NEIGHBOR EFFECTS IN MAST YEAR SEEDLINGS OF ACER SACCHARUM

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ABSTRACT

The size and age distributions of Acer saccharum Marsh. seedlings were studied in a mature hardwood forest in southeastern Ontario between 26 June and 26 September 1986. Ninety-one percent of the seedlings surveyed were produced in 1984 which was a mast year for this population of sugar maple. Mean height within quadrats was negatively correlated with the density of two-year-old seedlings in the first half of the sampling period, suggesting that competition may be an important factor affecting seedling size. A significant positive correlation in the second half of the sampling period, however, suggested a temporal shift in the pattern of seedling growth in which the shorter, more suppressed seedlings under the higher densities had increased their relative height in response to earlier competition. The sum of the heights of pairs of nearest neighboring seedlings sampled over the survey period was negatively correlated with the distance between them. The sum of the biomasses of pairs of nearest neighboring seedlings collected in October 1986, however, was positively correlated with the distance between them. Variation in the height of two-year-old seedlings was unaffected by light intensity but was to some extent accounted for by soil variables, and total percent cover of other species. The density of the two-year-old seedlings, however, accounted for the largest percentage of the variation in their mean height. The data suggest that competition between the seedlings derived from mast seeding in 1984 may represent an important component of the process of natural selection affecting this population.

Masting in trees has been proposed as an adaptive mechanism for predator avoidance. The periodic production of unusually large seed crops and subsequent poor seed crops may provide an effective defensive strategy in which predators are alternately satiated and starved (Janzen, 1971; Silvertown, 1980; Jensen, 1982; Crawley, 1983; Enoksson and Nilsson, 1983; Fenner, 1985). The spacing of mast years represents a compromise between the need to reduce predation and the need to maximize the opportunity for reproduction. Reproductively mature organisms which skip potential breeding seasons will generally have a lower fitness than those which reproduce at every opportunity (Bull and Shrine, 1979; Waller, 1979). In order for masting to be adaptive, there must be a greater proportion of seeds produced during mast years that survive to the adult stage. In Pinus albicaulis (Hutchins and Lanner, 1982) and Carya glabra (Sork and Boucher, 1977; Sork, 1983) for example, seed predation in nonmast years is so intense that significant recruitment is thought to be virtually confined to mast year cohorts.

The high seedling densities associated with masting will mean that those cohorts which generally have the highest probability of recruitment into the next generation (due to predator avoidance through satiation) will also experience the most intense competition with neighbors. The most dramatic neighbor effects among trees result from shading of seedlings by canopy trees (Peet and Christensen, 1987). The intense competition at the seedling stage among mast year cohorts however, may involve both above- and belowground neighbor effects and may represent an important component of the process of natural selection affecting these species. The actual process of competition in nature, like most forces of natural selection, can rarely be measured directly. A significant positive correlation between plant size and distance to nearest neighbor, however, provides convincing circumstantial evidence of competition between neighboring individuals (e.g., Pielou, 1960, 1961, 1962; Yeaton and Cody, 1976; Yeaton, Travis, and Gilsinsky, 1977; Inouye, Byers, and Brown, 1980; Fonteyn and Mahall 1981; Phillips and MacMahon, 1981) and enables measurement of both the intensity and importance (relative to other selection pressures) of competition un-

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nder natural conditions (Welden and Slauson, 1986).

No previous attempt has been made to document evidence for competition affecting plant size among tree seedlings resulting from mast seeding. The purpose of this study, therefore, was to search for evidence of neighbor effects in terms of variation in size in two-year-old seedlings of *Acer saccharum* Marsh. (sugar maple) that had resulted from masting within a mature population of sugar maple in southeastern Ontario in 1984. The sizes of mast-year seedlings were related to density, proximity to neighbors, soil variables, light availability, and abundance of other species.

**MATERIALS AND METHODS—Study species—** *Acer saccharum* Marsh. (sugar maple) is one of the largest and most important hardwoods in northeastern United States and Canada (Fowells, 1965). The tree flowers in the spring and the fruit ripens in about twelve weeks. Seeds fall in late October to November and germinate the following spring. Seeding mortality may be very high; Fowells (1965) reported that as little as 50% of new seedlings may survive the first year. The causes of mortality at either the seed or seedling stage however, are not well documented (Hett and Loucks, 1971). The seedlings are extremely tolerant of shade and may remain suppressed for many years in the shade of mature trees and still show a strong response to release (Fowells, 1965). Large fluctuations in yearly seed crop are characteristic of the species (Hett, 1971). A mast year for sugar maple occurred at the study site in 1984.

**Study site**—The study site was a 10-hectare woodland located on the property of the Queen's University Biology Station at Lake Opinicon in southeastern Ontario, Canada (44°34′02″N, 76°21′52″W). The area was logged in the last century, but the study site has since been free of any major disturbance from human activity. The site was bordered by the Opinicon Road on the north and a laneway on the east, west, and south, connected to the Opinicon Road at both ends. Sugar maple was the dominant tree species on the site. Less abundant canopy species included *Fraxinus americana* L., *Ostrya virginiana* (Mill.) K. Kock, and *Carya cordiformis* (Wang.) K. Koch.

**Field survey**—Most seedlings become established beneath the canopy of parent trees. Accordingly, 14 sugar maple trees within the population were randomly selected as sampling sites. Only trees with diameter at breast height (DBH) greater than 40 cm were chosen. The north, south, east, and west orientation of each of these trees was located with a hand compass, and the limit of the canopy in each compass direction was projected down to the ground by visual estimation and marked with a flag. These four points were connected by a meter tape to delimit a four-sided polygon. Quadrats, 1.0 m × 0.5 m, were placed randomly at one-, two-, or three-meter intervals along the perimeter of the polygon. If the positioning of a randomly placed quadrat was prevented by the presence of trees greater than 0.5 meters high, it was shifted to the next closest interval along the meter tape. A total of 185 quadrats were surveyed within the polygons of the selected trees between 26 June and 26 September 1986.

For each quadrat the following data were collected: age, height, and leaf number of each maple seedling or sapling less than 50 cm high, light intensity; soil magnesium, phosphorus, and potassium concentration, and pH; and percentage cover of herbaceous plants and non-maple tree seedlings.

The seedlings were aged by counting the annual bud scale scars. Light intensity was measured using a light meter (General Electric, Model 214) on cloudless days between 11 AM and 1 PM and expressed as a percentage of full sunlight. Five measurements of light intensity were recorded per quadrat—one at the center and one at each of the four corners. A single soil sample was collected from the center of each quadrat. The soil samples were sent to Agri-Food Laboratories Canada at Guelph for analyses. The percent cover of other species was estimated visually using a grid to partition the quadrat into smaller sections, each comprising 4% of the total quadrat area.

Within each quadrat, four two-year-old maple seedlings were randomly selected. The height and leaf number were recorded for each seedling and for its nearest neighbor. The distance between the neighboring seedlings was also recorded. A total of 638 neighboring seedling pairs were included.

**Seedling harvest**—In mid-October, the heights of 100 randomly selected two-year-old sugar maple seedlings and their nearest two-year-old neighbors were recorded as well as the distance between them. The seedlings were dug up, washed free of soil and debris, dried at 100 C to constant final weight, and weighed.

**Data analyses**—Product-moment correlation coefficients were calculated for variables recorded in the quadrat surveys. The relationship between the seedling height distribution...
of two-year-old sugar maple seedlings and seedling density (per quadrat) was determined from the correlation of the Gini coefficient (Weiner and Solbrig, 1984) for seedling height with quadrat density. The Gini coefficient is a measure of size inequality and ranges from 0 (when all individuals are of equal size) to a theoretical maximum of 1.0 in an infinite population where all individuals but one have a size of zero: the ultimate inequality (Weiner and Solbrig, 1984).

Forward, backward, and stepwise multiple linear regressions (SAS Institute, 1985) were used to select independent quadrat variables producing a significant regression model accounting for the most variation in the dependent variable, mean height of two-year-old maple seedlings. The independent variables tested included density of two-year-old seedlings, density of seedlings greater than two years old, total percent cover of other species, light intensity and soil variables (P, K, Mg, and pH), for each quadrat. Interactions between density of two-year-old seedlings and each of the other variables were also considered. The interaction of pH and two-year-old seedling density was omitted from the final regressions because of colinearity in the data.

The neighbor data were analyzed by product-moment correlations of the sum of the target’s and its nearest neighbor’s height or biomass (for the harvested seedlings) vs. the distance between the two neighbors (after Pielou, 1960).

**RESULTS**—A total of 10,038 sugar maple seedlings were aged. The two-year-old seedlings were produced in 1984 and represented 91% of the total number of seedlings. In the first four sites, seedlings greater than two years old were grouped into age classes (3–5, 6–10, 11–15, 16–20, and >20 years old). Seedlings for all other sites (5–14) were aged accurately by year. Figure 1 illustrates the age distribution of the accurately aged seedlings (N = 6,669). Two other relatively large cohorts were apparently produced in 1978 and 1976 (Fig. 1).

Correlations among variables recorded in the quadrat surveys are given in Table 1. Number of leaves on the two-year-old maple seedlings was positively correlated with potassium (P < 0.01), negatively correlated with sampling date (P < 0.001), and positively correlated with total percent cover of other species (P < 0.001) (Table 1). The density of two-year-old (mast year) sugar maple seedlings had a significant negative correlation with pH (P < 0.001), sampling date (P < 0.01), and total percent cover of other species (P < 0.01). The soil variables phosphorus, potassium, and magnesium were all negatively correlated (P < 0.001) with sampling date and were all positively correlated with each other (P < 0.001, P < 0.05, P < 0.001). Phosphorus was negatively correlated (P < 0.01) with density of sugar maple seedlings greater than two years old. Potassium was positively correlated (P < 0.001) with total percent cover of other species. Soil pH was positively correlated with potassium (P < 0.01) and with magnesium (P < 0.001). Light intensity had a significant positive correlation (P < 0.05) with magnesium (Table 1).

Figure 2 compares the correlations between mean height per quadrat and density of two-year-old maple seedlings for different intervals of the sampling period. In the first quarter, 26 June–7 July 1986, there was a significant negative correlation (P < 0.01) between mean seedling height and density per quadrat (Fig. 2a). A significant negative correlation (P < 0.001) between mean seedling height and density was also detected for the first half of the sampling period (26 June–31 July 1986) (Fig. 2b). In the second half of the sampling period, however, this relationship was significantly positive (P < 0.01) (Fig. 2c). For the last quarter of the sampling period the correlation was not significant (P > 0.05) (Fig. 2d). The Gini coefficient for seedling height (calculated for each quadrat) was positively correlated (r = 0.125) with seedling density, but this was not significant (P = 0.09).

The multiple regression models for each of the sampling intervals were highly significant (Table 2). The model for the first quarter of
<table>
<thead>
<tr>
<th>Leaf number</th>
<th>Density 2 yr</th>
<th>P</th>
<th>K</th>
<th>Mg</th>
<th>pH</th>
<th>Date</th>
<th>Percent cover</th>
<th>Light intensity</th>
<th>Density &gt;2 yr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height</td>
<td>0.03304</td>
<td>-0.01204</td>
<td>-0.03480</td>
<td>-0.00970</td>
<td>-0.06742</td>
<td>-0.02868</td>
<td>0.05559</td>
<td>0.00931</td>
<td>0.04615</td>
</tr>
<tr>
<td>0.6552</td>
<td>185</td>
<td>0.8708</td>
<td>0.6400</td>
<td>0.7703</td>
<td>0.8963</td>
<td>0.3645</td>
<td>0.6984</td>
<td>0.4524</td>
<td>0.9084</td>
</tr>
<tr>
<td>Leaf number</td>
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<td>0.00088</td>
<td>0.19420</td>
<td>0.11772</td>
<td>-0.03324</td>
<td>-0.30162</td>
<td>0.25386</td>
<td>0.00123</td>
<td>-0.04309</td>
</tr>
<tr>
<td>0.0937</td>
<td>185</td>
<td>0.9906</td>
<td>0.0084**</td>
<td>0.1125</td>
<td>0.6551</td>
<td>0.0001***</td>
<td>0.0005**</td>
<td>0.9879</td>
<td>0.5603</td>
</tr>
<tr>
<td>Density 2 yr</td>
<td>-0.03745</td>
<td>-0.07883</td>
<td>-0.10361</td>
<td>-0.30052</td>
<td>-0.21119</td>
<td>-0.22936</td>
<td>-0.02294</td>
<td>-0.05928</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>-0.32656</td>
<td>0.17990</td>
<td>-0.01967</td>
<td>-0.30205</td>
<td>-0.08086</td>
<td>0.01623</td>
<td>0.0111**</td>
<td>-0.23993</td>
<td></td>
</tr>
<tr>
<td>K</td>
<td>0.59132</td>
<td>0.21018</td>
<td>0.48761</td>
<td>0.27651</td>
<td>0.14091</td>
<td>0.01200</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mg</td>
<td>0.54459</td>
<td>-0.35627</td>
<td>0.13760</td>
<td>0.18940</td>
<td>0.01120</td>
<td></td>
<td></td>
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<tr>
<td>pH</td>
<td>0.05236</td>
<td>0.00975</td>
<td>0.08427</td>
<td>0.06786</td>
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<td></td>
<td></td>
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<tr>
<td>Date</td>
<td>-0.10953</td>
<td>-0.04986</td>
<td>0.01566</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent cover</td>
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<td>-0.06731</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Light intensity</td>
<td>-0.07645</td>
<td>0.03444</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</table>

* P < 0.05; ** P < 0.01; *** P < 0.001.
the sampling period accounted for the largest percentage of variation in mean seedling height ($r^2 = 0.36$). The regression coefficient for density of two-year-old seedlings was significantly negative for the first quarter ($P < 0.0001$) (Table 2a), and first half ($P < 0.0001$) (Table 2b) of the sampling period. In the second half of the sampling period, density * sampling date interaction and density * potassium interaction were the only significant ($P < 0.05$) independent variables affecting mean seedling height. Seedling density was not significant in the regression model for the fourth quarter of the sampling period. For the total sampling period, density * date interaction had the most significant regression coefficient ($P < 0.0001$) (Table 2e).

There was a highly significant negative correlation between the height of the target seedling and the distance to its nearest neighbor ($r = -0.1475, P = 0.0002, N = 638$ pairs). The negative correlation between the sum of the heights and the distance between target and nearest neighbor was also significant ($r =$
TABLE 2. Results from multiple linear regression analyses of mean height per quadrat of two-year-old sugar maple seedlings for different sampling periods. Independent variables accounting for the greatest amount of variation in seedling height (P values of the regression coefficients <0.01) where included in the models. Independent variables are defined as for Table 1

<table>
<thead>
<tr>
<th>Regression coefficient</th>
<th>( t )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) First quarter (26 June–7 July 1986)</td>
<td>( r^2 = 0.3600 )</td>
<td>( F = 7.686 )</td>
</tr>
<tr>
<td>Density (2 yr)</td>
<td>-0.0137</td>
<td>-3.741</td>
</tr>
<tr>
<td>Mg</td>
<td>-0.0034</td>
<td>-2.509</td>
</tr>
<tr>
<td>Density (2 yr) * %cover</td>
<td>0.0007</td>
<td>1.769</td>
</tr>
<tr>
<td>b) First half (26 June–31 July 1986)</td>
<td>( r^2 = 0.2566 )</td>
<td>( F = 7.249 )</td>
</tr>
<tr>
<td>Density (2 yr)</td>
<td>-0.0334</td>
<td>-4.169</td>
</tr>
<tr>
<td>pH</td>
<td>-0.2579</td>
<td>-1.954</td>
</tr>
<tr>
<td>Density (2 yr) * date</td>
<td>0.0004</td>
<td>2.808</td>
</tr>
<tr>
<td>Density (2 yr) * K</td>
<td>0.0002</td>
<td>2.194</td>
</tr>
<tr>
<td>c) Second half (4 August–26 September 1986)</td>
<td>( r^2 = 0.1933 )</td>
<td>( F = 5.332 )</td>
</tr>
<tr>
<td>K</td>
<td>-0.0163</td>
<td>-1.914</td>
</tr>
<tr>
<td>Density (2 yr) * pH</td>
<td>-0.0005</td>
<td>-1.704</td>
</tr>
<tr>
<td>Density (2 yr) * date</td>
<td>-0.0002</td>
<td>-2.207</td>
</tr>
<tr>
<td>Density (2 yr) * K</td>
<td>0.0006</td>
<td>4.268</td>
</tr>
<tr>
<td>d) Fourth quarter (9 September–26 September 1986)</td>
<td>( r^2 = 0.1836 )</td>
<td>( F = 4.836 )</td>
</tr>
<tr>
<td>P</td>
<td>-0.0582</td>
<td>-2.254</td>
</tr>
<tr>
<td>Date</td>
<td>1.0077</td>
<td>2.754</td>
</tr>
<tr>
<td>e) Total sampling period (26 June–26 September 1986)</td>
<td>( r^2 = 0.0811 )</td>
<td>( F = 5.325 )</td>
</tr>
<tr>
<td>Density (2 yr)</td>
<td>-0.0133</td>
<td>3.248</td>
</tr>
<tr>
<td>Date</td>
<td>-0.0165</td>
<td>-3.616</td>
</tr>
<tr>
<td>Density (2 yr) * date</td>
<td>0.0003</td>
<td>3.968</td>
</tr>
</tbody>
</table>

-0.1328, \( P = 0.0008 \). The negative correlation between height of the target’s nearest neighbor and distance between the target and its nearest neighbor was less significant (\( r = -0.0898, \ P = 0.0233 \)).

There was a significant (\( P < 0.01 \)) positive correlation between the sum of the biomass of neighboring seedlings harvested in October and the distance between them (Fig. 3). The sum of the heights of these neighbors was not significantly correlated with distance between them (\( r = 0.0710; \ P > 0.05 \)).

**DISCUSSION**—In a mast year cohort, more seedlings will germinate than can possibly survive to maturity. Such seedlings in sugar maple may survive for a considerable time in a suppressed state under the shade of canopy trees. Intense self-thinning can be expected when growth is released by canopy opening (Peet and Christensen, 1987) but the onset of neighbor effects may be much earlier. The effect of high neighbor densities may be absorbed by differential plant growth through plasticity as well as mortality (Bazzaz and Harper, 1976; Harper, 1977; Aikman and Watkinson, 1980). If size differences lead to fitness differences (e.g., Sohn and Policansky, 1977; Werner and Caswell, 1977; Solbrig, 1981), early competition with neighbors may represent an important selection pressure among mast year seedlings. Studies to date, however, have not established whether there are any significant neighbor effects among mast year seedlings.

Most of the sugar maple seedlings recorded in the quadrat surveys were produced in 1984 with relatively large cohorts also produced in 1976 and 1978 (Fig. 1). The number of seedlings found in cohorts prior to or directly following the 1984 mast year were much lower than the number of mast year seedlings. For example, only two three-year-old seedlings and not a single one-year-old seedling were recorded. This may reflect a drain on resources during the period of intensive seed production (Harper, 1977).

There were also relatively few seedlings in the older cohorts (e.g., >16 years old) compared with younger cohorts (Fig. 1), suggesting age-specific mortality in younger age classes. Heavy mortality among young seedlings is well documented (Hough, 1937; Hett and Loucks, 1968; Mulcahy, 1975). The majority of the mortality within the 1984 cohort clearly has yet to occur.

The two-year-old seedlings in the sampled population represent the survivors of selection in the previous year. The negative relationship between mean seedling height per quadrat and density in the first half of the sampling period (Fig. 2a, b) strongly suggests that earlier competition (including the previous year [1985])
was important in determining seedling height early in 1986. If seedling height reflects which seedlings are more likely to survive and reproduce, then competition may be an important factor affecting individual fitness in this population.

The data from the second half of the sampling period (Fig. 2c) shows a positive relationship between seedling height and quadrat density. This shift from significant negative to positive relationship is difficult to interpret. Both temporal and spatial effects may be involved. Intense competition early in the season may account for the negative relationship in the first half of the sampling period. The tallest individuals under high density conditions may realize little advantage by attaining greater heights later in the season; the more suppressed shorter individuals, however, would stand the most to gain by an increase in height relative to taller neighbors. Consequently, near the end of the growing season, dominant and suppressed individuals within the more crowded quadrats may have relatively similar heights. A significant negative correlation \( r = -0.2699, P < 0.001 \) between the standardized variance (variance/mean) in height (per quadrat) and sampling date supports this interpretation. The correlation between quadrat density and standardized variance in height shifts from significantly positive \( r = 0.1816, P < 0.05 \) in the first half of the sampling period to insignificantly negative \( r = -0.1339, P > 0.05 \) in the second half of the sampling period. This indicates that variation in seedling height is relatively high in crowded quadrats in the first half of the sampling period, but not later in the growing season. There was no significant correlation between mean height per quadrat and sampling date. However, mortality tends to be disproportionately high among smaller (shorter) individuals and consequently would also tend to equalize plant height. It is difficult to determine if self-thinning had begun in the seedlings in the present study, however, because a 1985 census of the 1984 seedlings is not available and the fates of individuals were not followed over the course of the study.

The apparent temporal changes in the relationship between mean seedling height and density (Fig. 2) may actually represent a spatial effect since different quadrats were surveyed at different times. The negative correlation between sampling date and phosphorus, potassium, and magnesium (Table 1) suggests that nutrient availability decreased over the sampling period. It is unclear however, whether this is a consequence of resource depletion due to plant growth (or microbial activity) over the growing season, or simply a consequence of sampling, by chance, the more resource-poor sites later in the season. In the later case, the most resource-poor sites might be expected to support seedlings which are not only relatively small but are also at relatively low densities. This could account for the positive relationship for later-surveyed quadrats (Fig. 2c).

A similar interpretation can be made for the significant negative correlation \( r = -0.1328, P = 0.0008 \) between the height sum of nearest two-year-old neighbors and the distance between them (i.e., neighbors that were closer together were generally taller). The presence of abiotic heterogeneity may produce variation in plant performance capable of masking the effects of local competition (Waller, 1981). Pielou (1960) attributed lack of evidence for competition to aggregate population distribution, where trees in nutrient-rich sites were not only in higher densities (i.e., closer together) but were also larger than those in less favorable sites.

Plant populations under the influence of competition typically consist of many small individuals and relatively few large individuals. Inequality (as measured by the Gini coefficient) may be used to describe the behavior of size distributions with changes in density (Weiner and Thomas, 1986). If competition is asymmetrical (i.e., larger individuals are able to get more than their proportional share of resources based on relative size, and grow at the expense of smaller individuals), then there would be greater inequality with increased density. The positive correlation between the Gini coefficient for seedling height within quadrats and quadrat density was not significant \( P = 0.09 \). The extremely high seedling density which is characteristic of mast year cohorts may cause seedlings to be regularly distributed despite random seed dispersal, and regular distributions show less of a size hierarchy than random distributions (Pielou, 1960). Furthermore, the distribution of plant height may not parallel the distribution of biomass (Harper, 1977). Despite the absence of a well-defined hierarchy of heights, it might be expected that the shorter seedlings in the first half of the sampling period would also have the smallest biomass and that the biomass hierarchy would be maintained throughout the growing season. In this case, biomass would more accurately reflect the variation in plant size in response to competitive interaction. Although biomass distribution within quadrats was not recorded, the significant \( P < 0.01 \) positive correlation between the separating distance and biomass sum of neighboring seedlings harvested in Oc-
tober (Fig. 3) strongly suggests that mast year seedlings are suppressed by close proximity to neighbors.

The negative correlation between number of leaves and seedling density (Table 1) suggests that interference with other seedlings may affect leaf production or result in leaf loss. Herbivores may also be attracted to high density patches of seedlings and therefore contribute to leaf loss. This might also explain the significant negative correlation between number of leaves and sampling date (Table 1). By later survey dates, more time had elapsed, and hence there was more opportunity for leaf loss. Seedlings might also drop a leaf in response to abiotic stress. Leaf number, however, was not significantly correlated with any of the abiotic factors that were recorded.

Competition between plants has been shown, in many cases, to be directly related to their distance apart (Mack and Harper, 1977; Weiner, 1982, 1984; Silander and Pacala, 1985). The positive correlation between the sum of nearest neighbor biomasses and the distance between them (Fig. 3) represents the strongest evidence for competitive interaction between mast year seedlings in the present study. Seedling size differences, however, may also be the result of genetic variation, differences in germination time, environmental heterogeneity, or the effect of herbivory, and these factors are likely to account for the unexplained variation in the data. Although genetic variation was not measured in this study, it may be considerable in Acer saccharum because it possesses an extremely effective outbreeding mechanism (Gabriel, 1968). Sugar maple grows most commonly on soil having a pH between 5.5 and 7.3 (Fowells, 1965). The highly significant negative correlation (Table 1) between seedling density and soil pH suggests that seedlings may be sensitive to low levels of pH. The total percent cover of other species was positively correlated \( P < 0.001 \) with number of leaves per seedling but negatively correlated \( P < 0.01 \) with seedling density. Those seedlings in quadrats with a high percent cover of other species may compete less with conspecifics. Alternatively, the presence of other species may provide a greater opportunity for beneficial interactions between species. The addition of these independent variables in the multiple regression analysis accounted for a greater proportion of variation in seedling height (Table 2), than the simple height vs. density regression (Fig. 2). Density (or density interactions with other variables), however, generally explained the largest proportion of variation.

These data indicate that sugar maple seedlings, even as early as in their second year of growth, may suffer size suppression due to the close proximity of neighboring cohorts. Which individuals survive to form the canopy of the next generation may therefore depend to a large extent upon neighbor effects occurring within the first two years following establishment, which may be long before growth is released by a canopy opening.

**LITERATURE CITED**


