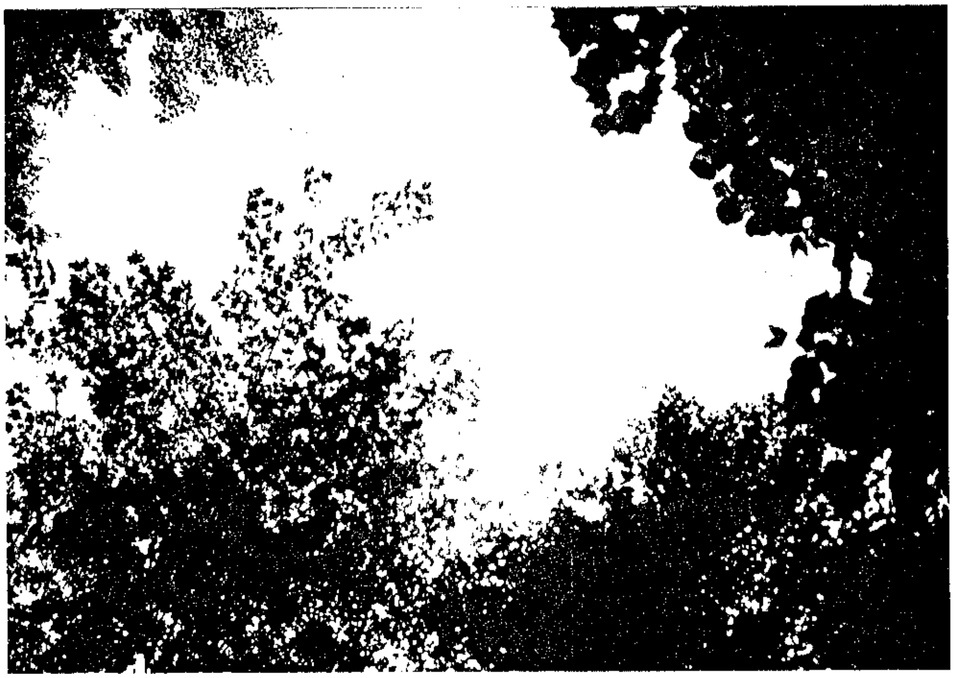


Figure 3. Canopy gaps in Plot 17 at Mt. Misery.

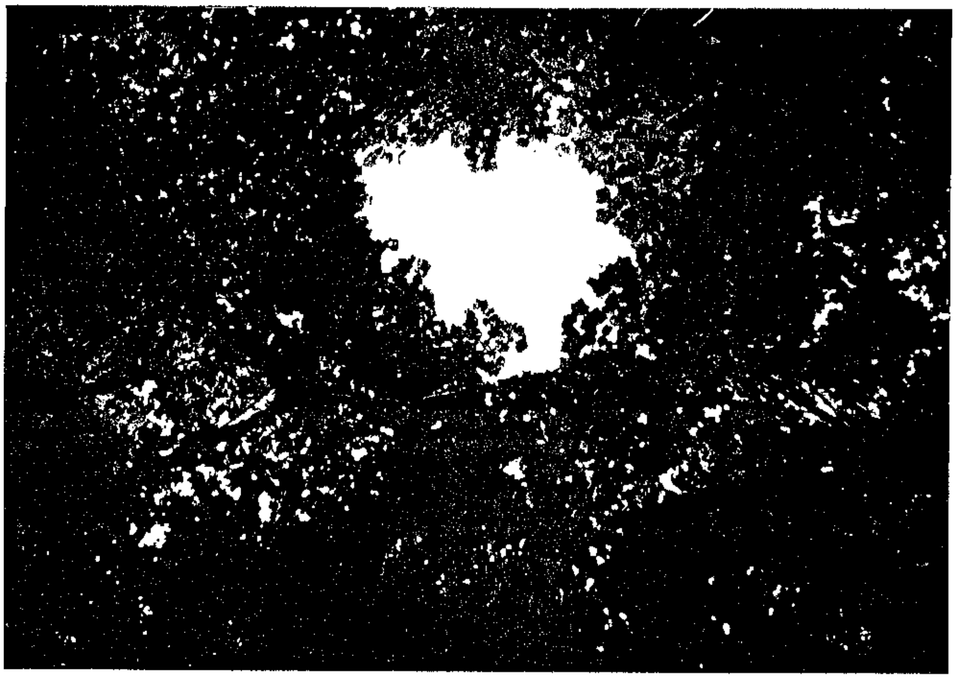
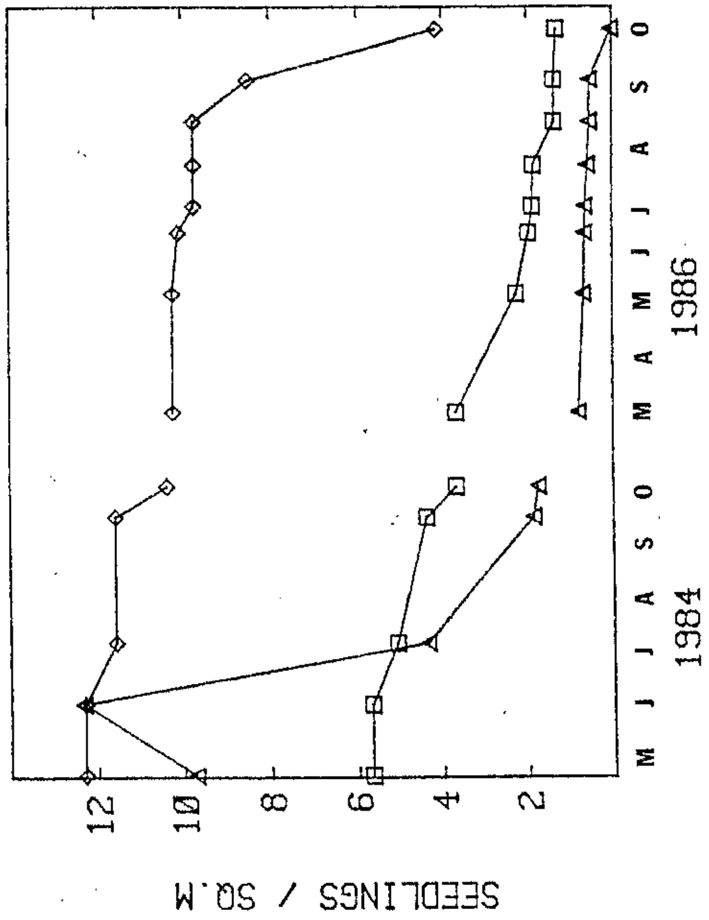


Figure 4. Canopy opening in the upper section of Plot T3.

Figure 5. Canopy opening in the lower portion of Plot T10.

Figure 6. Canopy of Plot D2, where all adult striped maples were removed in 1984.

Figure 7. Total number of living striped maple seedlings (m^{-2}) from the 1984 population, over the 1984 and 1986 growing seasons. Mortality rate for each plot was significantly linear ($p < .01$) with a negative slope. a) Plots 4, 17, and D2 b) Plots T3 and T10


SEEDLINGS / SQ.M
12
10
8
6
4
2
M J J A S O
1984
M A M J J A S O
1986

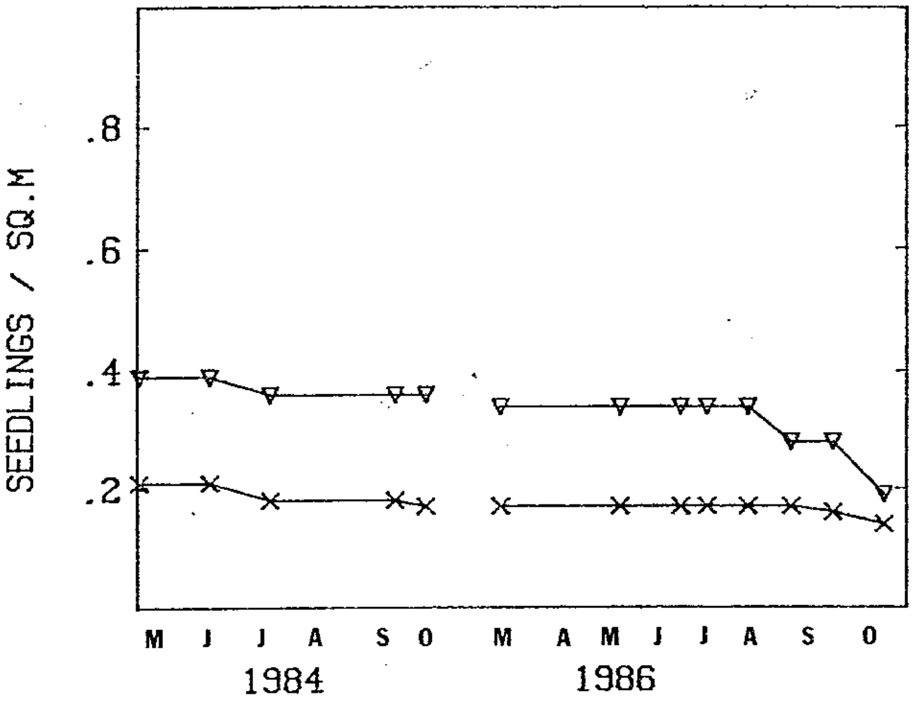
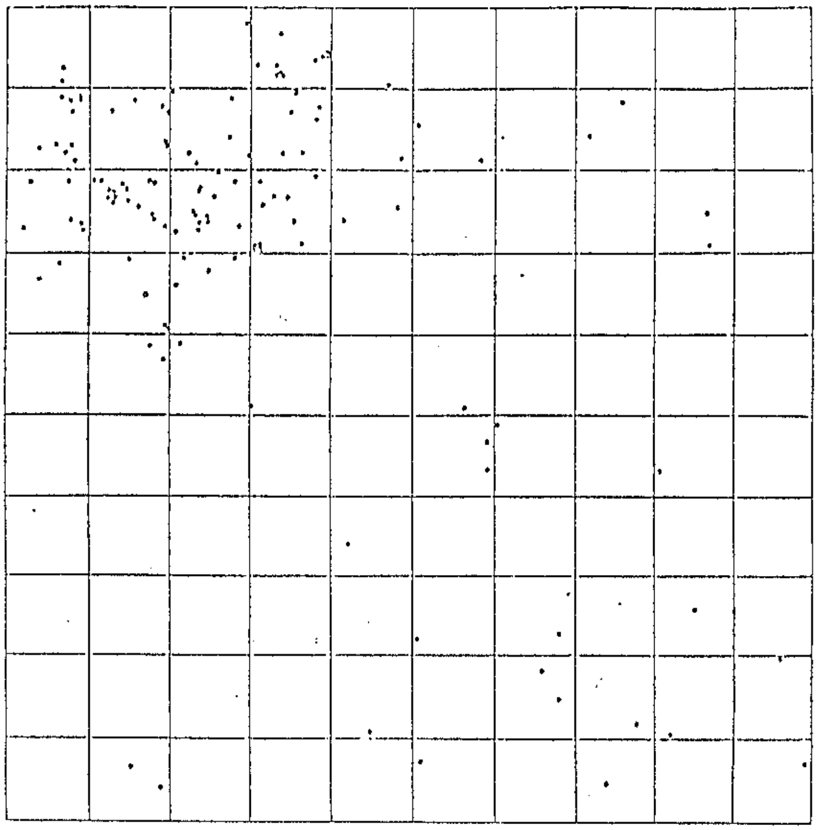
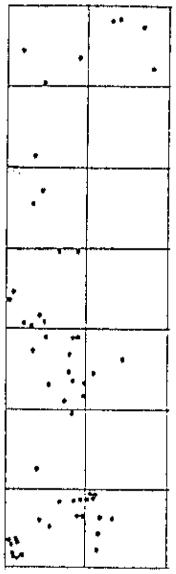

SEEDLINGS / SQ.M
.8
.6
.4
.2
M
J
J
A
S
O
M
A
M
J
J
A
S
O
1984
1986

Figure 8. a) Map of the distribution of the 1984 striped maple seedlings alive in Oct. 1986 in Plot 4 at Mt. Misery. The pattern of distribution was non-random (Kolmogorov-Smirnov goodness-of-fit; $p<.01$). Each square represents $1m^2$.



b) Map of the distribution of the 1984 striped maple seedlings alive in Oct. 1986 in Plot 17. The pattern of distribution was random. Each square represents $1m^2$.

c) Map of the distribution of the 1984 striped maple seedlings alive in Oct. 1986 in Plot D2. The pattern of distribution was non-random (Kolmogorov-Smirnov goodness-of-fit; $p<.01$). Each square represents $1m^2$.



d) Map of the distribution of the 1984 striped maple seedlings alive in Oct. 1986 in Plot T3. The pattern of distribution was random. Each square represents $1m^2$.

e) Map of the distribution of the 1984 striped maple seedlings alive in Oct. 1986 in Plot T10. The pattern of distribution was random. Each square represents $1 m^2$.

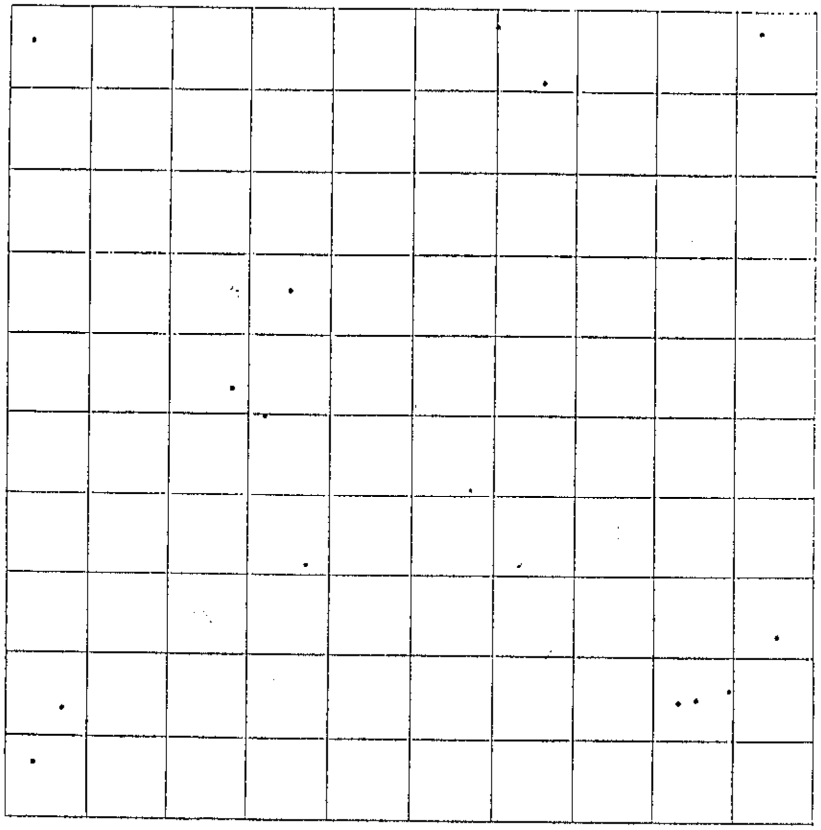
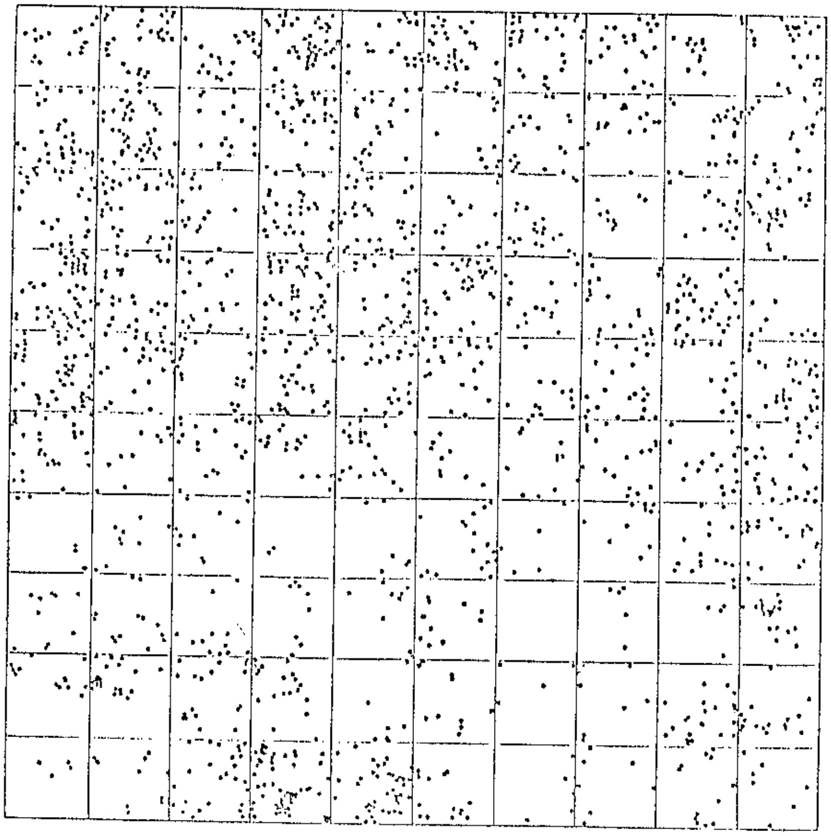


Figure 9. Distribution of (a) striped maple seedlings germinated in 1986 in Plot 4 , and (b) of surviving seedlings in Oct. 1986. Pattern of distribution in both cases was non-random (Kolmogorov-Smirnov goodness-of-fit; $p < .01$).



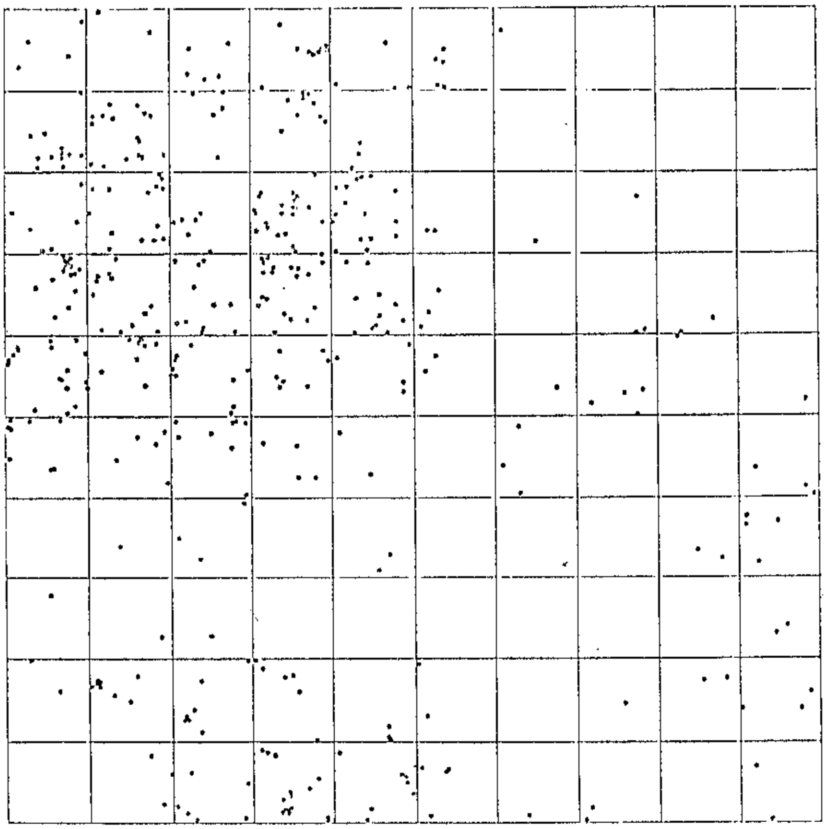


Figure 10. Distribution of (a) striped maple seedlings germinated in 1986 in Plot 17, and (b) of surviving seedlings in Oct. 1986. Pattern of distribution in both cases was random.

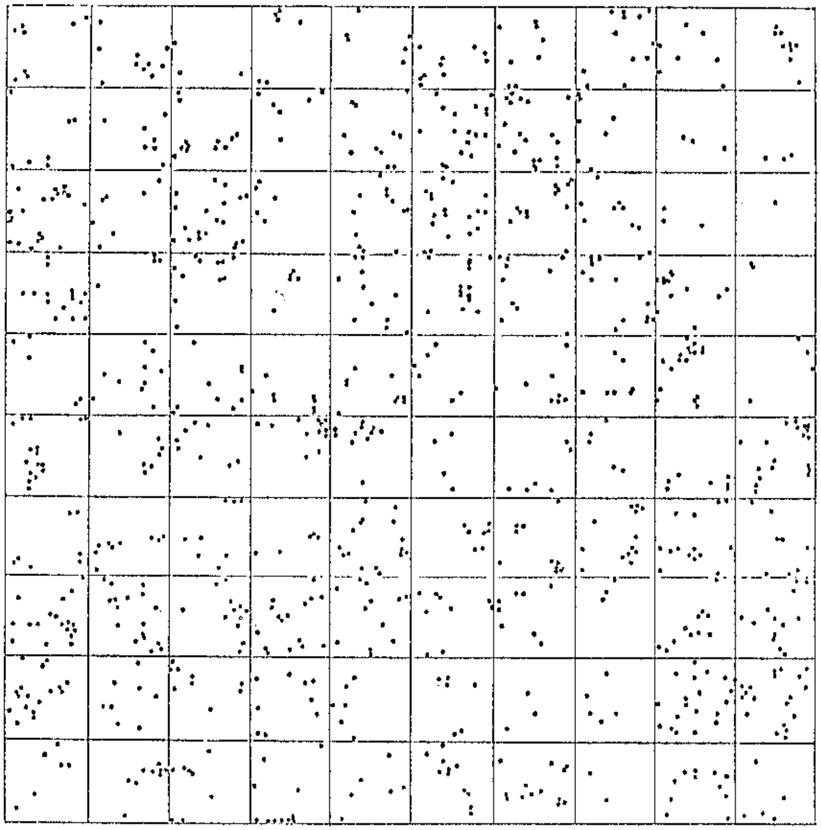
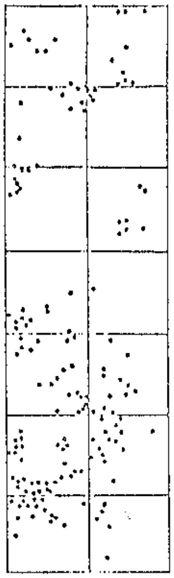
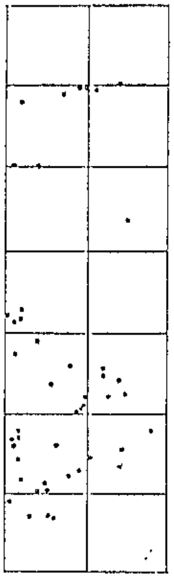


Figure 11. Distribution of (a) striped maple seedlings germinated in 1986 in Plot D2, and (b) of surviving seedlings in Oct. 1986. Pattern of distribution in both cases was non-random (Kolmogorov-Smirnov goodness-of-fit; $p < .01$).

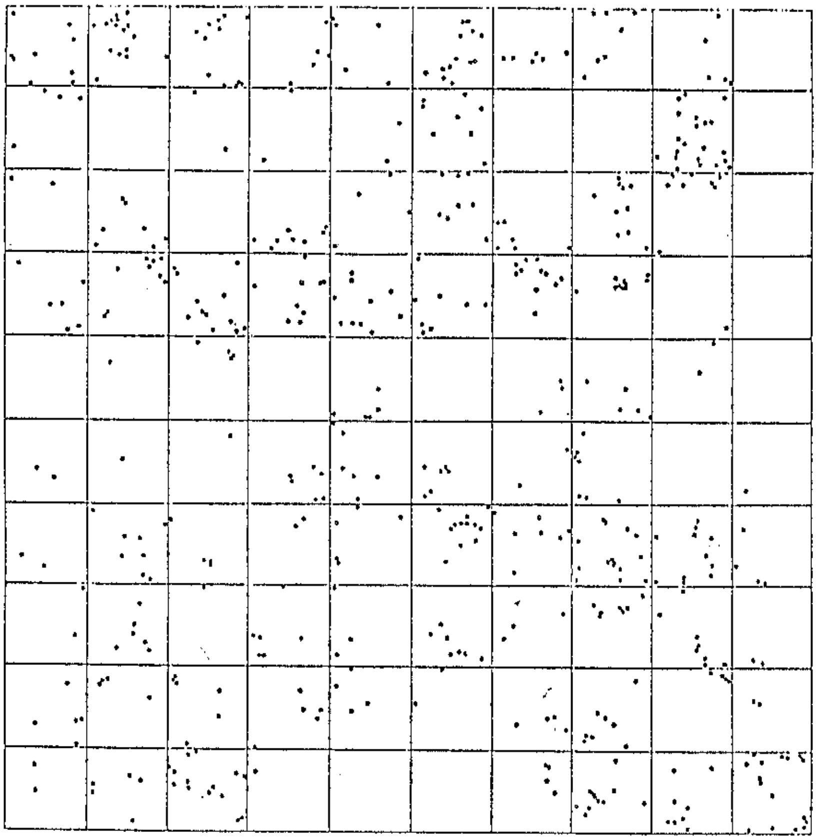


a



b

Figure 12. Distribution of (a) striped maple seedlings germinated in 1986 in Plot T3, and (b) of surviving seedlings in Oct. 1986. Pattern of distribution in both cases was non-random (Kolmogorov-Smirnov goodness-of-fit; $p < .01$).



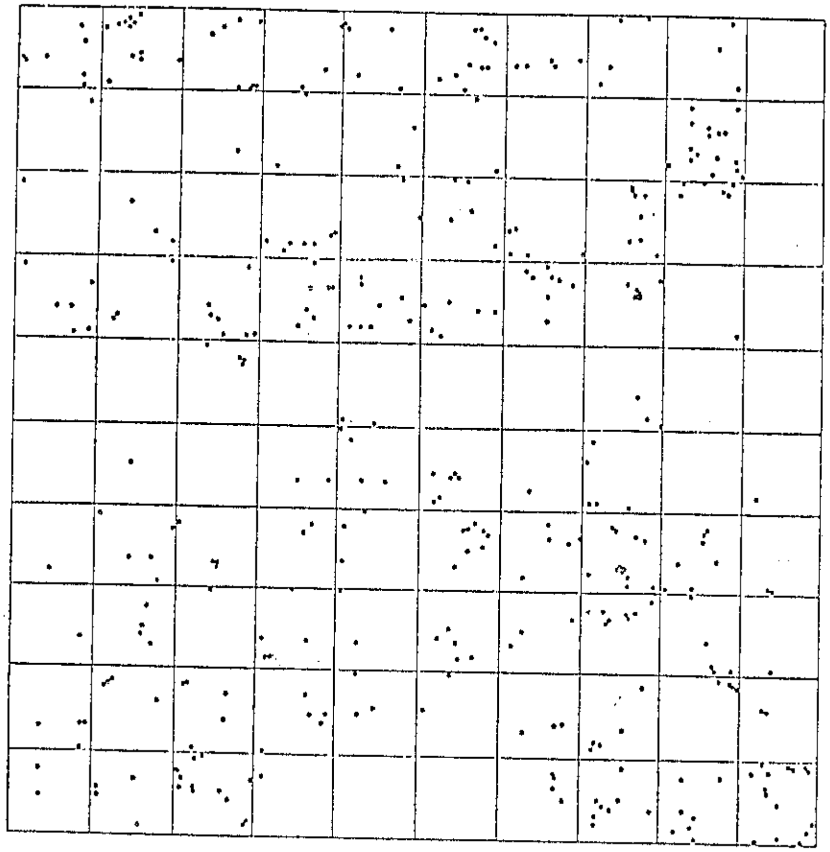
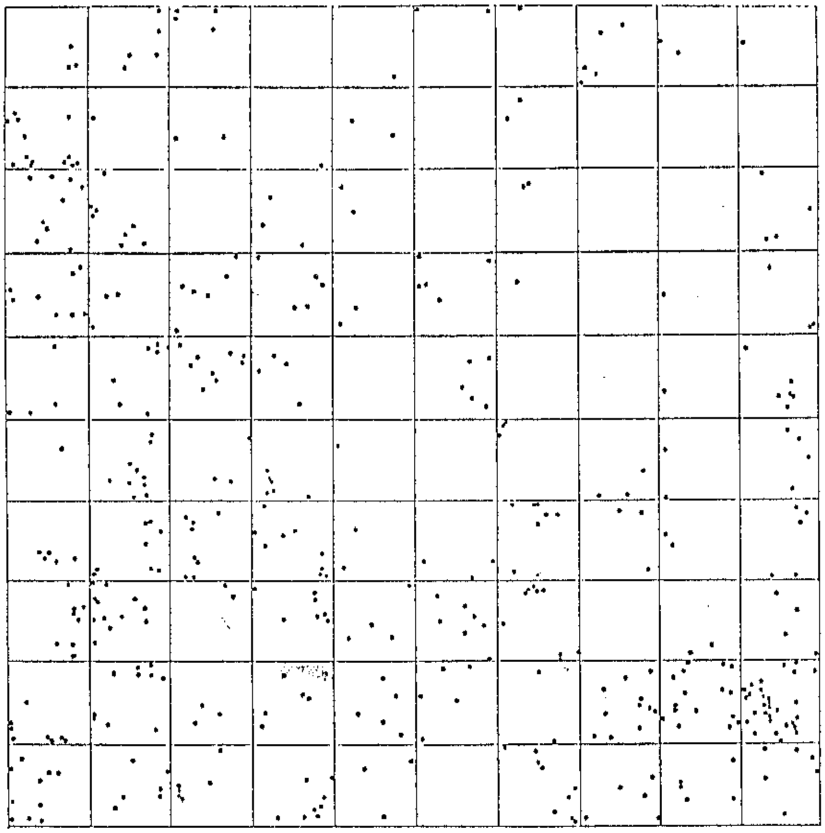


Figure 13. Distribution of (a) striped maple seedlings germinated in 1986 in Plot T10, and (b) of surviving seedlings in Oct. 1986. Pattern of distribution in both cases was non-random (Kolmogorav-Smirnov goodness-of-fit; $p < .01$).



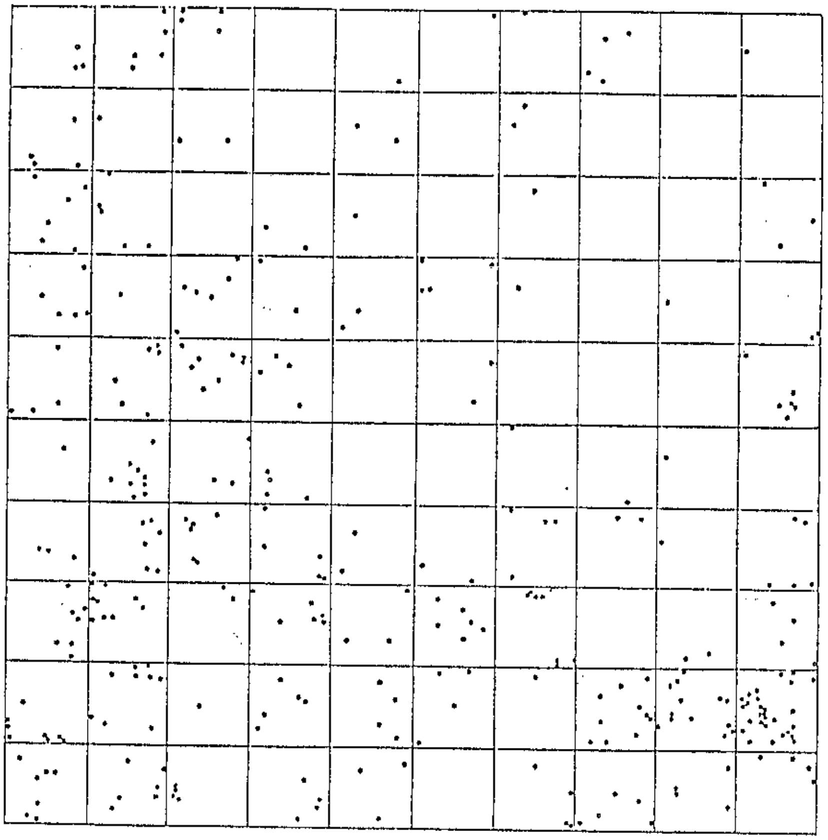
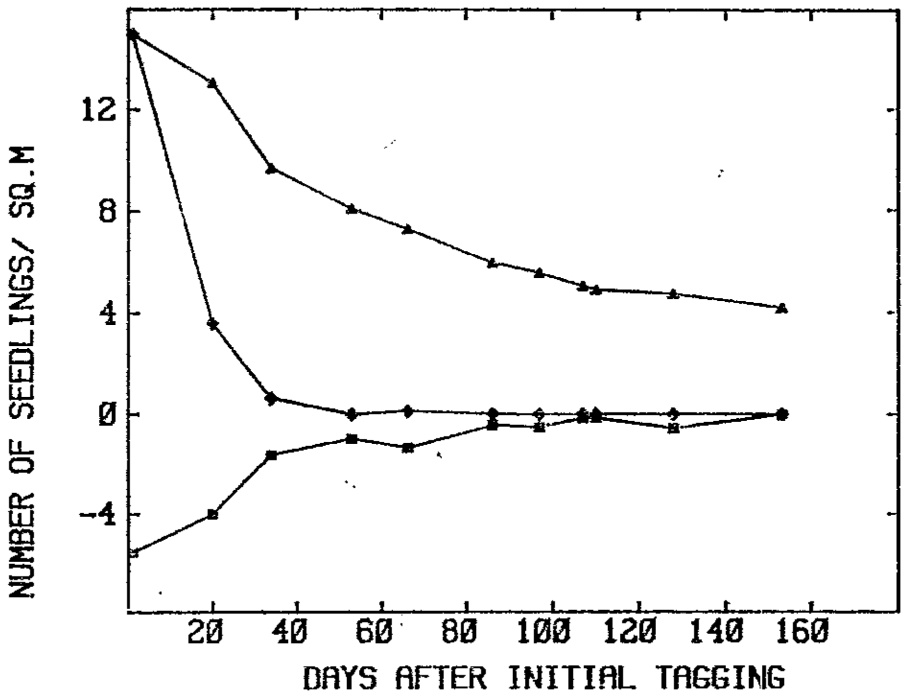
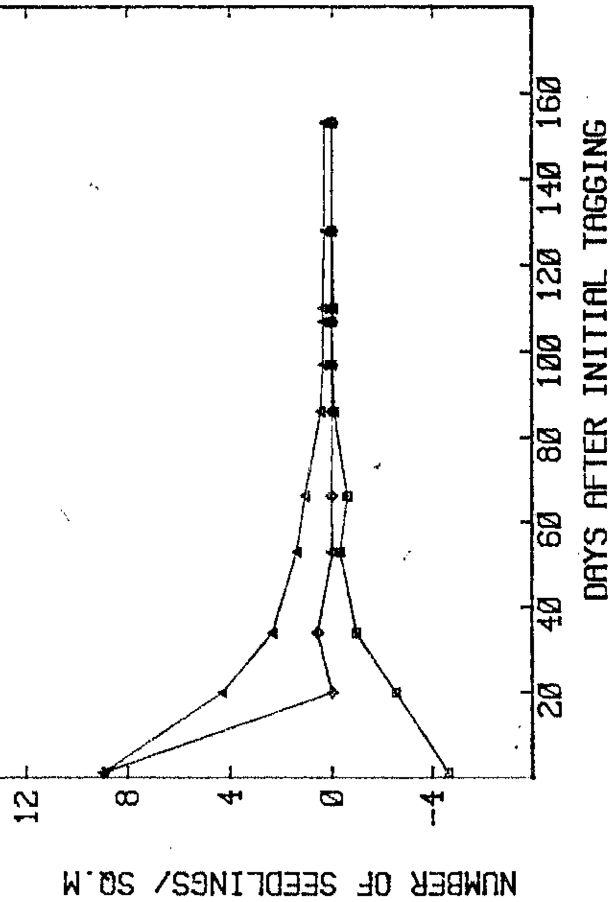


Figure 14. Population flux of the 1986 striped maple seedlings in Plot 4 at Mt. Misery. (▲ = number of live plants; ◆ = newly germinated seedlings; ■ = number of dead seedlings.)



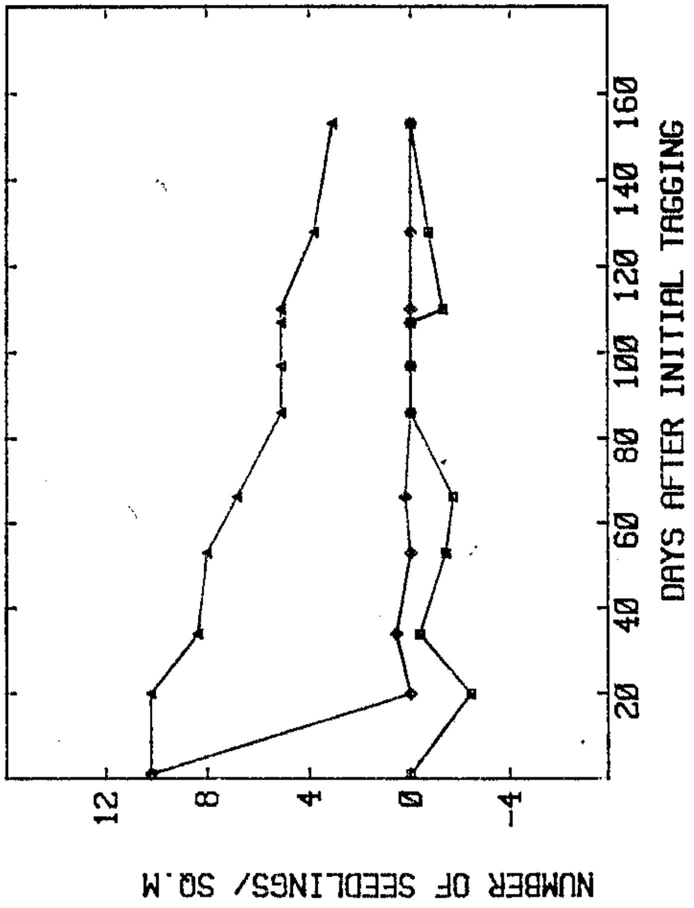
1986 POPULATION FLUX- PLOT 4

Figure 15. Population flux of the 1986 striped maple seedlings in Plot 17 at Mt. Misery. (▲= number of live plants; ◆ = newly germinated seedlings; ■ = number of dead seedlings.)



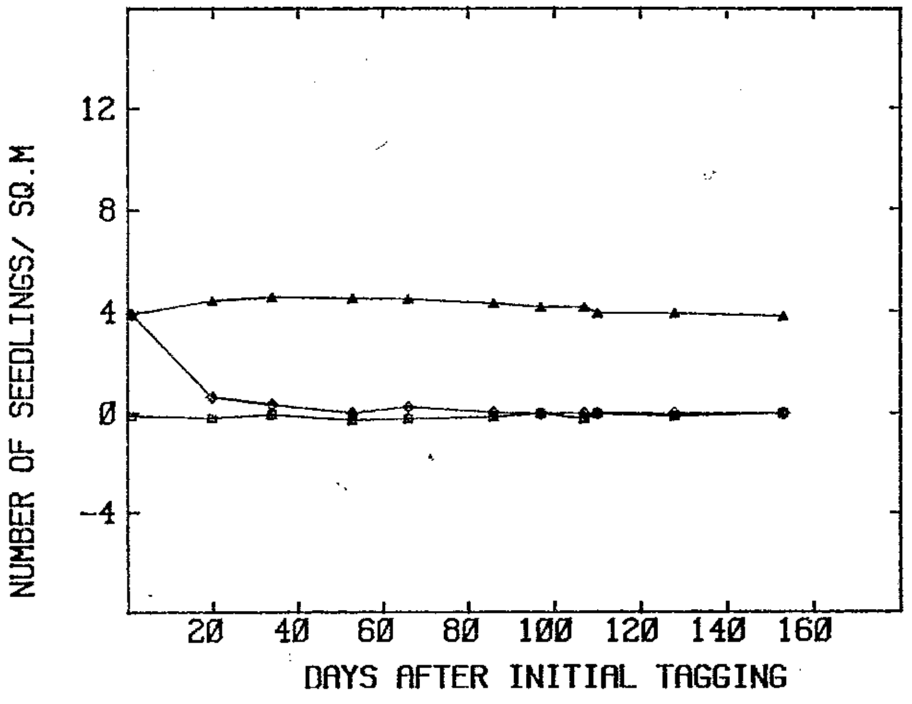
1986 POPULATION FLUX- PLOT 17

Figure 16. Population flux of the 1986 striped maple seedlings in Plot D2 at Mt. Misery. (▲= number of live plants; ◆ = newly germinated seedlings; ■ = number of dead seedlings.)



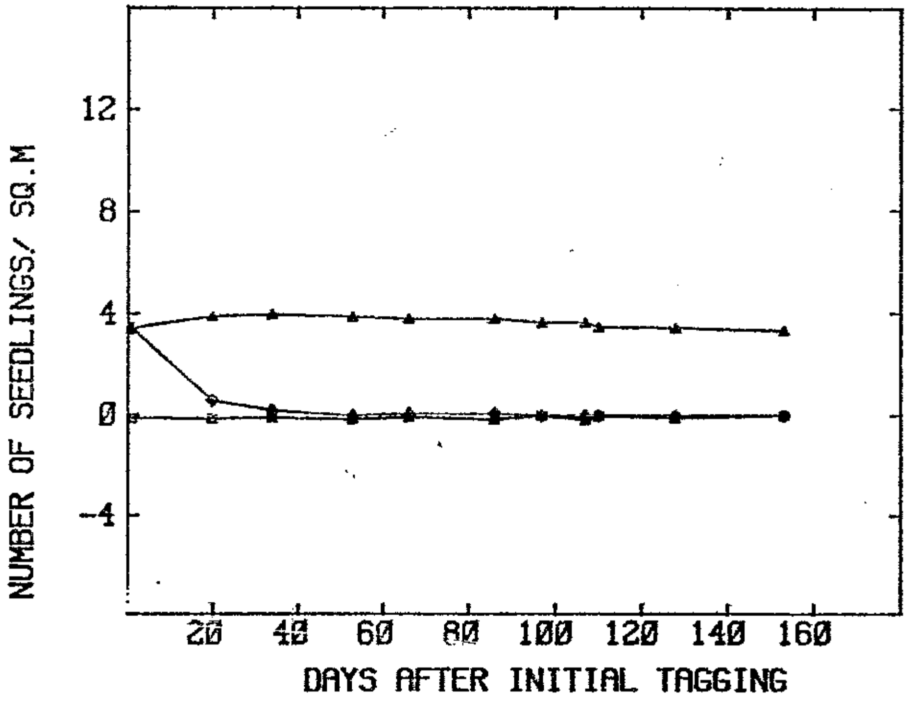
1986 POPULATION FLUX- PLOT D2

Figure 17. Population flux of the 1986 striped maple seedlings in Plot T3 at Mt. Misery. (▲= number of live plants; ◆ = newly germinated seedlings; ■ = number of dead seedlings.)



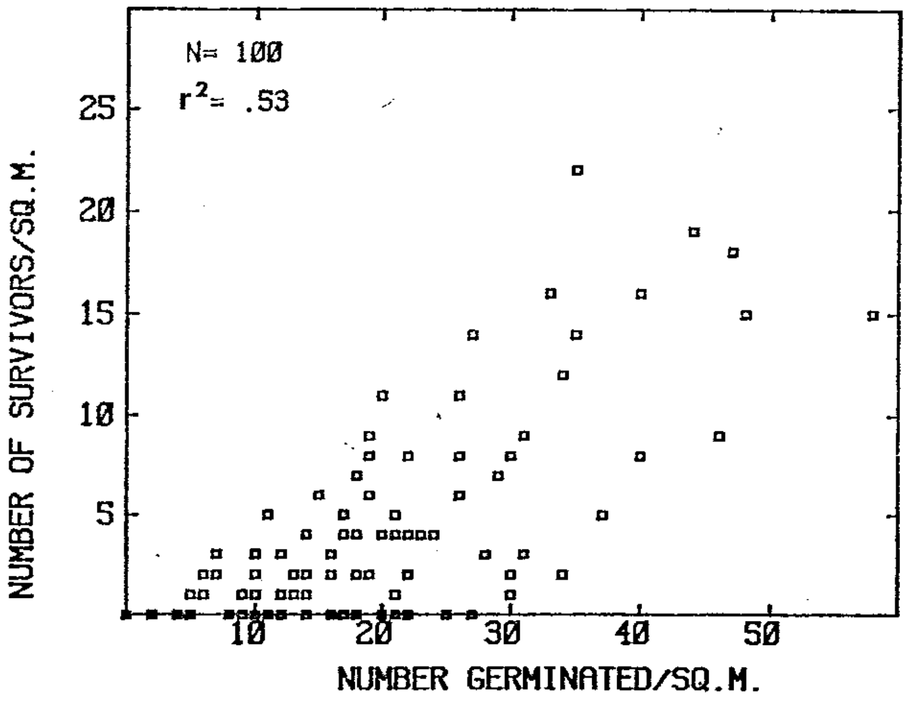
1986 POPULATION FLUX- PLOT T3

Figure 18. Population flux of the 1986 striped maple seedlings in Plot T10 at Mt. Misery. (▲ = number of live plants; ◆ = newly germinated seedlings; ■ = number of dead seedlings.)

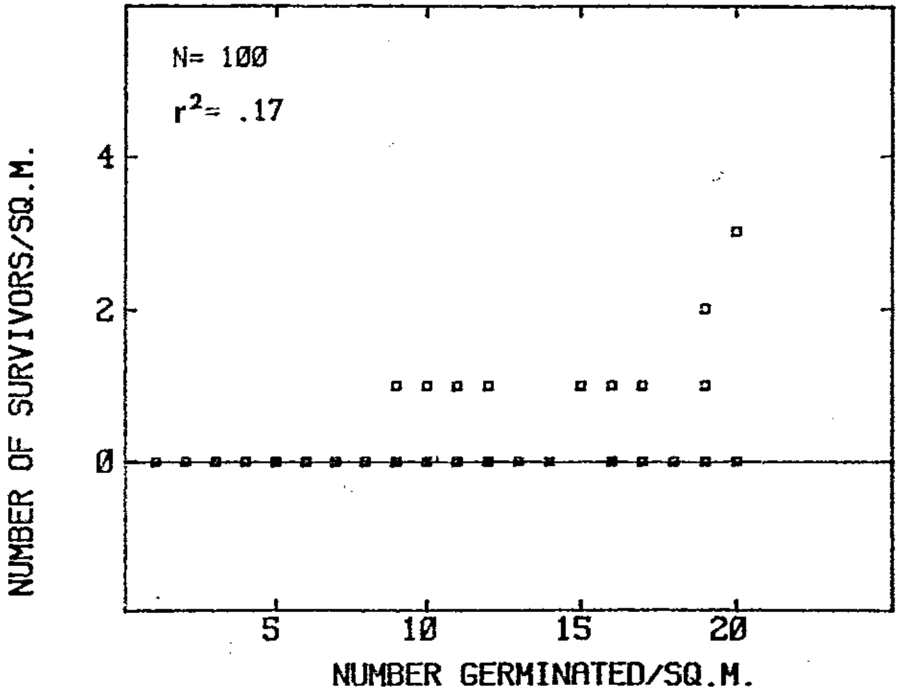


1986 POPULATION FLUX- PLOT T10

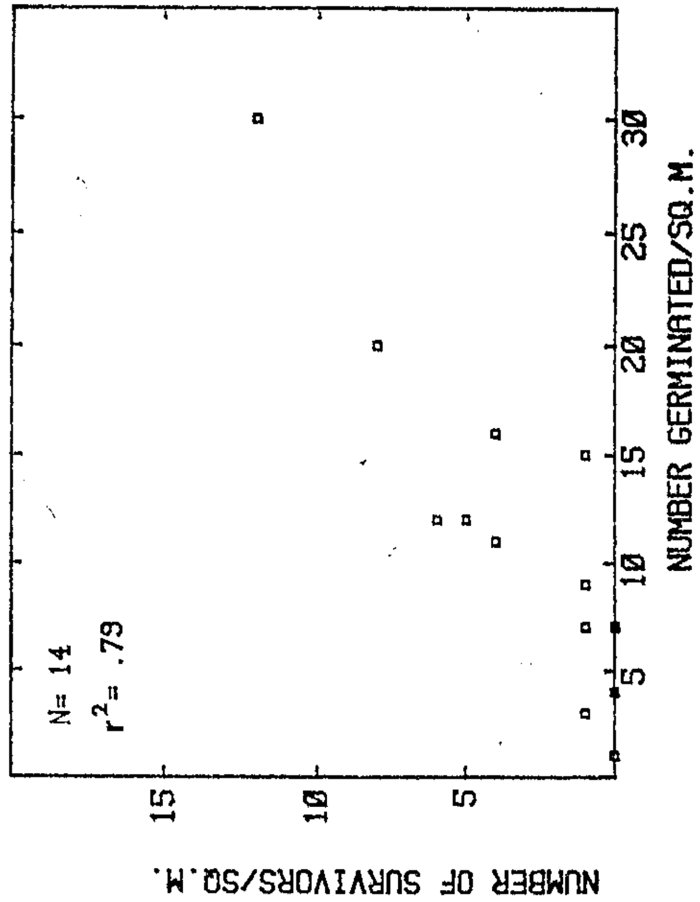
Figure 19a-e. Scatter plots of germination and survival of striped maple seedlings in 1986 in 5 study plots at Mt. Misery.



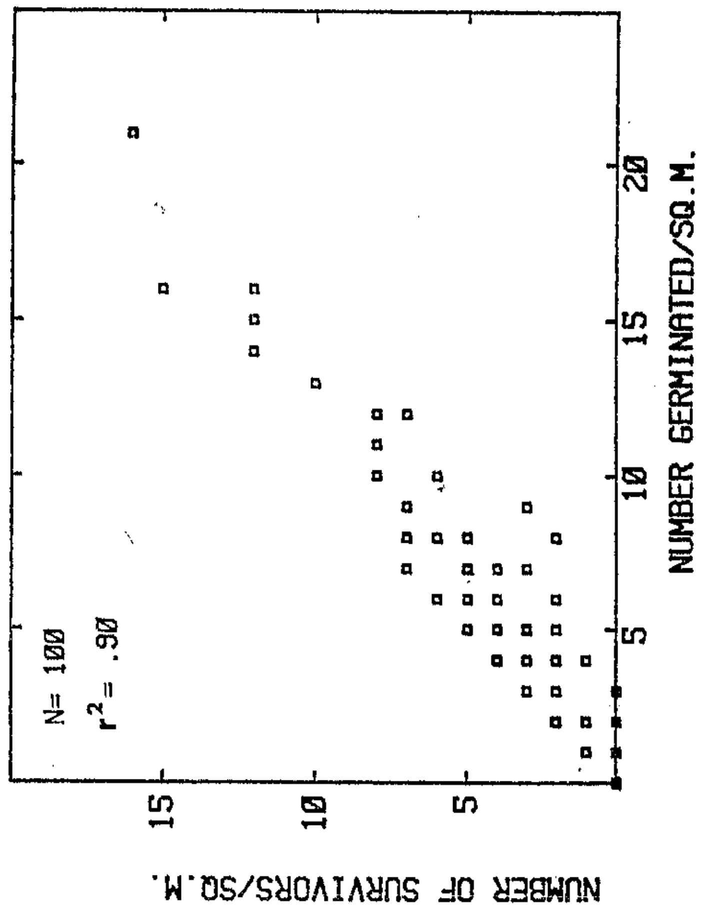
1986 POPULATION FLUX- PLOT 4



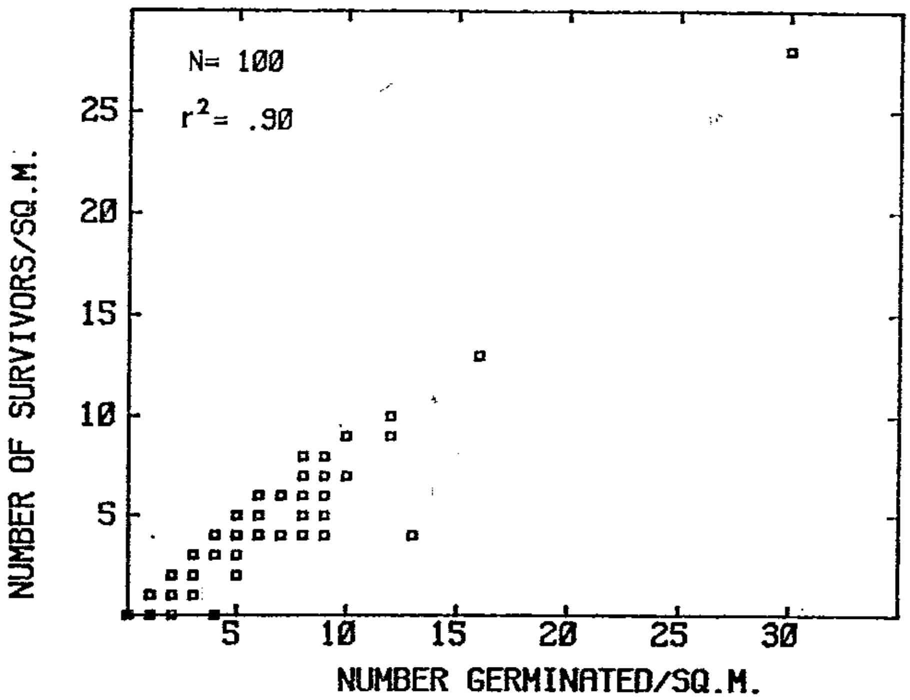
1986 POPULATION FLUX- PLOT 17



1986 POPULATION FLUX- PLOT D2

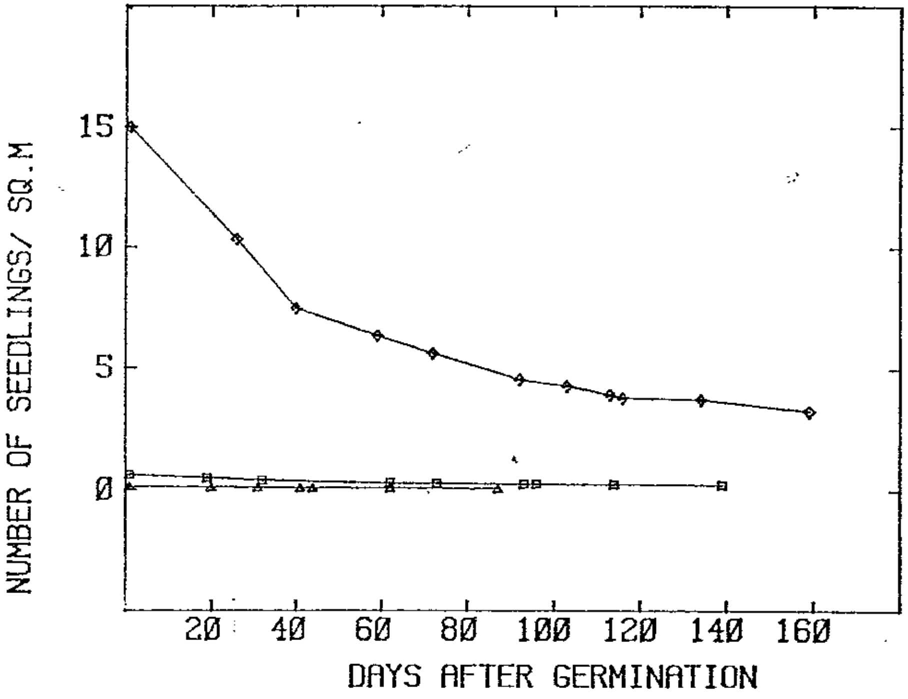


1986 POPULATION FLUX- PLOT T3

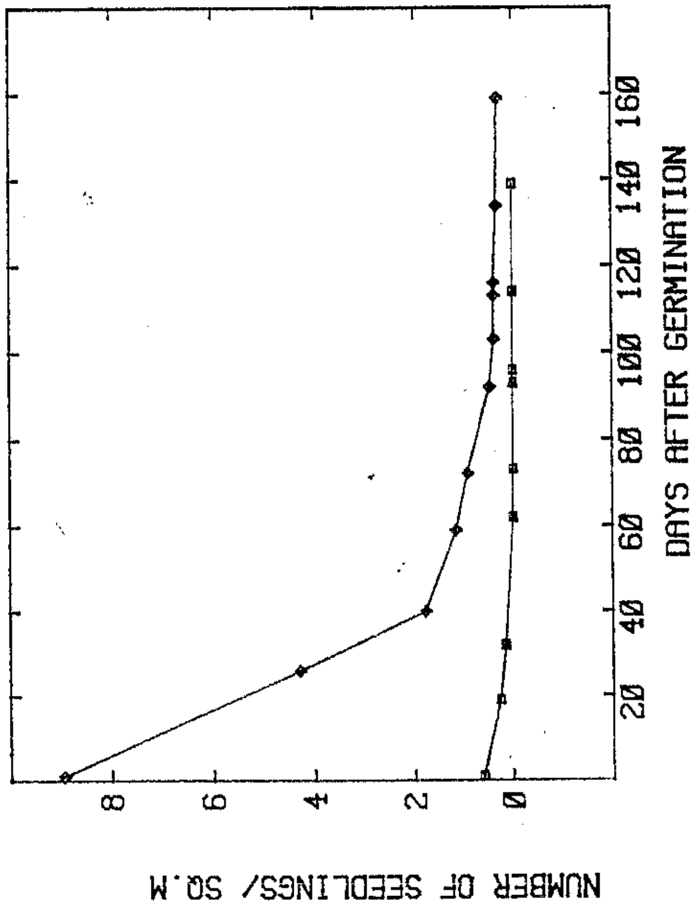


1986 POPULATION FLUX- PLOT T10

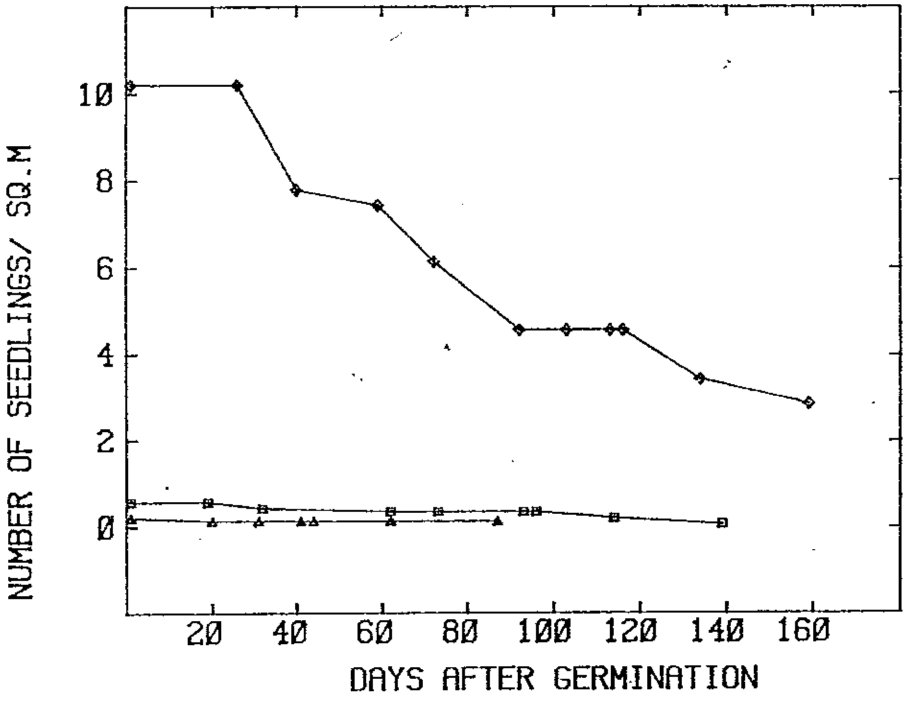
Figure 20. Mortality rates of early- (◆), mid- (■), and late- (▲) season cohorts in (a) Plot 4, (b) Plot 17, (c) Plot D2, (d) Plot T3, and (e) Plot T10.



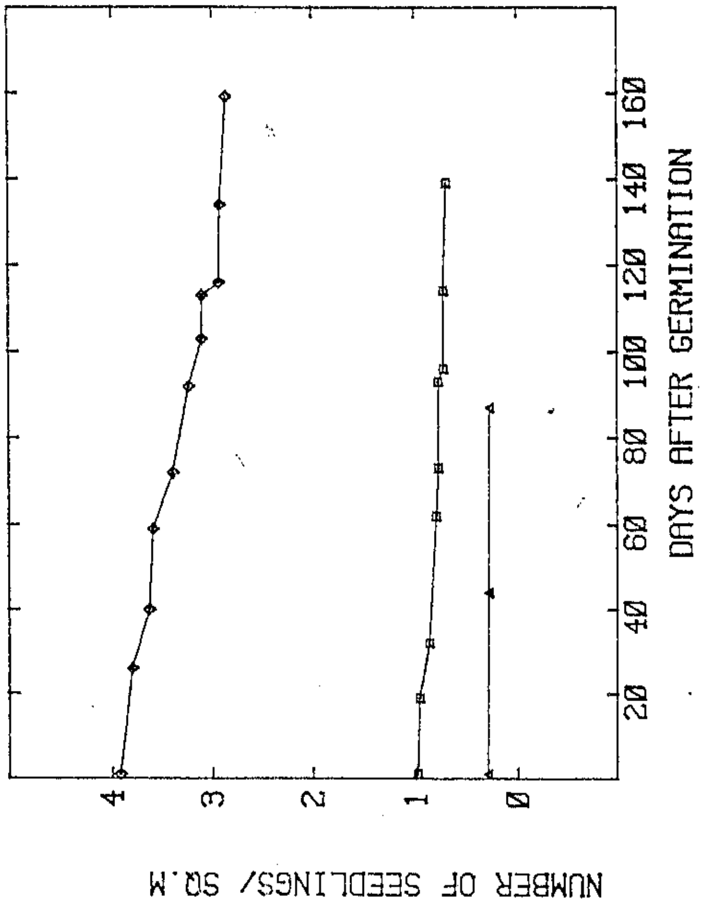
COHORT MORTALITY- PLOT 4



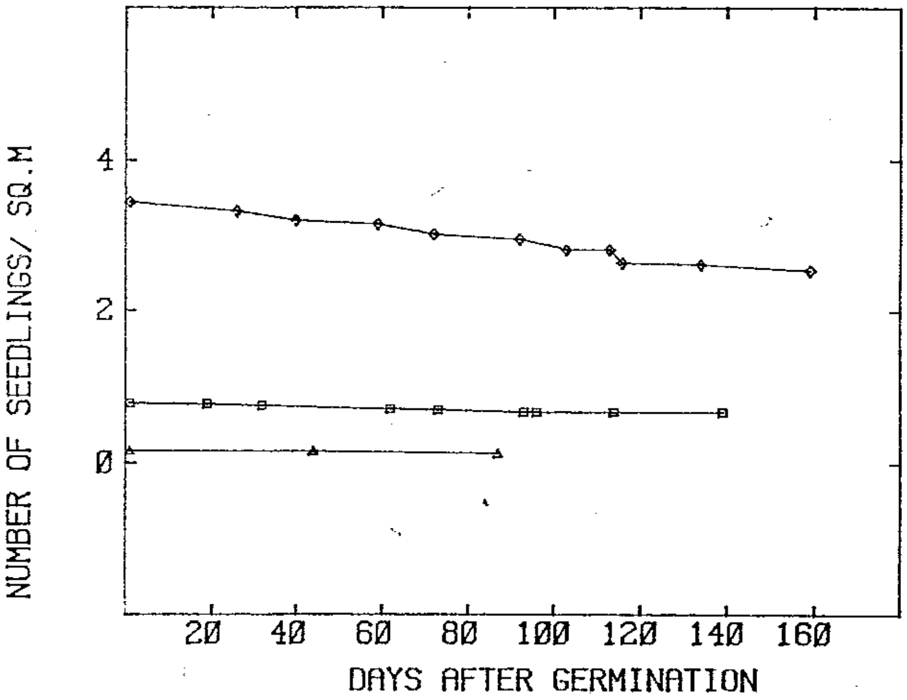
COHORT MORTALITY- PLOT 17



COHORT MORTALITY- PLOT D2

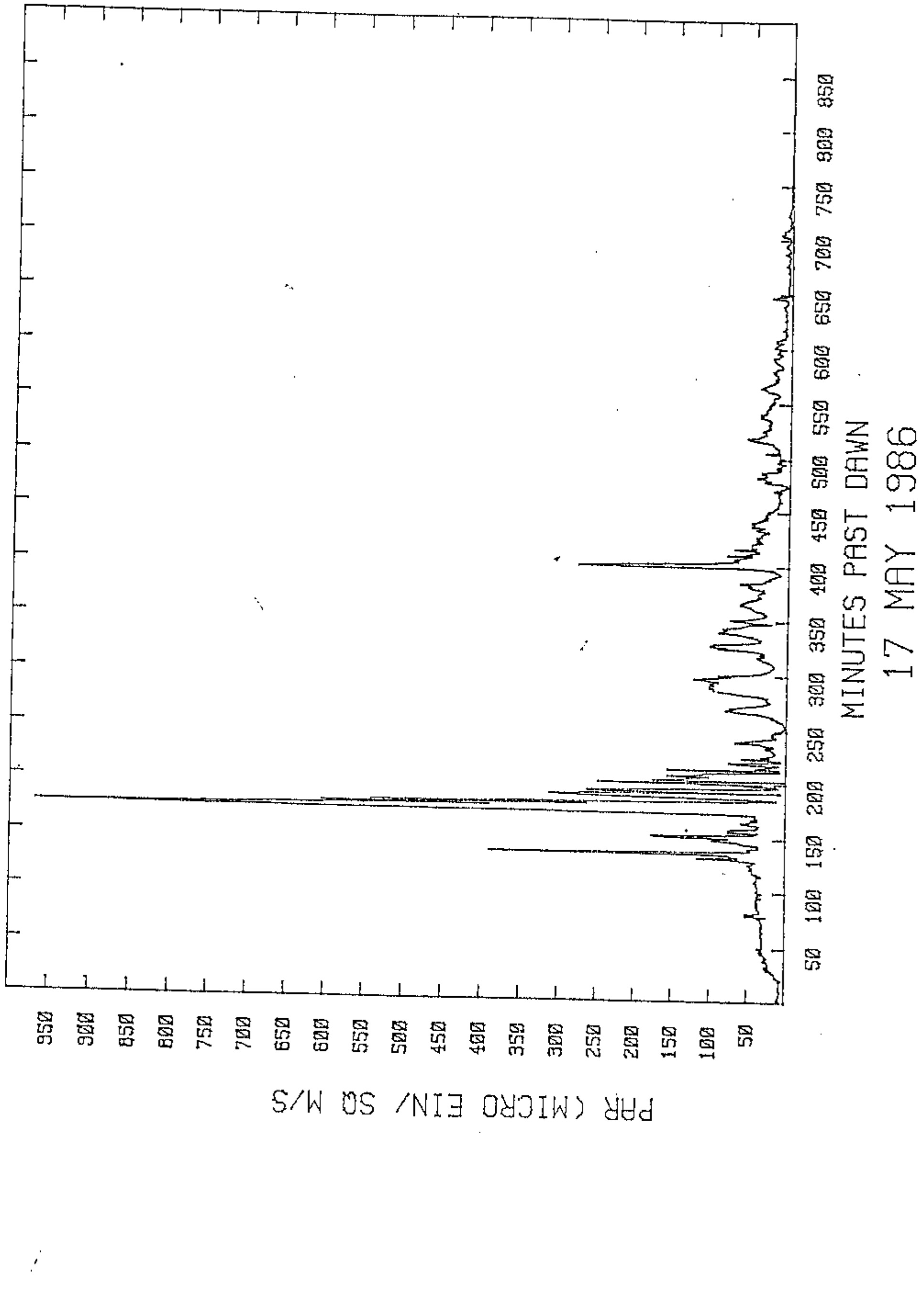


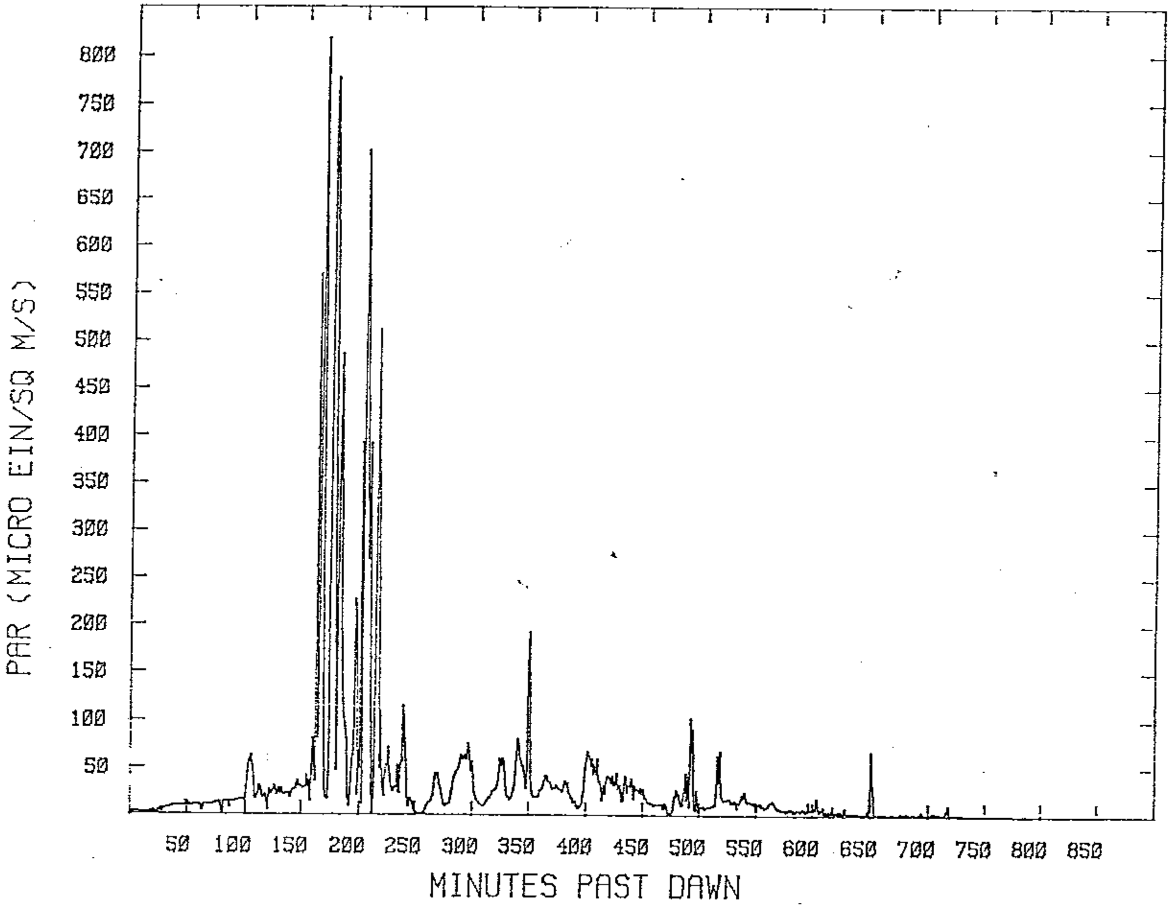
COHORT MORTALITY- PLOT T3



COHORT MORTALITY- PLOT T10

Figure 21. PAR ($\mu Em^{-2}s^{-1}$) measured from dawn to dusk on 17 May 1986 (a) in the gap center and (b) at the gap edge in Plot 4.


PAR (MICRO EIN/ SQ M/S
50
100
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
900
950
50
100
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
MINUTES PAST DAWN
17 MAY 1986


PAR (MICRO EIN/SQ M/S)
800
750
700
650
600
550
500
450
400
350
300
250
200
150
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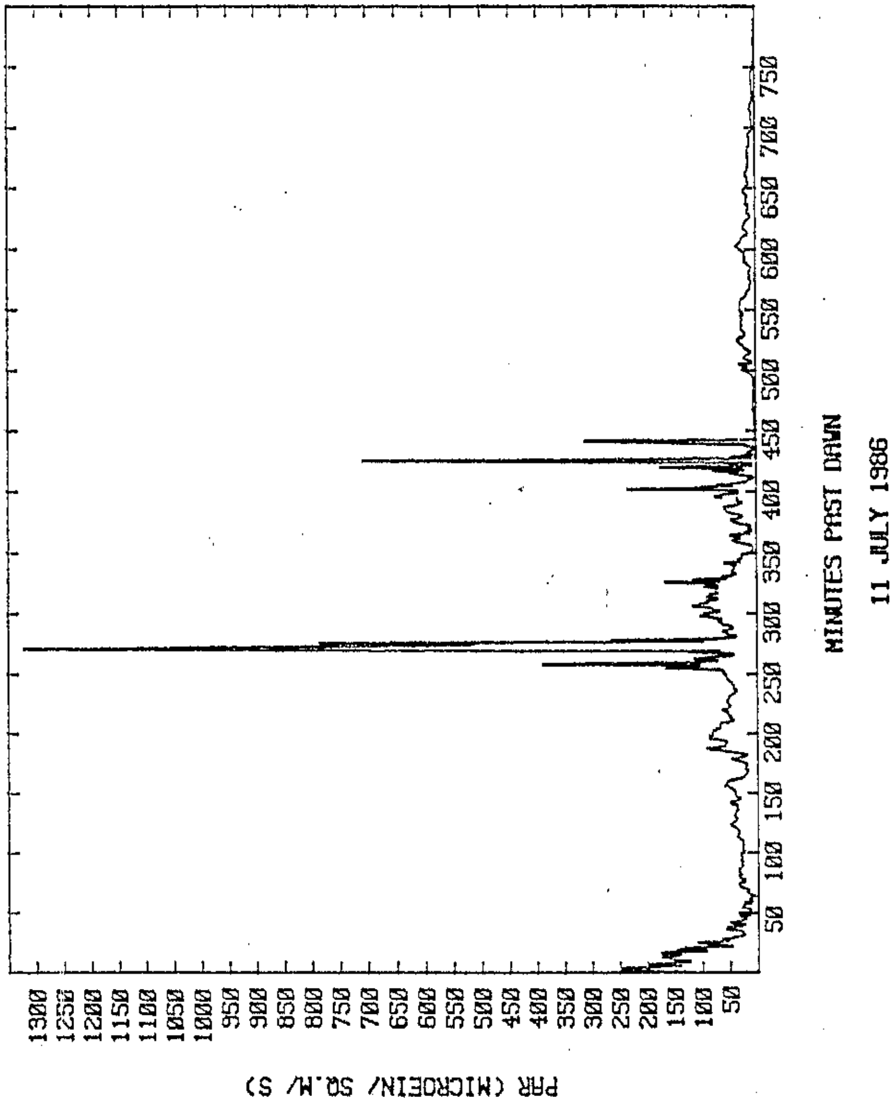
50
50
100
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
MINUTES PAST DAWN

17 MAY 1986

Figure 22. PAR ($\mu E m^{-2} s^{-1}$) measured from dawn to dusk on 11 July 1986 (a) in the gap center and (b) at the gap edge in Plot 4.


PAR (MICROEIN/ SQ.M/ S)
1300
1250
1200
1150
1100
1050
1000
950
900
850
800
750
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550
500
450
400
350
300
250
200
150
100
50
50
100
150
200
250
300
350
400
450
500
550
600
650
700
750
MINUTES PAST DAWN
11 JULY 1986

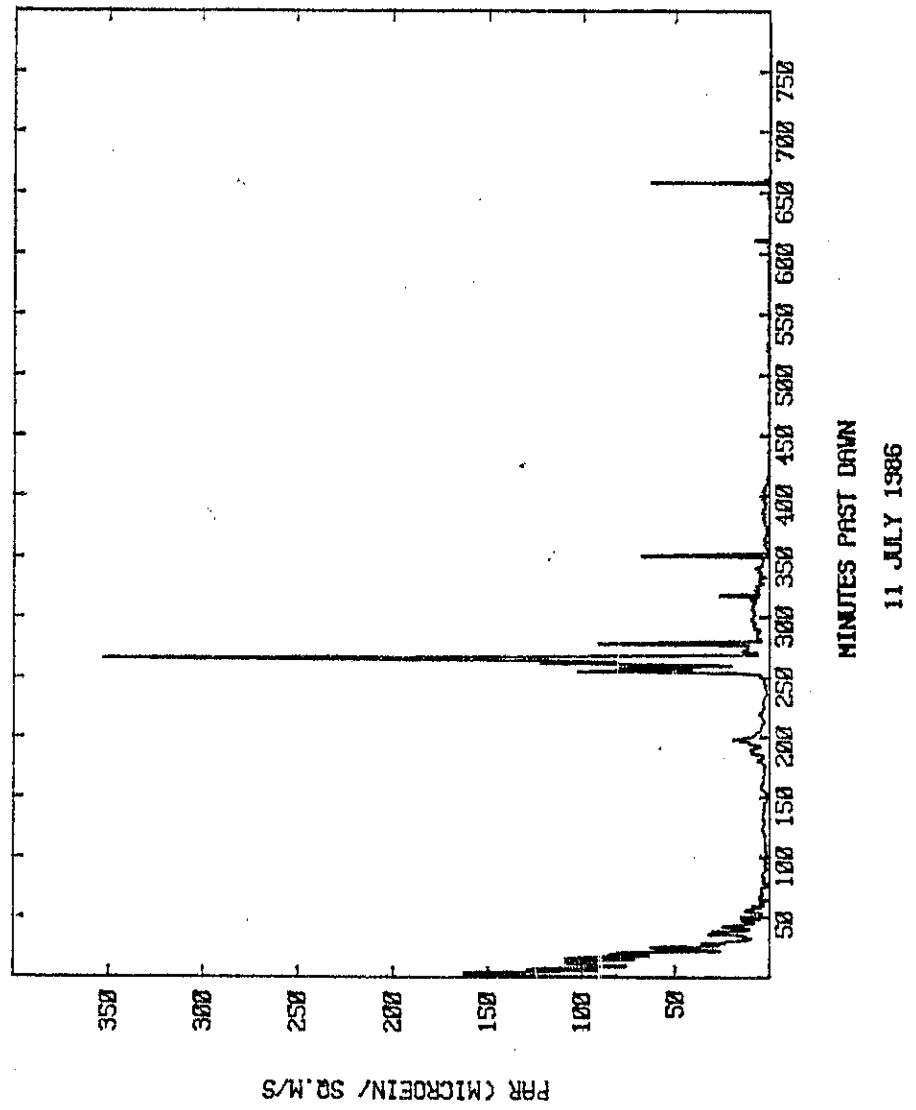
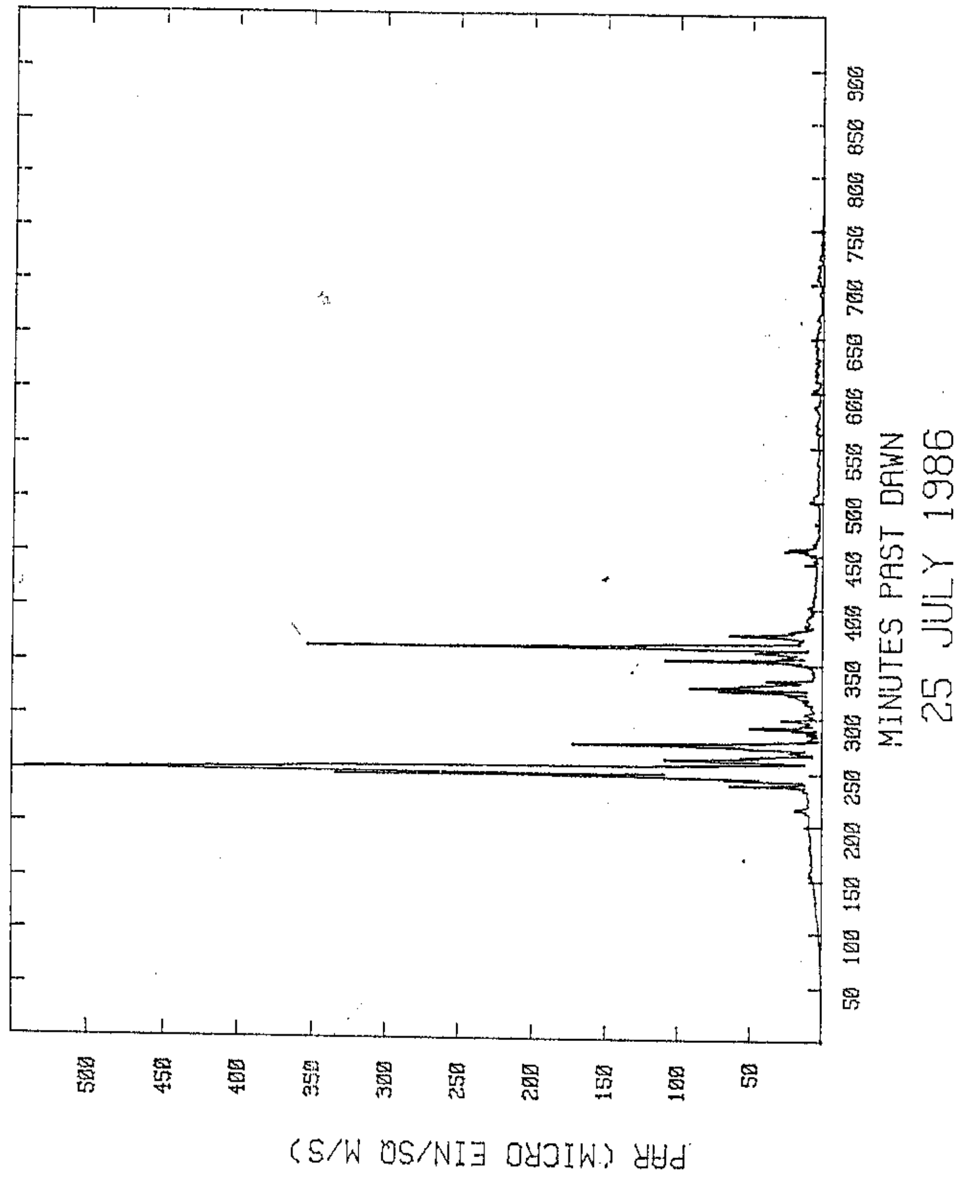
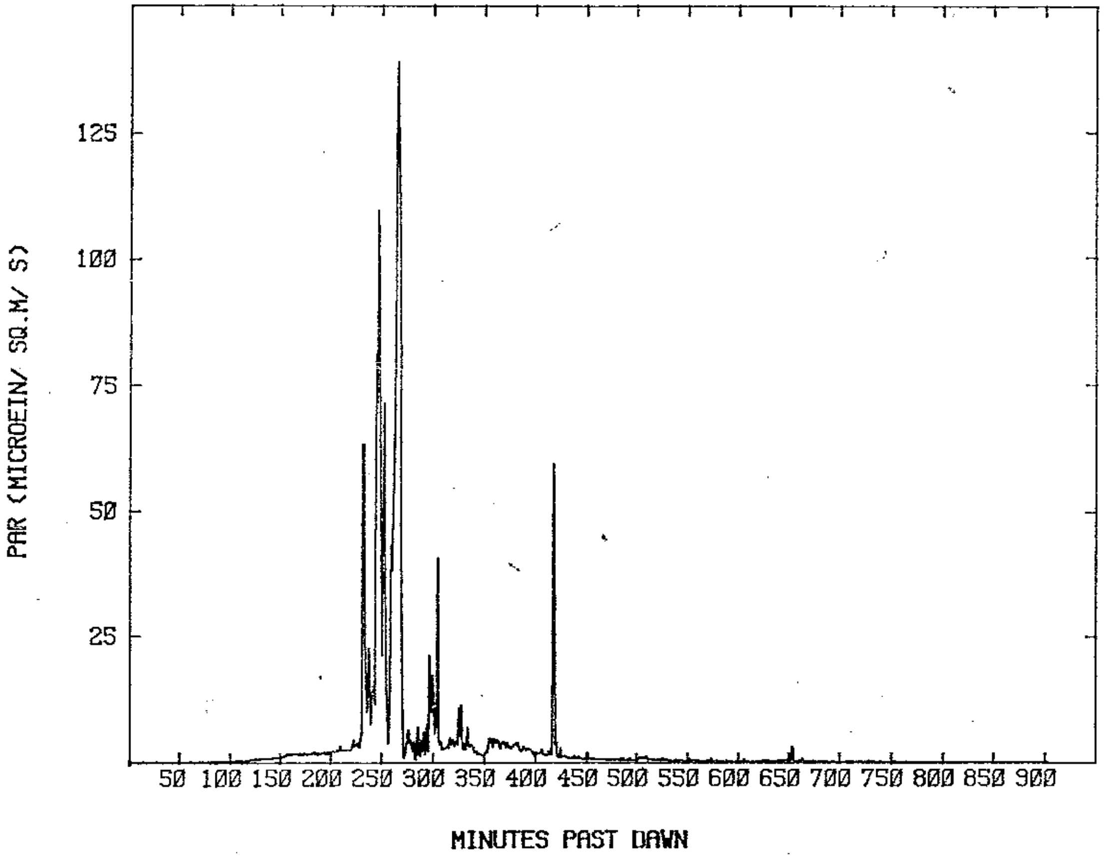

PAR (MICROEIN/ SQ.M/S
350
300
250
200
150
100
50
50
100
150
200
250
300
350
400
450
500
550
600
650
700
750
MINUTES PAST DAWN
11 JULY 1986

Figure 23. PAR ($\mu Em^{-2}s^{-1}$) measured from dawn to dusk on 25 July 1986 (a) in the gap center and (b) at the gap edge in Plot 4.



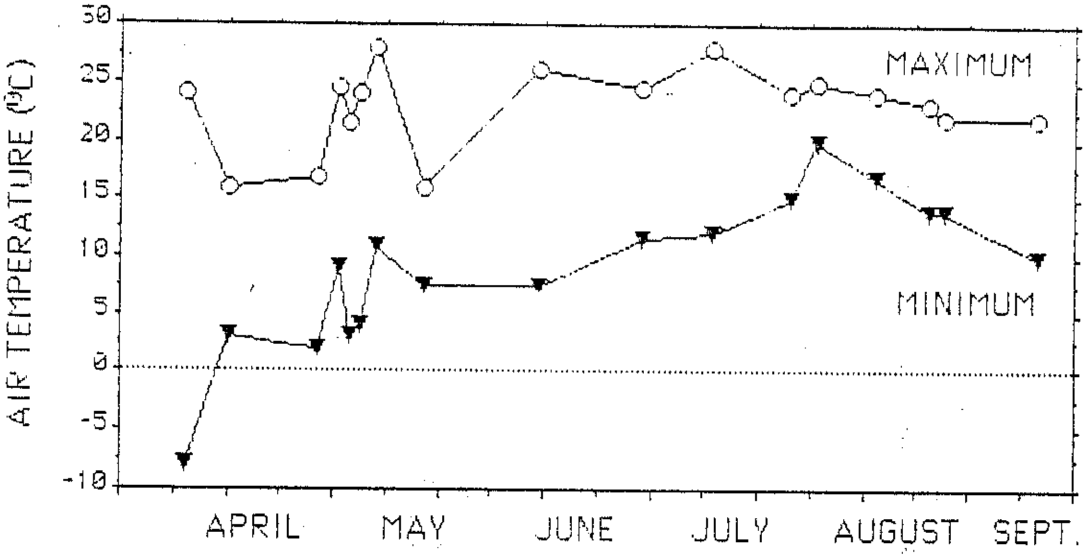
25 JULY 1986
MINUTES PAST DAWN
50
100
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
900
PAR (MICRO EIN/SQ M/S)
50
100
150
200
250
300
350
400
450
500


PAR (MICROEIN/ SQ.M/ S)
125
100
75
50
25
50 100 150 200 250 300 350 400 450 500 550 600 650 700 750 800 850 900
MINUTES PAST DAWN

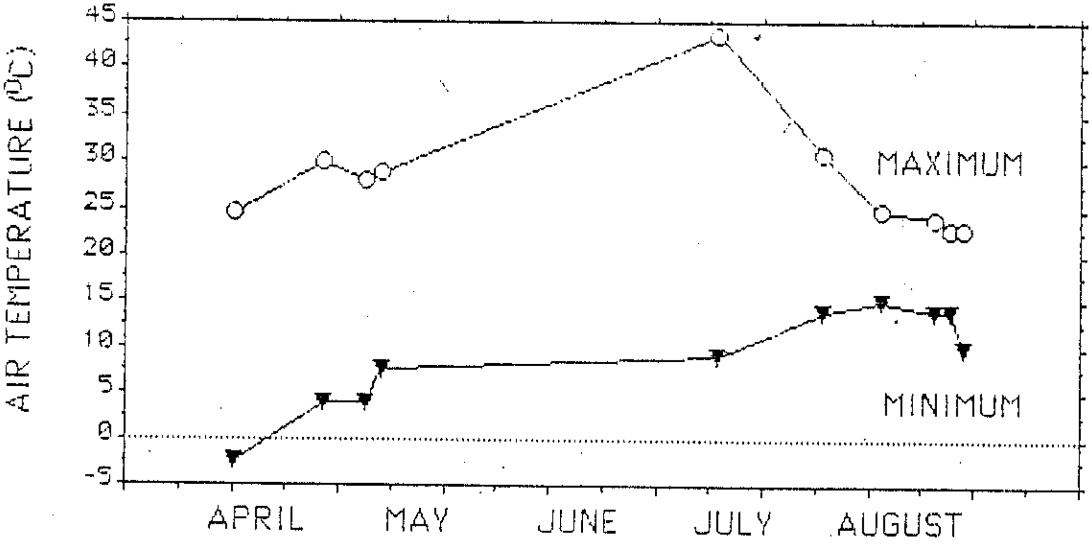
25 JULY 1986

Figure 24. Seasonal minimum and maximum air temperatures for the a) lower and b) upper Mt. Misery study sites.

(a)


AIR TEMPERATURE (°C)
30
25
20
15
10
5
0
-5
-10
MAXIMUM
MINIMUM
APRIL
MAY
JUNE
JULY
AUGUST
SEPT.

(b)


AIR TEMPERATURE (°C)
45
40
35
30
25
20
15
10
5
0
-5
MAXIMUM
MINIMUM
APRIL
MAY
JUNE
JULY
AUGUST