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JAPANESE MAPLE (*ACER PALMATUM* VAR. *MATSUMURAE*, ACERACEAE) RECRUITMENT PATTERNS: SEEDS, SEEDLINGS, AND SAPLINGS IN RELATION TO CONSPECIFIC ADULT NEIGHBORS[1]

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We analyzed the spatial patterns among seeds, seedlings, saplings, and conspecific adult trees of the cool-temperate tree species *Acer palmatum* var. *Matsumurae* in a conifer–hardwood mixed forest in northern Japan, using two models that consider the influence of each adult within the neighborhood of the offspring. The results showed that recruitment patterns of each stage could be characterized and that significant shifts occur between successive stages. Sound seeds were more widely dispersed than unsound seeds; the mean dispersal distance (MDD) was 41.5 m for sound seeds, but only 12.6 m for unsound seeds. Most seedlings were located near conspecific adult trees, with a MDD of 14.3 m. Saplings, however, were more dispersed away from conspecific adult trees, with an MDD of more than 35 m. Light and gap distributions did not strongly affect the spatial distribution of the offspring; most saplings were located under nonconspecific canopies. These results suggest that the recruitment pattern of Japanese maple offspring is strongly affected by conspecific adult neighbors, rather than by light and gap distributions, with close proximity to conspecific adult trees reducing the growth and survival of seedlings during the transition to saplings.

Key words: *Acer palmatum*; Aceraceae; recruitment; seed rain; spatial distributions.

The spatial distribution of plants within a population is first determined by the distribution of seeds during seed dispersal (i.e., the seed shadow sensu Janzen, 1971). After seed dispersal, numerous biotic and abiotic factors, including light intensity, soil condition, microtopography, and herbivory, influence seed fates (Bratton, 1976; Sydes and Grime, 1981; Beatty, 1984; Clark and Clark, 1984; Crozier and Boerner, 1984; Newbery et al., 1986; Schupp and Fuentes, 1995).

Although commonly locations of seedlings are assumed to determine the consequences of dispersal for a particular species, spatial variation in these factors may reshape the distribution of seedlings and saplings (e.g., Salomonson, 1978; Clark and Clark, 1981, 1984; McCanny and Cavers, 1987). Sites that are suitable for seedling germination and establishment may not be suitable for sapling growth (Schupp, 1995), and recruitment should not be defined as a single ''entry'' point, but rather as a multistage process, with potentially different factors operating at the different stages (Ribbens, 1995).

Howe and Smallwood (1982) proposed that two possible advantages of seed dispersal are the ability to colonize new areas or to escape high mortality rates due to agents associated with the current population location. One factor is likely to be stronger than the other for any given species, although the two factors are not necessarily mutually exclusive. As driving factors, colonization vs. escape are not distinguishable based solely on seed distribution. However, they will exert different forces to reshape the distribution of the offspring, and thus can be identified by examining changes in offspring distributions during development.

For forest tree species, if the principal advantage is escaping mortality agents, then survival will be highest in areas distant from conspecifics, particularly conspecific adults, because the presence of conspecific adults may reduce the growth and then survival of their offspring (Cypher and Boucher, 1982). In highly diverse tropical forests conspecific adult trees of some species negatively influence the spacing pattern of seedlings, due to distance- or density-dependent predation by animals which concentrate their foraging near adult trees (Janzen, 1970; Connell, 1971; Augspurger, 1983, 1984; Clark and Clark, 1984). Similarly, in temperate forests, Fox (1977) and Woods (1979) found that sugar maple (*Acer saccharum*) and beech (*Fagus grandifolia*) tend to establish saplings under crowns of the other species, although they expected that initial seed input would be higher near the conspecific canopies than the other canopies. These phenomena are not universal (e.g., Hubbell, 1980; Fleming and Heithaus, 1981; Condit et al., 1992), but when the escape hypothesis is an advantage of dispersion, we expect that the mean distance from adult trees to offspring will increase through time with the advance of growth stages.

If, however, the principal advantage of high dispersal

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distances is colonization, then seedling establishment and survival will be enhanced by high light levels (such as are typically found in treefall gaps). Shade-intolerant species are frequently clumped in large gaps where light conditions are better, whereas shade-tolerant species are not strongly associated with gaps (e.g., Nakashizuka and Numata, 1982a, b; Nakashizuka, 1984; Ishikawa and Ito, 1989; Leemans, 1991; Masaki et al., 1992). When the colonization hypothesis is an advantage of dispersion, we expect that light levels and locations within gaps will be correlated with offspring, increasing through time with the advance of growth stages.

We examined the spatial distribution of seeds, seedlings, saplings, and adult trees of Japanese maple, *Acer palmatum* var. *Matsumurae* Makino, by analyzing the spatial pattern of Japanese maple offspring with techniques developed by Weiner (1984) and Ribbens et al. (1994) to assess how conspecific adult trees affect the spatial patterns of their offspring. Our goal was to examine changes in the spatial patterns of Japanese maples as they progress through several stages in the regeneration process, and to evaluate these changes to identify probable driving mechanisms causing changes. Specifically, we wanted to evaluate the relative importance of seed dispersal, escape from conspecifics, and colonization into high light environments on Japanese maple sapling distributions, based on changes from the seed dispersal and seedling stages.

MATERIALS AND METHODS

Study site—*Acer palmatum* var. *Matsumurae* is a shade-tolerant forest species (Koike, 1988) commonly distributed in temperate forests of northern Japan. The seeds are samaras and primarily wind-dispersed, but sometimes they are secondarily dispersed by small rodents (N. Wada, personal observation).

The study site is a natural conifer–hardwood forest in the Tomakomai Experimental Forest (TOEF), Hokkaido University, northern Japan. In the summer of 1992, we set up a quadrat of 40 × 40 m in the forest. Although this forest was considerably disturbed by a typhoon in 1954 (Mishima et al., 1958), the forest stand within and around the quadrat remains relatively intact. *Acer palmatum* var. *Matsumurae, Quercus mongolica* var. *grosseserrata, Magnolia obovata,* and *Picea jezoensis* are dominants, comprising 18, 12, 12, and 23%, respectively, of the total basal area (26 m^2 / ha, trees >2 m tall). No other species occupy $>10\%$ of the total basal area in the forest. The terrain is nearly flat, and the forest floor is dominated by the fern *Dryopteris crassirhizoma.*

We divided the quadrat into 64 5 × 5 m subquadrats to facilitate mapping the location of all seedlings, saplings (<2 m tall), subcanopy trees (<10 m tall), and canopy trees (>10 m tall) of *Acer palmatum* var. *Matsumurae.* Saplings were divided into three height classes: small saplings, <0.5 m tall; midsized saplings, 0.5–1 m tall; and large saplings, 1–2 m). In this study, the term ''seedling'' denotes an individual that germinated and became established in the census year 1992.

In addition to mapping the locations of all individuals, we mapped the crown projection of all canopy trees in the quadrat. In this study, we defined regions within the quadrat where the canopy was <10 m tall as a gap. Based on the diagram of the crown projection, we calculated the coverage of Japanese maple canopies, the canopies of the other species, and gaps by using an automatic area meter (Hayashi Denkoh Co., Ltd., Tokyo, Japan) to calculate the area of the conspecific canopy, the canopies of the other species, and gaps.

To assess seed dispersion, in late September we uniformly distributed 64 seed traps (0.5 m^2 each) by putting a trap on the center of each subquadrat to record the dispersal of Japanese maple seeds. Every week we collected the seeds through December. We dissected all seeds collected and counted the numbers of sound and unsound seeds. Sound seeds had a well-developed embryo, but unsound seeds had a smaller (or missing) embryo that was either immature or eaten by predispersal seed predators.

We measured the photosynthetic photon flux density relative to a standard open site (RPFD) at the center and the four corners of each subquadrat on an entirely overcast day in mid-August 1994 by positioning a LI-COR, LI-190S quantum sensor (LI-COR, Lincoln, NB) at 2 m above the ground ($N = 145$ points). The contour plots were drawn by SYSTAT (SYSTAT, 1992), using the method of Lodwick and Whittle (1970), combined with linear interpolation.

Weiner spatial analysis—To assess the effect of conspecific adults on spatial distribution of seeds, seedlings, and saplings, we first divided the 40 × 40 m quadrat into subquadrats, and counted the number of seeds, seedlings, and saplings in each subquadrat from map data. We analyzed the spatial pattern between offspring and adults using Weiner's neighborhood influence statistic and using the spatial dispersion analysis of Ribbens et al. (1994).

The neighborhood influence (W) statistic of Weiner (1984) is calculated as:

$$W = \sum_{i=1}^{N} \times \frac{A_i}{d_i}$$

where N is the total number of neighbors defined below, A_i is the size (cross-sectional trunk area) of adult i, and d_i is the distance from the trunk base of ith tree to the center of a given 5 × 5 m subquadrat. Neighboring trees were defined as all individuals within 20 m from the center of each subquadrat with a dbh (diameter at breast height) >10 cm. We assumed an individual <10 cm in dbh would produce few or no seeds and would have a low impact on the survival of seedlings and saplings.

Because W reflects accumulated effects of conspecific adult neighbors, it will have a higher value at sites where conspecific adults are densely located. Thus, we assumed that the influence of each adult decreased with increasing distance from the offspring and increased with size of each adult. We calculated W at the center of each subquadrat (using the total seeds, seedlings, or saplings mapped in the subquadrat), and analyzed the relationship between W and density of offspring within the subquadrat (seeds, seedlings, and saplings) using Spearman rank correlation ($\hat{r}_s$).

RECRUITS analysis—We estimated the mean dispersal distance (MDD) of seeds, seedlings, and saplings with the spatial model of dispersion (RECRUITS) developed by Ribbens et al. (1994). The RECRUITS program statistically estimates recruitment parameters (i.e., number of offspring produced by a standard-sized tree and mean dispersal distance from the tree) from map data by taking the influence of each adult within the 40 × 40 m quadrat, as well as all adults within a 20 m wide strip, into account. This method assumes that the influence decreases with increasing distance from the offspring, as in Weiner's model.

RECRUITS uses maximum likelihood statistics to calibrate parameters for a Poisson-based dispersal function, via a searching algorithm that finds those parameters that give the closest fit between the predicted number of recruits and the actual number found in each square meter (the number of seeds counted or seedlings or saplings mapped). Furthermore, the RECRUITS program fits 95% confidence intervals to the parameters, and calculates the product-moment correlation of fit between observed recruits (seeds, seedlings, or saplings) and predicted recruitment distributions. These correlations are a conservative measure of the ability of the function to track the observed distributions (see Ribbens et al., 1994 for details).

The number of recruits (R) predicted for a tree of m metres away from a quadrat is represented as follows:

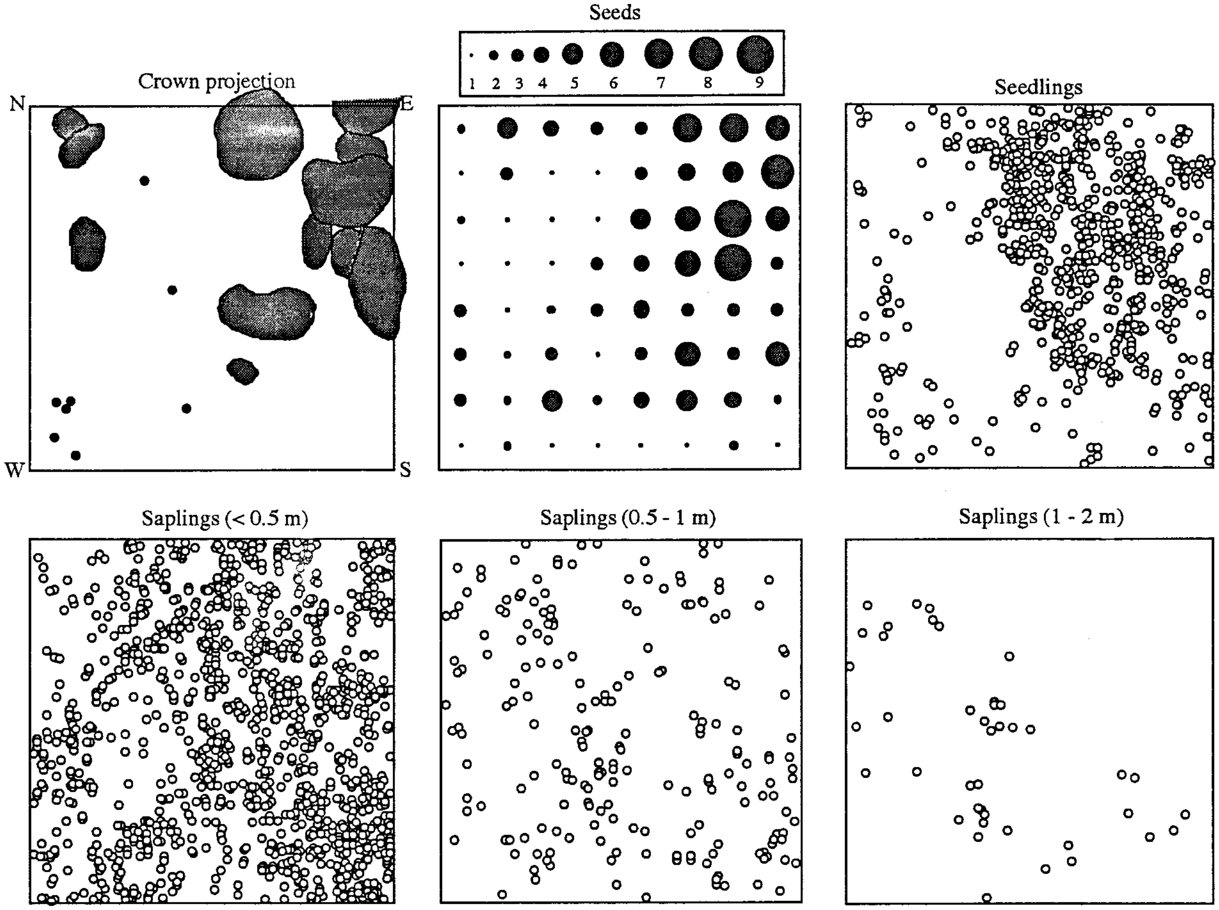

Fig. 1. Spatial distributions of adult and subcanopy trees, seeds, seedlings, and saplings of Japanese maple. In the figure of crown projections (top left), canopy outlines of the adult trees (>10 m tall) are shown by dark shaded areas, and trunk locations of subcanopy trees (<10 m tall) are shown by solid circles. The seed shadow figure (top middle) shows only sound seeds: the number of dispersed seeds in a subplot is proportional to the size of the solid circle: 1, 1–7; 2, 8–10; 3, 11–14; 4, 15–18; 5, 19–21; 6, 22–25; 7, 26–29; 8, 30–32; 9, 33–36.

$$R = \left[\mathrm{STR} \times \left(\frac{\mathrm{dbh}}{30}\right)^2\right] \times \frac{1}{n} \times [e^{-D \times m^3}]$$

where the parameters being calibrated are STR (the total number of recruits produced by a tree 30 cm in dbh), *D*, which determines how rapidly the dispersion of recruits around the tree decreases with increasing distance, and *n*, a normalizer used to decouple the two halves of the equation. Briefly speaking, the first half of the equation expresses the total number of offspring produced by the tree, and the second half of the equation describes the mean density of offspring to be found in the quadrat at the given distance *m* from the adult tree. We chose to scale STR relative to a 30 cm dbh tree, because this is both close to the mean dbh for the mapped area, and because it facilitates comparisons with the results of Ribbens et al. (1994). Because *D* is completely correlated with the more intuitively interpretable mean dispersal distance (MDD), we also calculated MDD values, which indicates the average dispersal distance from parent to offspring.

RESULTS

There were 12 adult Japanese maples (*Acer palmatum* var. *Matsumurae*) in the 40 × 40 m quadrat established in the TOEF. Seven adult maple trees (>10 m tall) were aggregated in the eastern corner, and five were clustered in the western corner (Fig. 1). Eight small maple trees (<10 m tall) were distributed apart from the conspecific adult trees. Because no fallen Japanese maples were observed on the forest floor in this quadrat, the location of adult maples was thought to have been constant for at least the past several years.

In the 64 seed traps, 5870 Japanese maple seeds were collected, of which 884 (15%) were considered sound. The seeds were dispersed heterogeneously in space, so the number of seeds in each trap varied from 1 to 36 (mean ± 1SD: 13.8 ± 8.1, $N = 64$) sound seeds and from 32 to 175 (77.9 ± 37.1) unsound seeds. Many seeds were dispersed near conspecific adult trees around the eastern corner, while few seeds were found in the other corner (Fig. 1).

Figure 2 shows the relationships between both sound and unsound seeds and the neighborhood influence (*W*) of conspecific adult trees. The number of dispersed seeds was significantly positively correlated with *W* for both sound ($r = 0.582$, $P < 0.001$) and unsound seeds ($r = 0.684$, $P < 0.001$). However, the slope of the regression line was significantly different between sound seeds and unsound seeds ($F_{1,124} = 34.2$, $P < 0.001$, analysis of covariance); sound seeds had a more horizontal slope of regression than unsound seeds, and thus were more widely dispersed than were unsound seeds.

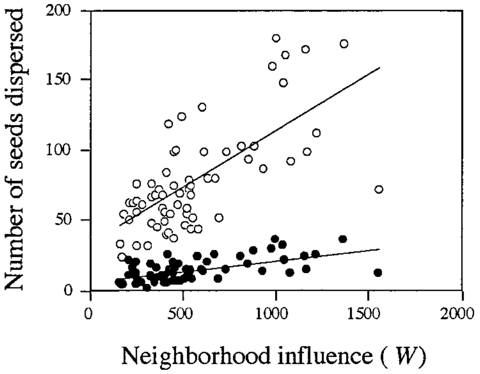

FIG. 2. Relationship between dispersed seeds and neighborhood influence (*W*) of conspecific adult trees. Open circles, unsound seeds; solid circles, sound seeds.

We estimated standardized total recruit production (STR) and mean dispersal distance values (MDD) for all categories of seeds, seedlings, and saplings with the RECRUITS program (Table 1), and found MDD values of 41.6 m for sound seeds and 12.6 m for unsound seeds. Correlations between observed and predicted distributions (r) of both sound and unsound seeds were significant ($P < 0.001$), with correlations of 0.587 for sound seeds and 0.735 for unsound seeds. Thus, both methods of analysis indicated that sound seeds were dispersed much farther than unsound seeds.

Although seedlings were also clustered in the eastern corner (Fig. 1), the MDD was considerably different between sound seeds (41.6 m) and seedlings (14.3 m). Large Japanese maple saplings showed a negative association with both the seed shadow and the seedling abundance (Fig. 1). Although many seeds and seedlings were distributed below the conspecific crowns, the tallest saplings were located away from the clump of seven adult trees, suggesting a negative impact of Japanese maple adult trees on the growth and survival of seedlings to saplings.

We confirmed this hypothesis by comparing offspring abundance with neighborhood influence (W) of the conspecific adult trees (Table 2). The density of sound seeds was significantly positively correlated with W as well as that of seedlings. With growth, however, the correlation coefficients changed from positive to negative values, showing a gradual change of offspring distributions away from conspecific adult neighbors (Fig. 1; Table 2). Supporting this, the RECRUITS analysis determined that predicted sapling distributions were much less correlated with observed distributions ($R < 0.1$), indicating that saplings were losing their spatial association with conspecific adult trees (Table 1). Furthermore, saplings were widely dispersed; the MDD was 35.7 m for small saplings, 36.1 m for mid-saplings, and 72.0 m for large saplings. Thus, we found that mean dispersal distance from offspring to conspecific adults increased with growth from seedlings to saplings.

We also examined the densities of seedlings and saplings in three habitats: under conspecific canopies, under nonconspecific canopies, and in gaps (Table 3). The density of seedlings was highest under conspecific adult canopies, but for saplings the density was significantly higher under nonconspecific canopies, rather than gaps or conspecific canopies (see χ^2 statistics in Table 3). Light distribution did not strongly affect the sapling distributions (Fig. 3), and we were unable to detect any influence of light levels on recruitment patterns using RECRUITS. A multiple regression analysis of W and RPFD for each stage of growth found that light was significant only for large saplings, but the influence of light (standardized coefficent) was not as strong as the neighborhood influence (Table 4). The relationship between neighborhood influence (W) and RPFD (light) was also not significant ($N = 145$, $r = 0.038$, $P = 0.651$). These results demonstrate that the spatial patterns of seeds, seedlings, and saplings were strongly affected by the location, size and density of conspecific adult trees, but there is only weak evidence that light levels influenced survival, at least based on the current light levels.

TABLE 1. Recruitment parameters. MDD (mean dispersal distance), STR (Standard Total Recruitment), observed-expected correlation (r), normalizer, and D values for seeds, seedlings, and saplings of Japanese maple.

Growth stage	MDD	STR	r	Normalizer	D[a]
Sound seeds	41.6	14845.8	0.587*	8978.2	561.0
Unsound seeds	12.6	13554.1	0.735*	824.3	20180.2
Seeds (total)	12.5	15914.0	0.567*	818.3	20404.3
Seedlings	14.3	87.6	0.278*	1058.7	1.4
Saplings (<0.5 m)	35.7	717.9	0.090	6643.6	<0.1
Saplings (0.5–1 m)	36.1	116.1	0.076	6789.6	<0.1
Saplings (1–2 m)	72.0	97.2	0.075	26973.2	<0.1

* Significant at $\alpha = 0.05$.

[a] D values equal $D \times 10^4$.

TABLE 2. Spatial correlation between the density of Japanese maple offspring and neighborhood influence (W) of the conspecific adult neighbors ($N = 64$).

Growth stage	Sound seeds	Seedlings	Saplings[a]		
			S	M	L
Spearman's r_s	0.556	0.604	0.110	−0.266	−0.366
P	<0.001	<0.001	0.384	0.035	0.004

[a] S saplings < 0.5 m; M saplings 0.5–1 m; L saplings 1–2 m.

DISCUSSION

We have characterized Japanese maple recruitment patterns of seeds, seedlings, and several sizes of saplings, and demonstrated that substantial shifts in dispersal pat-

TABLE 3. Densities (m^2) of maple offspring under conspecific and nonconspecific canopies and gaps.

Class	Canopy: conspecific	Other	Gap	χ^2 test (df = 2)
Seedlings	0.732	0.437	0.256	$\chi^2 = 397.17$***
S saplings[a]	0.839	0.871	0.667	$\chi^2 = 659.96$***
M saplings	0.084	0.179	0.093	$\chi^2 = 95.23$***
L saplings	0.000	0.051	0.011	$\chi^2 = 41{,}449.98$***
Area (m^2)	380.0	777.5	442.5	

*** $P < 0.001$.

[b] See Table 2 footnote for description of sapling categories.

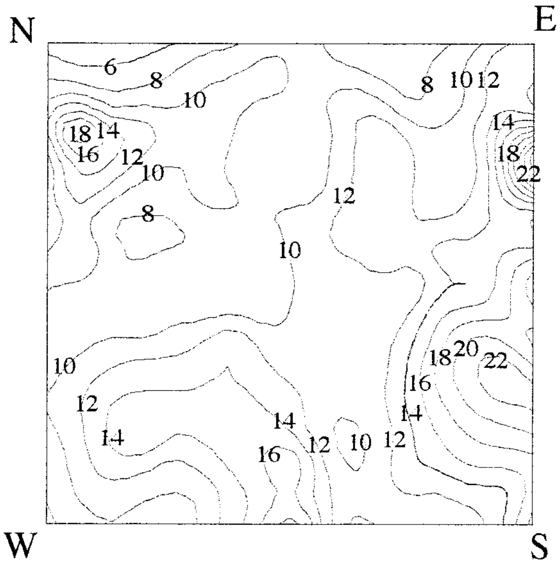

Fig. 3. Spatial distribution of light intensity, drawn by SYSTAT. The numerals show relative photon flux density (RPFD) isoclines.

terns occur with advancing growth. One purpose of this study was to determine if escape or colonization were important benefits of seed dispersal (Howe and Smallwood, 1982). We found that the numbers of seeds and seedlings were positively correlated with neighborhood influence (*W*) of conspecific adult trees, and we were able to fit Poisson functions to seed and seedling distributions. Clearly, seedlings are not uniformly distributed across space. Furthermore, the distribution of seedlings was not strongly associated with gap and light distributions. This indicates that this species does not depend on gaps for the germination and emergence of seedlings, and that, at least for initial establishment, colonization does not appear to be important for this species.

Saplings were more widely dispersed from conspecific adult trees than were seedlings, with a MDD >35 m for all size classes. Mid-sized and large saplings were especially negatively correlated with neighborhood influences, suggesting conspecific adult trees strikingly reduced the growth and/or survival of seedlings as they matured into saplings. Because the spacing change from seedling stage to sapling stage was not explained only by light and gap distributions, it is unlikely that shading effects by conspecific canopies were the main factor preventing tallest saplings from being found near the crown. Interestingly, oak (*Quercus mongolica* var. *grosseserrata*) saplings were relatively abundant under the clump of Japanese maple canopies, while maple saplings were located near the oak canopies in this quadrat (Wada, 1995).

Therefore, throughout growth colonization of high light environments does not appear to be an important driving factor for dispersal. Rather, the escape hypothesis of Howe and Smallwood (1982) appears to be important. Species-specific factors other than shading are probably affecting the growth and survival of seedlings and saplings of Japanese maple under the conspecific adults. It is possible that widely dispersed offspring escape high mortality due to pathogens, herbivores, or seed predators concentrated around adult conspecifics, although further study is needed to identify specific agents.

TABLE 4. Multiple regression analysis of neighborhood influence (*W*) and current light intensities (RPFD) for sound seeds, seedlings, and three stages of saplings. Calculations were done using *W* values and RPFD values at the center of each 5 × 5 subquadrat (*N* = 64). W and RPFD values in this table show standard coefficients of the multiple regressions.

Growth stage	r^2	$F_{(2,61)}$	*P*	W	RFPD
Sound seeds	0.321	15.877	<0.0001	0.569***	0.065
Seedlings	0.259	12.008	<0.0001	0.541***	−0.095
S saplings[a]	0.007	1.234	0.298	0.000	0.197
M saplings	0.078	3.652	0.032	−0.272**	0.240
L saplings	0.186	7.345	0.001	−0.402***	0.271*

* Significant at $P < 0.05$; ** significant at $P < 0.01$; *** significant at $P < 0.001$.

[a] See Table 2 footnote for description of sapling categories.

Although Houle (1992) reported that seed or seedling mortality of *Acer saccharum* was not strongly related to its abundance in a deciduous forest of Quebec, Canada, Taylor and Aarssen (1989) found density-dependent seedling growth of *Acer saccharum* in Ontario, Canada. Seedling size was negatively correlated with initial densities, suggesting competition between seedlings even in this early growth stage. In a temperate deciduous forest of Japan, Shibata and Nakasizuka (1995) demonstrated that seedling emergence was significantly negatively correlated with seed fall density and was not correlated with distance from conspecific adults for four *Carpinus* species. However, 1st-yr seedling survival was significantly positively correlated with the distance from conspecific adults in two of the four species, suggesting different species-specific mortality factors occurred with different growth stages, even in these early seed and seedling stages. Although these studies did not consider the spatial variation of mortality-causing agents, it is likely that density- or distance-dependent mortality of seeds or seedlings mediated by conspecific adults is one of the important factors causing the significant spacing shifts with the growth of seedlings into saplings.

Evidence for escape from density-dependent mortality agents associated with adults has been documented in several studies. For example, Woods (1979) reported that *Acer saccharum* sapling mortality was higher under conspecific canopies than under nonconspecific *Fagus grandifolia* canopies. Woods and Whittaker (1981) speculated that, rather than shading effects, root competition or some other factors cause higher mortality of saplings under conspecific canopies. However, Condit et al. (1992) found support for density-dependent mortality only for a few of the many species they examined, and Augspurger (1984), who carefully examined nine species of tropical trees for shifting patterns of mortality as seedlings advanced in age, determined that, while there was support in some species for density-dependent mortality agent, most species were best characterized as supporting the colonization hypothesis.

We found that sound seeds were more widely dispersed than unsound seeds. Why were sound seeds dispersed much farther? One might expect that unfilled seeds would be lighter and thus have a slower rate of descent. Al-

Table 5. STR (Standard Total Recruitment), MDD (Mean Dispersal Distance), observed-expected correlations, normalizer, and *D* values for Japanese maple and several North American wind-dispersed tree species (from Ribbens et al., 1994), sorted by MDD.

Species	STR	MDD	*r*	Normalizer	*D*§
Sugar maple	182.42	8.150	0.513*	345.63	0.74350
Red maple, rep. 1[b]	417.71	9.525	0.425*	472.03	0.46581
Red maple, rep. 2	219.33	11.591	0.239*	698.85	0.25856
Japanese maple	87.62	14.315	0.278*	1058.71	1.37753
White ash	26.18	16.341	0.163*	1388.87	0.09228

* Significant at $\alpha = 0.05$.

[a] Rep. = replicate.

[b] *D* values equal $D \times 10^4$.

though we did not measure the ability of seed traits such as seed mass, samara area, and wing morphology to affect MDD, one possible explanation for this result is that many unsound seeds appeared to have deformities, tended to fall in pairs, and thus had a less effective wing-lift to promote maximum dispersion (Greene and Johnson, 1992). In contrast, sound seeds were frequently dispersed individually, might have a stronger abscission zone, and were more likely to dehisce during a strong wind (N. Wada, personal observation). These traits may result in increasing maximum dispersion by releasing seeds preferentially during high-wind periods.

In wind-dispersed species, seed dispersal distance is affected by many interacting factors, including seed mass, wing morphology, velocity, and height of attached seeds (Augspurger and Franson, 1987; Greene and Johnson, 1989; Sipe and Linnerooth, 1995), which makes the determination of exact mechanisms favoring long-dispersal distances difficult. Loubry (1993) reported unsound fruits being dispersed more widely by wind than sound fruits; however, in contrast to Japanese maple, the *Dicorynia guianensis* fruits he studied contain one to several seeds, and single-seeded fruits were more likely to be attacked by predispersal seed predators. Sound seeds were also dispersed more widely than seedlings. One possible explanation for this is that, because dispersed seeds were not from the same year as seedlings, different seed dispersal dynamics between years could drive the different MDD between sound seeds and seedlings.

The dispersal distances we calculated for Japanese maple seedlings are somewhat higher than dispersal distances previously calculated by Ribbens et al. (1994) for two species of North American maples (Table 5). Japanese maple seedling dispersal distances are more similar to white ash, another species with large samaras that preferentially releases seeds during high winds. STR values are lower than those calculated for red maple and sugar maple seedlings, but higher than white ash seedlings. Thus, Japanese maple fits into the general pattern of large samaras dispersed by wind, with good seedling production and a mid-range dispersal ability.

We conclude that the recruitment pattern of Japanese maple offspring was strongly affected by escape from conspecific adult neighbors. This study is the first paper in which the spacing pattern of offspring from the seed dispersal stage to the large sapling stage was analyzed, using two separate methods of analysis that take neighborhood effects of conspecific adults into account. Clearly, conspecific adults exert strong influences over seed, seedling, and sapling distributions, and recruitment probabilities decrease as distance to an adult increases. Spacing patterns shifted substantially among the different stages of growth; seedlings were more tightly clustered around adults than were saplings.

However, it is not still known what mechanisms were driving the shift in spacing from seedlings to saplings. It does not appear to be due to light levels or canopy gap dynamics, and may be due to density-dependent mortality agents concentrated in the vicinity of adults. Finally, this study illustrates that although the analysis of spatial patterns at multiple stages within the life cycle is complicated, it is clear that, as Schupp and Fuentes (1995) pointed out, simply examining the pattern at one stage is not sufficient to determine either spatial dynamics or to assess its impacts on community structure and dynamics.

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