Seed production and dispersal patterns in populations of *Liriodendron tulipifera* at the northern edge of its range in southern Ontario, Canada

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Seed production, viability, and dispersal patterns were examined for populations of *Liriodendron tulipifera* L. (tuliptree) at the northern edge of its range in Ontario, Canada, to determine whether these factors could account for its locally limited distribution. Seed production was measured by estimating the number of samara cones present in the canopy, and samaras collected in traps were dissected to determine potential seed viability under different stand conditions. Seed-trap collections were used to delineate seedfall patterns around individual tree stems and within high-density stands. Results indicate that seed production in Ontario begins when trees reach approximately 25 cm diameter at breast height and increases with maturity. Large trees often produce more than 2000 cones in good years, a level similar to more southern populations. The proportion of samaras containing filled seed increases with stand density, ranging from approximately 8–10% for isolated trees to over 20% for old-growth, high-density stands. Although low, these values are comparable to those reported elsewhere in the species' range. Seedfall patterns followed a leptokurtic distribution about individual stems. Life-history attributes other than seed viability may therefore be the cause of the restricted distribution and low population levels of *L. tulipifera* in Ontario.

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La production, la viabilité et les patrons de dispersion des graines ont été étudiés chez des populations de liriodendron tulipier (*Liriodendron tulipifera* L.) situées à la limite nord de l'aire de distribution de cette espèce en Ontario, Canada, dans le but de déterminer si ces facteurs peuvent expliquer sa distribution localement restreinte. La production de graines a été mesurée en évaluant le nombre de cônes à samare présents dans le couvert tandis que les samares collectées dans des trappes furent disséquées pour déterminer la viabilité potentielle des graines dans différentes conditions de peuplement. Les collections obtenues dans les trappes ont servi à tracer les patrons de chute des graines autour de la tige d'arbres individuels et à l'intérieur des peuplements à densité élevée. Les résultats indiquent, qu'en Ontario, la production de graines commence quand les arbres atteignent environ 25 cm de diamètre à hauteur de poitrine et augmente avec l'âge. Les gros arbres produisent souvent plus de 2000 cônes lors des bonnes années, soit une quantité comparable à celle des populations plus au sud. La proportion de samares contenant des graines pleines augmente avec la densité du peuplement, allant d'environ 8–10% chez les arbres isolés à plus de 20% dans les vieux peuplements à densité élevée. Quoique faibles, ces valeurs sont comparables à celles rapportées ailleurs dans l'aire de distribution de l'espèce. Les patrons de chute des graines suivaient une distribution leptokurtique autour des arbres individuels. Des caractéristiques du cycle vital autres que la viabilité des graines pourraient donc être la cause de la distribution restreinte et des faibles populations de *L. tulipifera* en Ontario.

[Traduit par la revue]

Introduction

Among plant species, life-history attributes such as flowering frequency, seed production, seed dispersal, and seedling establishment are crucial ecological determinants of recruitment success. In turn, the recruitment of new individuals into a population directly influences the size of a local species' population and is a measure of the degree to which extant populations may be maintained or new ones established (Harper 1977). The availability of seeds in suitable sites for germination is considered to be a critical factor affecting seedling establishment and hence the regeneration and maintenance of plant species' populations (Grubb 1977). Ultimately, therefore, life-history attributes that influence the demographic characteristics of a population play a significant role in determining the abundance of a species and the dynamics of its range.

For some tree species, recruitment of new individuals near the range margin is low compared with populations near the centre of the range (Kavanagh and Kellman 1986). In these situations, lower rates of seedling recruitment among peripheral populations may reflect reduced flowering or an inability to set viable seed. Among plant species that do not reproduce vegetatively, a reduction in the numbers of viable propagules might lower the rate of recruitment, which, in turn, could result in lower population densities.

In southern Ontario, Canada, a number of temperate tree species reach their northern range limits (Fox and Soper 1952; Maycock 1963; Hosie 1979; Argus and White 1982–1987). Many of these tree species are now considered rare in the province (Argus and White 1982–1987), which, in part, may be the result of significant forest clearance across much of the region. The remaining populations tend to be small and generally restricted to scattered woodlots in a highly fragmented landscape. Few studies (e.g., Maycock 1963; McCaw 1985) have investigated the population ecology of these tree species in the Canadian sector of their ranges.

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Liriodendron tulipifera L. (tulip-tree), a tree species reaching its northern geographical limits in southern Ontario, is found throughout much of the eastern deciduous forest zone (Beck and Della-Bianca 1981). Although its Canadian distribution has apparently never been extensive (Fox and Soper 1952; Cruise 1969), the species has recently been listed as rare in Ontario (Kavanagh *et al.* 1987). Among southern Ontario populations of *L. tulipifera*, little is known about its local ecology and population attributes. It is a minor component of most forest stands when present and appears to suffer from competition with *Acer saccharum* Marsh. and *Fagus grandifolia* Ehrh. on mesic sites (Maycock 1963). Elsewhere, *L. tulipifera* is a prolific invader of disturbed forest sites and abandoned farmland across a range of edaphic conditions (Fowells 1965; Beck and Della-Bianca 1981). In Ontario, however, *L. tulipifera* appears to be more conservative in its distribution. It is most abundant on wet-mesic or dry-mesic sandy soils (Maycock 1963) and is rarely observed invading abandoned farmland or cut-over areas in significant numbers (personal observation).

The primary objective of this study is to examine the fecundity and seed dispersal patterns of *L. tulipifera* in southern Ontario. Results are compared with seed productivity and dispersal data from studies in other parts of its range in an attempt to determine whether these life-history attributes can account for the observed limited distribution of *L. tulipifera* at the northern edge of its range.

Study area

Forest stands in southwestern Ontario with *L. tulipifera* were examined for seed production in both Rondeau (42°17′N, 81°51′W) and Pinery (43°15′N, 81°52′W) provincial parks and in three forest stands (Backus Woods (42°39′N, 80°30′W), Landon's Woods (42°47′N, 80°22′W), and the Smith Tract (42°44′N, 80°27′W)) in Norfolk County. Figure 1 indicates the location of these sites within the known range of *L. tulipifera* in Ontario. Seed traps were established in Landon's Woods (n = 47), a second-growth woodlot approximately 50–65 years old, and Backus Woods (n = 40), a predominantly old-growth forest. The density of *L. tulipifera* ranges from 3.8–15.3 stems/ha for the relatively isolated trees upwards to 24.2–31.9 stems/ha for the high-density stands. Differences between the low- and high-density stands are most apparent in the dominance of *L. tulipifera*, with basal areas ranging from 1.32–1.64 m^2/ha for the low-density stands to 4.10–4.46 m^2/ha for the high-density sites (Table 1).

Methods

Seed production

Estimates of total seed production per tree were made through the late autumn and winter following leaf fall (November–March). Seeds are produced in singe-winged samaras that are aggregated into conelike clusters (Harlow *et al.* 1979), which henceforth will be referred to as cones. Since the bottom whorl of samaras remain attached to the central stalk until the following spring, the mature, conelike fruiting bodies are clearly visible at this time. Visual counts of cones were obtained using 7 × 35 wide-angle binoculars. Between two and four cone counts per tree canopy were made. The final estimate recorded each year was therefore a mean of two or more individual counts. Estimated totals of 150–950 cones per tree were rounded to the nearest 50, whereas estimates of 1000+ cones per tree were rounded to the nearest 100. Since each flower produces a cone whether or not successful pollination occurs (Wright 1953; Boyce and Kaeiser 1961; McNight and Bonner 1961), these counts also reflect flowering intensity. The mean number of samaras per cone was determined by counting the number of samaras in each of 148 intact cones collected from 31 individual trees (maximum of 6 cones per tree). This measure was then used to estimate total samara production per tree.

Individual trees (n = 146), ranging in size from 17.0 to 88.0 cm in diameter at breast height (dbh), were monitored over a 3-year period (1984–1986) to estimate annual variation in total seed production. Data from marked trees were augmented with data from additional trees in 1985 (total n = 231) and 1986 (total n = 341) by including all *L. tulipifera* stems $>$10.0 cm dbh within 20 m of transects taken through forest stands in all study sites. Mature trees $>$70.0 cm dbh tended to be under-represented; therefore, additional searches were conducted to increase the number of estimates of seed production for tree stems in the larger size classes.

To assess total samara production, intact seed cones collected in autumn of 1983 from trees in Rondeau Park and Norfolk County were dissected. A maximum of five cones were collected from any one individual.

Seed viability

Samaras from Backus and Landon's woods were collected in seed traps placed beneath *L. tulipifera* canopies and were dissected to determine the number containing either single or paired filled seeds. Seed traps were monitored between 1983 and 1985 during autumn and early winter. Seed-trap design varied through the sampling period. In 1983, polyethylene bags were suspended from four anchored corner posts approximately 0.5 m above ground level. Small puncture holes in the base of each bag provided drainage. The mean surface catchment area of this trap design was 0.138 m^2. As a result of the destruction of several polyethylene traps following a severe windstorm in 1983, in 1984 and 1985, polyethylene bags were replaced by plastic trays with drainage holes at most locations. The surface area of this type of trap was fixed at 0.136 m^2. Mixed with the plastic trays were fifteen 0.4 m tall plastic buckets with a circular surface area of 0.068 m^2.

Seeds in plastic trays at ground level were susceptible to predation by small mammals, although predation of ripened *L. tulipifera* seed in the canopy by several species of birds (e.g., evening grosbeak (*Coccothraustes vespertinus*), purple finch (*Carpodacus purpureus*)) was also noted during fieldwork in late October and November. Several other animal species are reported to eat *L. tulipifera* seeds, including two species of deer mouse (*Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis*) (Hamilton 1941), golden mouse (*Ochrotomys nuttalli*) (Linzey and Linzey 1973), fox squirrel (*Sciurus niger*), gray squirrel (*Sciurus carolinensis*) (Trippensee 1948), and several species of seed-eating birds (e.g., northern cardinal (*Cardinalis cardinalis*) and American goldfinch (*Carduelis tristis*) (Tenes 1968)). Evidence of seed predation in the trays usually consisted of opened samaras left on location. Samaras destroyed in this manner were tabulated separately during the 1985 season.

Seed traps were monitored weekly in 1983 during the main seedfall period (October–December). During 1984 and 1985, seed traps were monitored less frequently, although the collection period was extended until mid-April for the 1984 seed year. This extended period was implemented to determine if any significant contribution of filled seed occurred beyond the main seedfall episode in late autumn. Counts of filled seed were expressed as a percentage of all samaras collected.

Seedfall and dispersal patterns

Seed traps were arranged radiating outward along four main axes (approximating north, east, south, and west) from three individual *L. tulipifera* stems (41.0, 59.0, and 81.5 cm dbh). These trees were located in low-density *L. tulipifera* stands on mesic sites. Three traps were placed at distances of approximately 2, 7, and 16–20 m (depending on understory characteristics) along each of the four main axes. In addition, four individual traps were placed 5–7 m from the main stem in positions corresponding to northeast, southeast, southwest, and northwest. A fourth mesic site tree (66 cm

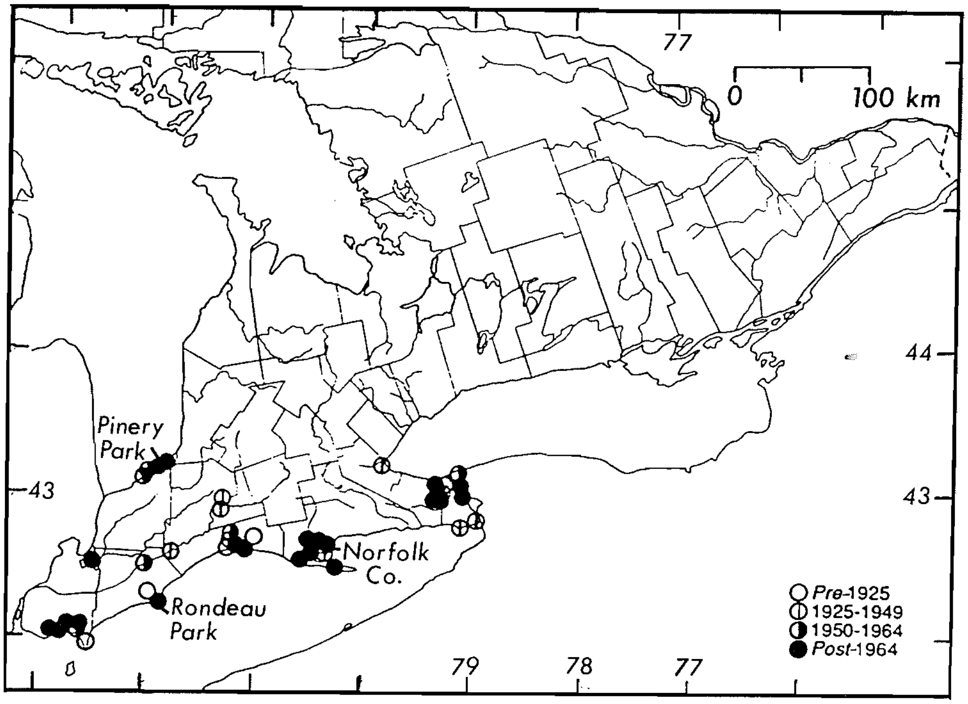

FIG. 1. Distribution of *Liriodendron tulipifera* in southern Ontario (after Kavanagh *et al.* 1987) indicating both historical and extant populations. Locations of the major study sites (Norfolk County, Rondeau, and Pinery provincial parks) are also indicated.

TABLE 1. Stand characteristics of the *Liriodendron tulipifera* study sites

Site	Mean dbh (cm)	Estimated age of seed trees (years)*	Density of *L. tulipifera* (stems/ha)	Basal area *L. tulipifera* (m^2/ha)
Low density				
Landon's Woods				
Tree 1	35.5	58	15.3	1.64
Tree 2	39.9	65	11.5	1.59
Backus Woods				
Trees 3 and 4	64.7	150 (tree 3) 167 (tree 4)	3.8	1.32
High density				
Landon's Woods	41.0	63-68	31.9	4.46
Backus Woods	51.4	120-150+	24.2	4.10

NOTE: Plots are centered on the individual tree or stand and represent circular areas with a radius of 50 m. Values include only *L. tulipifera* stems >15 cm dbh.

*Denotes the age of individual *L. tulipifera* seed trees for trees 1-4 and estimated range of ages for seed-bearing trees in high-density stands.

dbh) was sampled with eight seed traps radiating outward along the four principal cardinal points. Seed traps were placed along each axis at 2- and 10-m distances from the stem.

In addition, two higher density *L. tulipifera* stands, representing a second-growth and an old-growth stand on wet-mesic sites, were monitored with regularly placed grid networks of 15 and 16 traps. Sampling frequencies were as described earlier. Seedfall patterns were obtained for the 3-year period 1983-1985. Samara and filled-seed totals (1983-1985) were plotted on base maps showing all *L. tulipifera* canopy outlines within a 50 m radius circular plot originating at the centres of seed-trap plots. Isopleths of equal seedfall rain were then interpolated by hand to illustrate seed dispersal patterns.

Results

Seed production

Cone production for the 146 trees monitored from 1984 to 1986 is shown in Fig. 2. No significant differences were noted between this sample group and the additional trees sampled in 1985 and 1986, hence only results from the 146 trees are illustrated in Fig. 2. The overall pattern indicates an increasing cone production with stem diameter. Trees generally begin producing cones when they reach approximately 20-25 cm dbh, corresponding to ages of approximately 30-40 years (K.C. Kavanagh, unpublished data). At this stage of development, many trees do not appear to produce cones annually, although sporadic, light flowering was observed in trees as small as 14.5 cm dbh. Cone production became well established in trees larger than 35 cm dbh and increased through to the 75+ cm dbh size class where mean cone production levels reached 2200 cones per tree. Heavy seed production (>1000 cones per tree) begins once trees reach approximately 55-50 cm dbh. Maximum seed production recorded for an individual tree was 4000 cones (Rondeau Provincial Park, 1986; dbh = 97.0 cm).

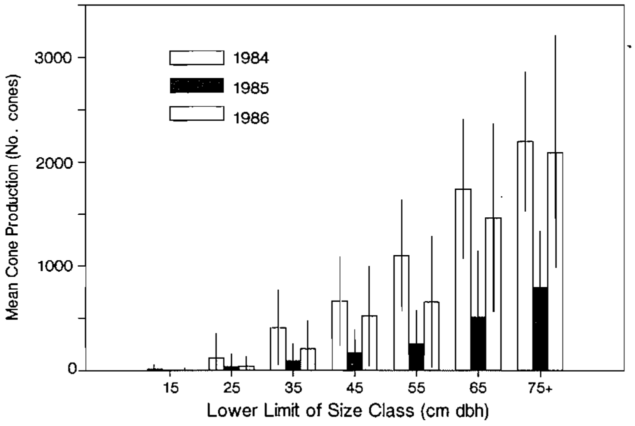

FIG. 2. Mean cone production per tree from 1984 to 1986 for Ontario populations of *Liriodendron tulipifera*. Error bars indicate one standard deviation unit on either side of the mean.

TABLE 2. Coefficients of variation for mean cone production among different size classes in Ontario populations of *Liriodendron tulipifera*

Size class (cm dbh)	*n*	Coefficient of variation 1984	1985	1986
<25	8	241.7	279.0	278.6
25-34.5	28	191.2	321.5	221.7
35-44.5	37	88.9	180.1	114.3
45-54.5	29	63.9	108.4	97.8
55-64.5	19	50.3	137.0	84.7
65-74.5	21	39.5	88.8	61.0
>74.5	4	30.4	85.9	35.3

Cone production levels in 1985 fell markedly across all size classes, many classes showing declines of 300-400% when compared with levels of 1984 (Fig. 2). In most size classes, cone production recovered in 1986 to similar levels recorded in 1984. Many trees in the smaller size classes (>35 cm dbh), however, continued to yield reduced quantities of cones even in 1986, with some individuals ceasing cone production altogether after 1984. Variation in cone production was greatest among individuals in small size classes and increased among all size classes in 1985, when the seed crop generally failed (Table 2). This pattern is indicated by the coefficients of variation for mean cone production, which ranged from 191.2 to 278.6% for small size classes and from 30.4 to 114.3% for large size classes in 1984 and 1986. In 1985, these values ranged from 279.0 to 321.5% among the small size classes and from 85.9 to 180.1% among the large size classes.

The mean numbers of samaras per cone (±1 SD) were 108.0 ± 14.2 (n = 76) and 114.4 ± 12.3 (n = 72) for Norfolk County and Rondeau Provincial Park, respectively. Individual cones ranged in size from 66 to 140 samaras.

Seed viability

The total number of samaras containing filled seed is listed in Table 3. The four trees occurring in low-density situations had the lower mean levels of samaras containing filled seed, ranging from 8.1 to 11.9% for the combined 1983-1985 period. These levels are lower than those for trees representative of high-density stands, where mean values for the same period were 15.2% (Landon's Woods) and 21.5% (Backus Woods). In Landon's Woods values ranged from 11.2% (1983) to 19.0% (1984). The higher 1984 value of filled-seed production coincides with a major increase in total cone production. Values for Backus Woods were markedly uniform, varying between 20.7% (1985) and 21.7% (1983). Samaras collected beneath trees with stems ranging in size from 21.5 to 95 cm dbh (all in relatively high density populations) in Rondeau Provincial Park (1984 data only) indicated that 17.0% contained filled seed. A linear regression was performed between (*i*) stand basal area of *L. tulipifera* (within circular plots of 50 m radius) and (*ii*) seed viability levels for the four trees in low-density stands and the two high-density stands. Results indicated a positive relationship ($r^2 = 0.67$; $p < 0.05$) between stand basal area and seed viability.

Samaras from the base of the cone were always empty and persisted on the tree well beyond the main seedfall period, often into the following spring. These samaras are reported to function as a support structure for samaras developing farther along the central stalk (Boyce and Kaeiser 1961). Most samaras near the tip of the cone were also empty and underdeveloped. A few samaras were found to contain two filled seeds. Such occurrences were lowest for trees in low-density stands (0.9%) and increased slightly to 3.6% for high-density stands (e.g., Backus Woods). Mean seed predation in the traps for 1985 was 15.5%. The value was highest in Backus Woods, at 21.4%. Undoubtedly, some of these samaras contained filled seed. The similarity in relative numbers of samaras with filled seed between 1985 and 1983 when traps were rodent proof for Backus Woods and Landon's Woods, however, indicates that only minor reductions in the filled seed count may have occurred as a result of seed predation on the ground.

Seedfall and dispersal patterns

Seedfall began in mid-October and continued until mid-November. By this time approximately 80-90% of the samaras had been released (Fig. 3). Trees in sites located inland from the shores of the Great Lakes (e.g., Landon's Woods) began dropping seed nearly 2 weeks earlier than those in sites in close proximity to the Lake Erie shoreline (e.g., Backus Woods). In 1984, some seed continued to fall throughout the winter, but this did not contribute more than 1-2% of the annual filled seed total.

Dispersal patterns of samaras generally indicated that a majority of samaras fall within a short distance of individual tree canopies (Fig. 4). High seedfall densities were limited to areas immediately below the canopy and outward for 5-10 m. Seedfall distributions are best described as leptokurtic in the vicinity of isolated trees. Patterns were less well defined in high-density stands but also suggested a majority of seed falling within close proximity of canopy trees (Figs. 5 and 6). A seed shadow to the east of the high-density stand in Landon's Woods is weakly defined (Fig. 5).

For the high-density stand in Backus Woods, there was an annual maximum of 353 filled seeds/m^2 recorded, with a 3-year maximum of 555 seeds/m^2. The 3-year total is an important consideration for seedling establishment since seeds often lose viability after this period, although some may remain viable in the soil for up to 7 years (Clark and Boyce 1964). In Landon's Woods, the annual maximum was 198 filled seeds/m^2, with a 3-year maximum of 380 seeds/m^2.

TABLE 3. Seed viability for *Liriodendron tulipifera* populations in Ontario

Site	Year	Samaras per filled seed	% samaras with filled seed	% samaras with 2 seeds
Low density				
Landon's Woods				
Tree 1	1983–1985	555/45	8.1	
Tree 2	1983–1985	707/84	11.9	
Backus Woods				
Tree 3	1983–1985	487/53	10.9	
Tree 4	1983–1985	260/28	10.8	
Total	1983–1985	2009/209	10.4	0.9
High density				
Landon's Woods	1983	663/74	11.2	
	1984	906/172	19.0	
	1985	536/73	13.6	
	1983–1985	2105/319	15.2	2.0
Backus Woods	1983	1164/252	21.7	
	1984	1538/332	21.6	
	1985	542/112	20.7	
	1983–1985	3244/696	21.5	3.6
Rondeau Provincial Park	1984	890/151	17.0	2.9
Overall total		8248/1375	16.7	

Discussion

Seed production

Seed production, as indicated by seedfall, in the Ontario populations of *L. tulipifera*, does not appear to be significantly different from that of more southerly populations (Carvell and Korstian 1955; Engle 1960; Tryon and Carvell 1960; Beck and Della-Bianca 1981). Although some point sources beneath high-density stands in Ontario indicated that the annual seedfall levels were significantly higher than those previously reported (up to approximately 1000/m^2), these areas were small and restricted to particularly high-density patches within larger stands.

Despite similarities in seedfall estimates, measurements of cone production in relation to tree size in Ontario are approximately half those reported for the piedmont of North Carolina (Carvell and Korstian 1955). The magnitude of this difference, however, may be artificial, as no sample size was given for that study and cone production in some Ontario trees was noted to approach those values reported for the piedmont. Furthermore, results from Ontario indicate that there can be significant annual variation in seed production. This suggests that measures of seed output for several years may be needed to obtain accurate estimates.

Viable seed production in *L. tulipifera* is consistently low or high among individual trees, indicating that some of the variation in seed production found within the size classes may be the result of inherent differences among individual trees (Wean and Guard 1940; Limstrom 1959). Drought stress may also influence seed production in some trees; a response that has been documented for other plant species (Harper 1977). For example, in 1984, a year that followed an unusually warm and dry summer in 1983, many trees of small stem diameter flowered but failed to do so in 1985 or 1986. This response may account for the large variation detected in cone production among trees in small-diameter classes. Variation in cone production in larger stem size classes was also believed to be influenced by drought, but could also be attributed to differences in canopy size due to breakage from windstorms and ice storms.

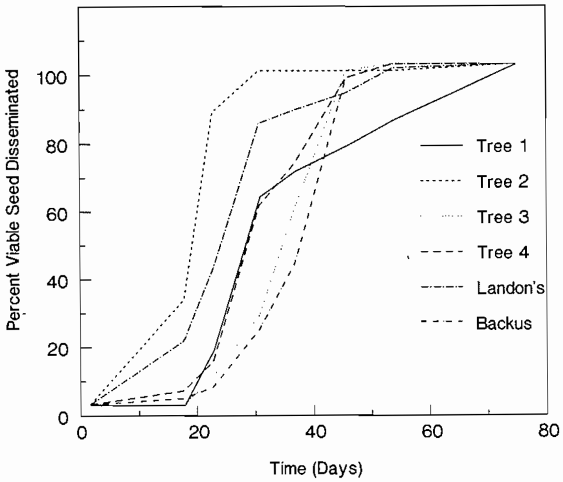

FIG. 3. Dissemination of viable seed through time for the four individual trees and two high-density stands monitored in 1983. Day 0 = October 4, 1983.

Seed viability

Among Ontario populations of *L. tulipifera*, the samaras produced on comparatively isolated trees contained fewer filled seed (approximately 10%) than samaras produced on trees in high-density stands (approximately 20% filled seed). Steinhubel (1962*b*) similarly reported that seed viability was twice as high for trees growing in groups as for isolated individuals. Ontario levels of seed viability are generally within the ranges reported for *L. tulipifera* populations in the central and southern parts of its range (Wean and Guard 1940; Guard and Wean 1941; Carvell and Korstian 1955; Boyce and Kaeiser 1961; Goebel and McGregor 1973).

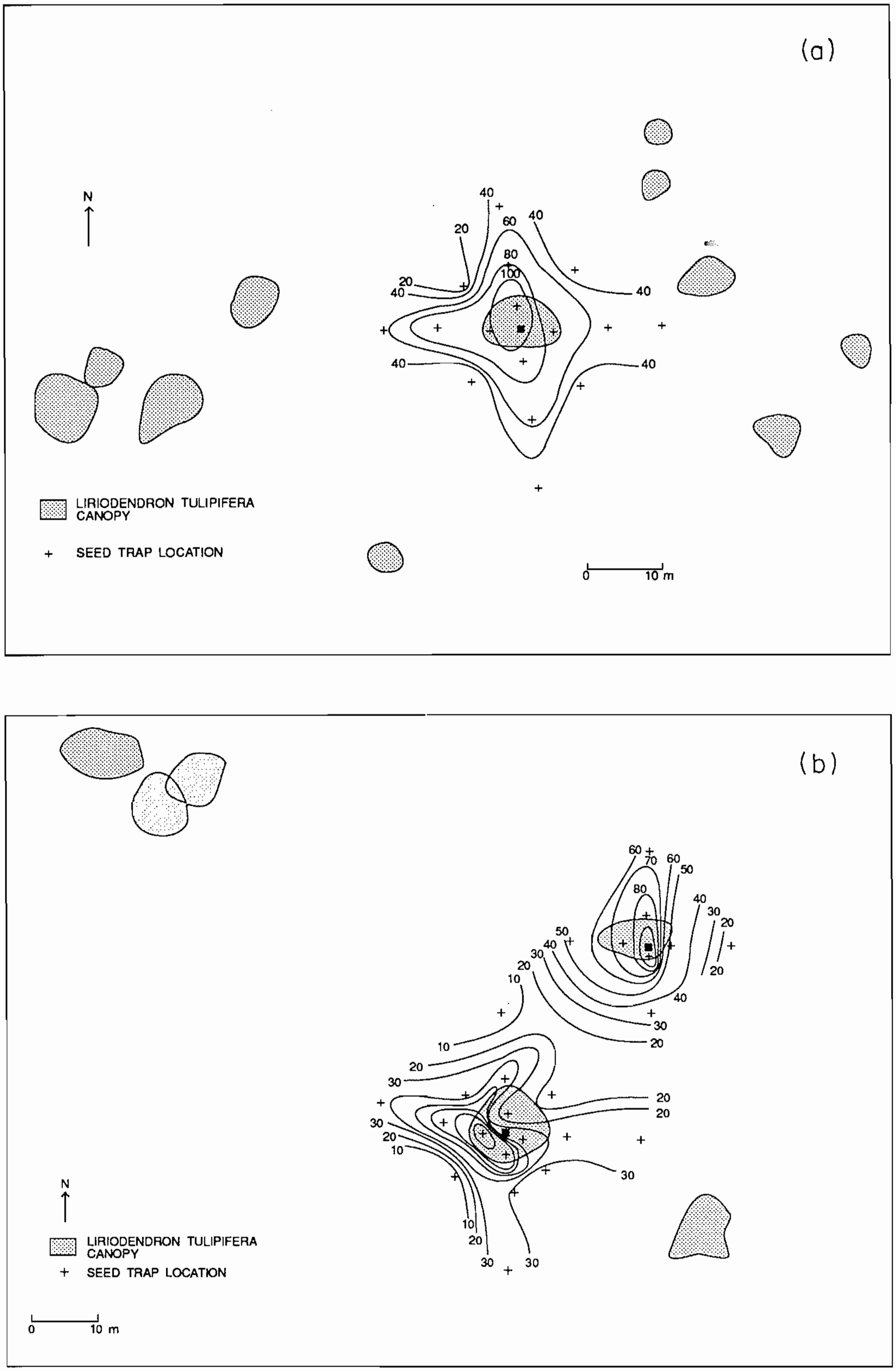

FIG. 4. Dispersal patterns of filled seed for three relatively isolated *Liriodendron tulipifera* trees (■) in Ontario for the period 1983-1985. (*a*) Tree No. 2 (65 years) from Landon's Woods. (*b*) Two mature trees in Backus Woods (aged 150 and 167 years). Isolines are hand drawn and represent equivalent values of seedfall input (no./m^2) at ground level.

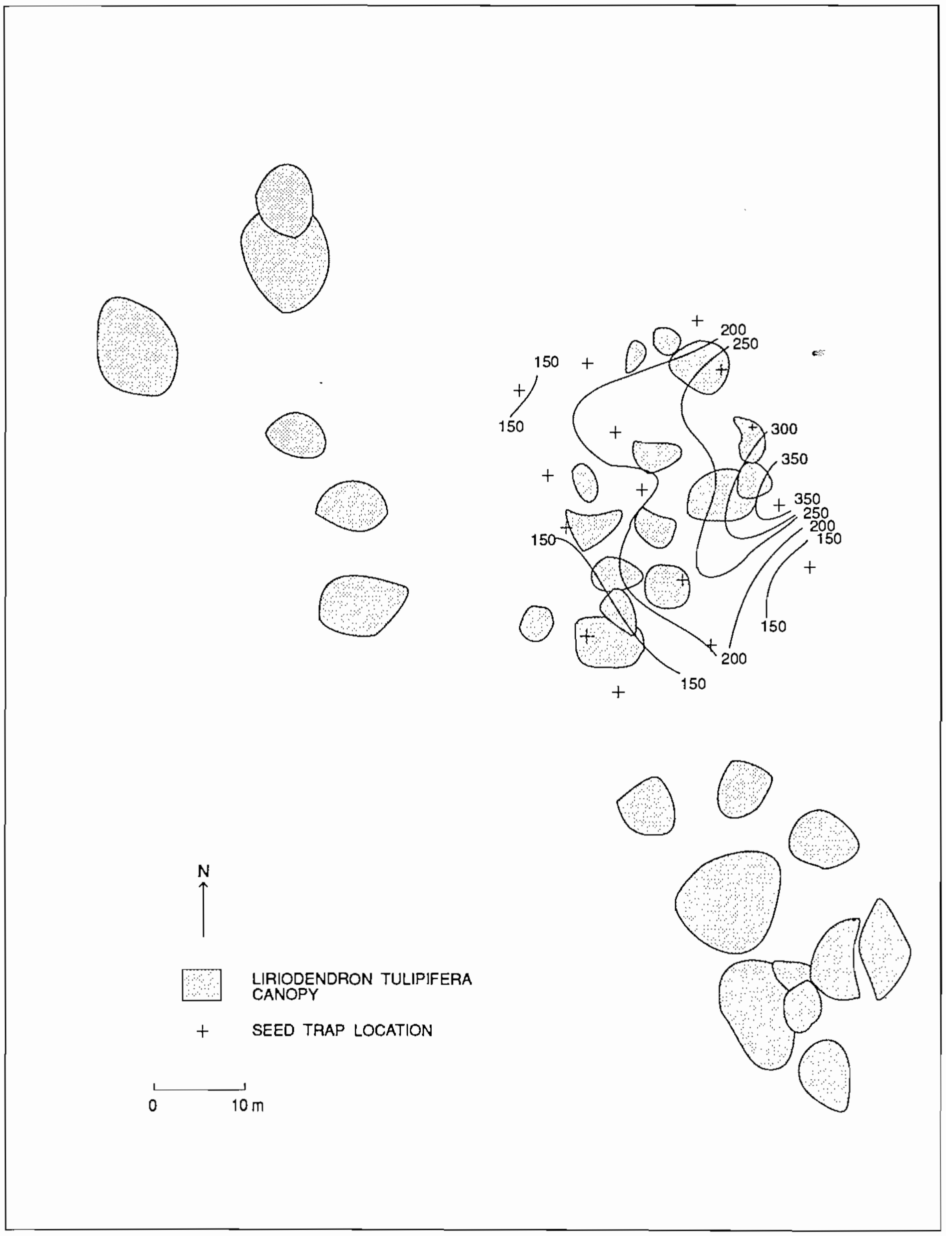

FIG. 5. Dispersal patterns of filled seed in a high-density, second-growth *Liriodendron tulipifera* stand in Landon's Woods for the period 1983–1985. Isolines are hand drawn and represent equivalent values of seedfall input (no./m^2) at ground level.

The low numbers of filled seed noted for *L. tulipifera* in Ontario are characteristic of the species and have generally been attributed to ineffective pollination. Although *L. tulipifera* is self-compatible, the number of filled seed produced by selfing is low. Even with cross-pollination, rarely more than 30% seed set is evident (Carpenter and Guard 1950; Wright 1953; Boyce and Kaeiser 1961; Wilcox 1963; Taft 1966; Thor *et al.* 1976). Under artificial conditions, pollination success is improved either through controlled pollination or when trees separated by significant distances (i.e., several kilometres) are crossed (Carpenter and Guard 1950; Steinhubel 1962*a*, 1962*b*, as cited by Schoenike 1980). Boyce and Kaeiser (1961) conclude that since *L. tulipifera* is not freely interbreeding under natural conditions, a low rate of gene interchange occurs among stands.

Thor *et al.* (1976) report that open-pollinated flowers produce fewer filled seed than those that were hand-pollinated. Their results suggest that pollinators do not travel far enough among neighboring trees to produce effective cross-pollination. Several studies indicate that selfing is common in *L. tulipifera* since most insect pollinators tend to travel from anther to stigma on the same flower or work principally on individual trees (Wright 1953; Steinhubel 1962*a*, as cited by Schoenike 1980; Taft 1966). Chemical treatments, girdling, and removal of a portion of the flowering buds have had little effect on seed yield (Istratova 1966, as cited by Schoenike 1980). This indicates that pollinator limitation, rather than resource allocation, is primarily responsible for the low pollination success and seed set. Therefore, differences in seed set between the high-density, young stand (50-year-old Landon's Woods) and the old-growth stand (Backus Woods) may, in part, be the result of differential pollination success. In 1983 and 1985, total samara counts were much lower at both sites than in 1984,

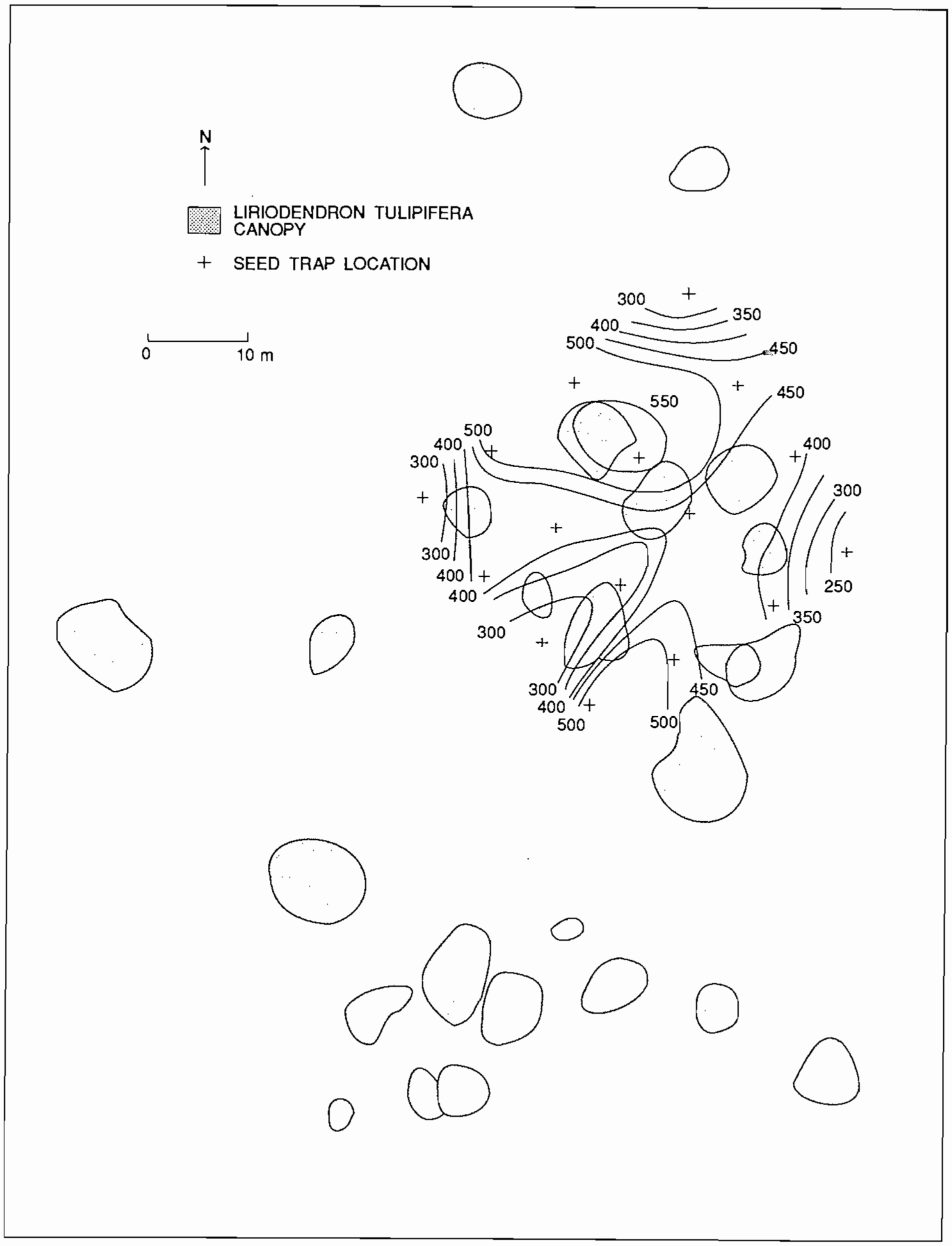

FIG. 6. Dispersal patterns of filled seed in a high density, old-growth *Liriodendron tulipifera* stand in Backus Woods for the period 1983–1985. Isolines are hand drawn and represent equivalent values of seedfall input (no./m^2) at ground level.

reflecting a reduction in flowering intensity during those years. While filled seed levels fluctuated with flowering intensity in Landon's Woods, relative filled seed levels were constant throughout the period in Backus Woods regardless of flower production. This may indicate that within the old-growth stand, flowering was consistently maintained above some minimum threshold for achieving successful pollination and maximum seed set.

Alternatively, the issue of tree compatibility must be considered. The old-growth, uneven-aged character of Backus Woods may have produced a heterogeneous population. This contrasts with Landon's Woods, where the majority of flowering *L. tulipifera* trees are relatively even aged, increasing the probability of close neighbors of similar parentage. Here, heavy flowering may be required to attract pollinator activity and increase the probability of long-distance outcrossing with compatible neighbors. Therefore, high-density, old-growth stands may be the most productive and stable in terms of maximizing viable seed output in Ontario.

An additional consequence of low rates of pollen exchange in *L. tulipifera* is that the vigor of seedlings that result from selfing is lower than that of seedlings that are derived from outcrossing. Thus, relatively few and less vigorous seedlings may establish in low-density *L. tulipifera* stands (Carpenter and Guard 1950; Wilcox 1963; Taft 1966; Thor *et al.* 1976).

Seedfall and dispersal patterns

Seedfall patterns surrounding the trees in this study are similar to those described for *L. tulipifera* elsewhere in its range (Engle 1960). Such leptokurtic seedfall distributions have also been reported for other tree species in forest stands with wind-dispersed seeds (Jemison and Korstian 1944; Boyer 1958; Cayford 1964; Cremer 1966; Gashwiler 1969;

Mair 1973; Dobbs 1976; Harper 1977; Green 1980; Hughes and Fahey 1988). Given seeds of similar size and weight, McCutchen (1977) found that seeds of *L. tulipifera* descend faster than some other wind-dispersed tree species (e.g., *Acer*). Their spinning motion, however, is more stable than samaras of other species, which may be an advantage in gusty winds. This facilitates relatively long flight distances (McCutchen 1977).

As *L. tulipifera* establishes in gaps (Barden 1979, 1980; Lorimer 1980), there appears to be little advantage to depositing a majority of seed in the low-light environment beneath a parent tree. *Liriodendron tulipifera*, however, can create large gaps with the death of mature individuals. The concentrated pattern of seedfall in close proximity to the parent tree may thus increase the probability of self-replacement. Given this seedfall pattern, it is predicted that the highest probability of seedling recruitment, following disturbance, will be in close proximity to the parent tree, regardless of stand density. In high-density stands, however, overlapping shadows of seedfall will collectively increase the seed rain at more distant sites. Consequently, population expansion outward from the main stand and the establishment of new populations may be more frequent adjacent to high-density stands.

Although seedfall patterns reported in this study show that dispersal of *L. tulipifera* seed is concentrated near the tree, the leptokurtic distribution implies that some viable seed must be dispersed well beyond the 30-m limits examined here. Nonetheless, the probability of large numbers of viable seed reaching safe sites more than 500–1000 m from the parents is low. Engle (1960) reported that only a few scattered seeds were collected 183 m (600 ft) from source trees.

Despite prevailing westerly winds in southern Ontario, strongly skewed seedfall distribution patterns were not apparent in most of the study plots. Engle (1960) found that the combined seedfall pattern after 2 years was displaced to the north and northeast of the tree canopies since most seedfall occurred during warm, dry weather with southerly or southwesterly winds. It was noted, however, that seedfall patterns in any given year could vary depending on weather conditions (Engle 1960).

Although results reported in this study indicate that measures of fecundity for *L. tulipifera* in Ontario are similar to populations elsewhere in its range, the continued isolation of these small populations is of concern. Dispersal patterns of seed indicate little opportunity for population expansion in the fragmented landscape of southern Ontario. Logging of remaining stands has increased the uniformity of size- and age-class structures, thereby potentially reducing levels of successful cross-pollination and seed set owing to reduced compatibility among neighboring trees of similar parentage. In combination, these factors may result in declining reproductive success, particularly where populations have been reduced to low densities.

Conclusions

Measures of fecundity in Ontario populations of *L. tulipifera* indicate that there is little overall difference in seed production, seed dispersal patterns, or seed viability in comparison with more southerly populations. Therefore, other life-history attributes of *L. tulipifera* may be determining its restricted distribution and low population levels in Ontario.

It is predicted that continued isolation of populations in the fragmented landscape of southern Ontario, together with limited long-distance dispersal of seed, will result in infrequent establishment of new populations. Reduced population densities may further produce lower quantities of filled seed and (or) vigorous seedlings, thereby lowering the probability of successful seedling recruitment. These two features require careful consideration in regard to conservation and management techniques for *L. tulipifera* in Canada.

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