

POLLEN PRODUCTION AND PLANT DENSITY AFFECT POLLINATION AND SEED PRODUCTION IN *TAXUS CANADENSIS*¹

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Abstract. Mean pollen production and mean nearest neighbor distance were recorded for several populations of *Taxus canadensis* and correlated with the proportion of ovules pollinated and seed set. Distance and pollen production together explained 86% of the variation in pollination success, each variable significantly adding to the regression when adjusting for the other. Seed set was correlated significantly with pollen production and nearest neighbor distance separately, but the multiple regression including the latter two variables was not significant. Seed set was correlated most strongly with pollination success and mean ovule production ($R^2 = 0.71$), suggesting that variation in seed set among *Taxus* populations was a combination of differences in pollen and resource availability.

Key words: *Apostle Islands*; plant density; pollen availability; pollen production; pollination efficiency; seed production; *Taxus canadensis*; wind pollination.

INTRODUCTION

The efficiency of wind pollination is generally assumed to decrease as the concentration of airborne pollen decreases (Regal 1982, Whitehead 1983). This low efficiency may be due to large distances between conspecifics, low pollen production by individuals, and poor pollen dispersal. These conditions are assumed to affect both ovule fertilization and seed production negatively.

Measurements of wind-borne pollen from point sources show highly leptokurtic dispersion (e.g., Wright 1952, 1953, Faegri and van der Pijl 1979), and consequently, as plant spacing increases, the probability of pollination is assumed to decrease. Studies of agricultural species (Bateman 1947, Sarvas 1968) support this assumption, but evidence from natural plant populations is limited and indirect (see, for example, Lemmen 1980, Farris and Mitton 1984). No quantitative relationships between pollination efficiency and pollen availability have been developed for natural populations of wind-pollinated species.

Determining the relationship between pollen availability and seed production in wind-pollinated species is important because of the potential for gene flow among populations and the influence of pollen availability on sex expression. Models of gene flow between plant populations, for example, are typically based on pollen dispersion curves from point sources (Koski 1970), but the behavior of a pollen cloud from point sources vs. that originating from diffuse population sources may be different (Levin and Kerster 1974).

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Most theories on sexual allocation strategies of plants assume that pollen availability typically does not limit seed production in plant populations (Charnov 1982, Willson and Burley 1983). Supporting studies usually involve a single population of a particular species. Pollen limitation of seed production has been observed in several species (Bierzychudek 1981), and pollen availability may vary among populations of a species (Allison 1987).

The difficulties in describing the relationship between pollen availability and pollination efficiency are: (1) finding plant populations covering a wide range of plant abundance; (2) simultaneously measuring pollen production and seed production in several populations; and (3) long-distance pollen dispersal among populations that complicates the dynamics of pollen dispersal within populations (Lanner 1966, Koski 1970). Long-distance pollen dispersal may cause significant pollination in otherwise presumably isolated populations (Squillace 1967).

Here I report on the relationship between plant spacing, pollen production, and pollination efficiency (estimated by both the proportion of ovules pollinated and ovules matured as seeds) in *Taxus canadensis* Marsh. All data discussed in this paper were collected from naturally occurring *T. canadensis* populations.

METHODS

T. canadensis is an evergreen, wind-pollinated, coniferous shrub found in the understory of moist deciduous and mixed deciduous-coniferous forests in the northeastern United States and southeastern Canada (Martell 1974). It is monoecious, producing separate male and female strobili on the same plant (Chamberlain 1966, Allison 1987). Female strobili are uni-

TABLE 1. Means of male strobilus and ovule production per branch, nearest neighbor distance, pollination success, and seed set of study populations in 1985. Data were calculated as described in the Results section. All sites are in zone 15.

Site	No. plants sampled	Male strobilus production*	Ovule production*	Nearest neighbor (m)*	Pollination success	Seed set	Site coordinates†
Apostle Islands							
Basswood Island	50	0.46	0.25	3.13	.231	.103	6 ₇₃ 700 m E/51 ₉₂ 500 m N
Rocky Island	97	1.90	0.28	3.13	.463	.134	6 ₇₆ 500 m E/52 ₁₁ 000 m N
Otter Island	57	4.20	2.24	0.20	.791	.541	6 ₇₃ 100 m E/52 ₀₆ 000 m N
Outer (closed)	92	22.17	3.06	0.11	.853	.393	6 ₉₃ 500 m E/52 ₁₆ 600 m N
Stockton Island	45	23.48	11.77	1.58	.576	n.a.‡	6 ₈₆ 700 m E/51 ₉₈ 100 m N
Outer (gap)	25	163.30	35.82	0.03	.932	.212	6 ₉₆ 100 m E/52 ₁₆ 500 m N
Cedar Creek	25	0.97	0.46	0.15	.473	.284	4 ₈₄ 300 m E/50 ₂₈ 100 m N
North Grey Cloud	31	87.25	9.24	0.03	.913	.309	5 ₀₀ 400 m E/49 ₆₂ 200 m N

* Means of male strobilus production, ovule production, and nearest neighbor distance are back-transformed from \log_{10} transformations of individual plant values. Transformed means were used in comparisons of means among populations (Allison 1987).

† Universal Transverse Mercator (UTM) Grid coordinates of the study sites (described in the Methods section).

‡ Not available.

ovulate; after fertilization, a female strobilus produces a single seed surrounded by a red, fleshy aril.

The forest understory is typically cooler than the canopy, creating a temperature inversion that restricts vertical movement of pollen (Levin and Kerster 1974). The decreased turbulence and wind velocity of the understory will also reduce pollen transport (Raynor 1967, Tauber 1967). As a result, the influence of long-distance pollen dispersal should be minimized, and pollination within a *T. canadensis* population should be most strongly determined by the plant density and pollen production within that population.

Most data were collected from several *T. canadensis* populations at the Apostle Islands National Lakeshore, an archipelago of 21 islands near the south shore of Lake Superior, where there is considerable variation in plant density and pollen production among *T. canadensis* populations (Allison 1987). In addition data were collected on sexual reproduction at two study sites in southeastern Minnesota. Precise location of all study sites is listed in Table 1.

At all sites I selected *T. canadensis* ramets or plants along transects that were systematically placed in each of the study populations. I recorded the distance to the nearest neighbor of each sample plant to the nearest centimetre. Mean nearest neighbor distance was then calculated for each population. I measured the production of male and female strobili and seeds in the sample plants in these populations in 1983, 1984, and 1985. Female strobili are uniovulate; thus female strobilus production is equivalent to ovule production. Regression analysis showed a strong correlation between the size of male strobili and the number of pollen grains per strobilus ($r^2 = 0.89$). I recorded no significant differences in the mean size of male strobili among several populations (Allison 1987). Counts of male strobili, therefore, are good estimates of plant pollen production.

I counted the number of developing ovules on sam-

ple plants ≈ 1 mo after the 1983 spring census on the Apostle Islands and at all study sites in 1984 and 1985. Earlier observations indicated that no mortality of developing seeds had occurred by this time. Ovules that did not develop were still present on plants but were yellow-white in color and small, easily distinguished from the green, swollen, developing ovules. Circumstantial support for the conclusion that developing ovules have been pollinated comes from hand-pollination experiments that increase the number of developing ovules (Allison 1987). Although fertilization of ovules typically occurs within 1 mo of pollination in *T. canadensis* (Dupler 1917), in the absence of direct, cytological evidence I cannot be certain that developing ovules were fertilized. Thus, I used this census to estimate pollination success (proportion of ovules pollinated) in the various populations. Ovules not developing at this time were assumed to have received no (or insufficient) pollen.

Seed set (proportion of ovules that become seeds) was measured in all populations beginning in mid-July and continuing into September. Ripe seeds were counted when I observed either a brown seed surrounded by a red, fleshy aril, or an expanded receptacle indicating that a ripe aril with seed had been removed. Considerable mortality of developing ovules occurs during the summer, although the proximate mechanisms controlling ovule abortion in *T. canadensis* are unknown.

RESULTS

Mean male strobilus and ovule production per ramet, nearest neighbor distance, pollination success, and seed set for all populations in 1985 are listed in Table 1. This was the last year data were collected and is representative for data from other years that were included in the regressions. Means of male strobilus production, ovule production, and nearest neighbor distance are back-transformed from \log_{10} transformations

of individual plant values. Transformed means were used in comparisons of means among populations (Allison 1987), and therefore were also used in regressions.

I plotted weighted means of pollination success and seed set against mean male strobilus production per plant and mean nearest neighbor distance for each population. Weighted means of pollination success and seed set were used in the regressions to reduce the effect of plants that produced only one or two ovules on population means and variances. These were calculated by multiplying each plant's ovule production by the number of ovules produced by that plant divided by the mean ovule production for the population. No significant differences were observed among years in the regression of either pollination success or seed set versus pollen production and nearest neighbor distance; thus the data from different years were combined into one regression (e.g., see Fig. 1).

Pollination success is a rapidly saturating positive function of male strobilus production (Fig. 1A) and a negative function of nearest neighbor distance or plant spacing (Fig. 1B). Regressions performed on \log_{10} transformations of both independent variables produced significant straight-line functions (male strobili: Fig. 2A, Table 3a; nearest neighbor distance: Fig. 2B). \log_{10} transformation of the independent variables was used to improve the fit of linear functions to the data, although it is apparent from Fig. 2A that some non-linearity remains. Because percentage data are obviously constrained while pollen production data are less so, some nonlinear relationship is inevitable.

Nearest neighbor distance and mean male strobilus production of a population were significantly negatively correlated (Table 2); high-density *T. canadensis* populations tended to have high male strobilus production per plant (see Table 1). This reflects the influence of past deer history on Apostle Islands populations used in the regression (see Discussion). Enough variability in the data set existed, however, so that both variables contributed significantly to the regression after adjusting for the other. Stepwise regression on pollination success indicated that male strobilus production contributed more to pollination success than did distance to nearest neighbor. Together male strobilus production and nearest neighbor distance accounted for 86% of the variance observed in pollination success among sites (Table 3b).

Seed set was not as well correlated with male strobilus production (Table 2 and Table 3c) or nearest neighbor distance (Table 2), although both correlations were significant. Stepwise regression showed that neither variable significantly added to the regression when adjusting for the other. Seed set is also indirectly related to these two variables by pollination success (Table 2; $P < .005$).

Ovule production is another factor that might influence pollination success and seed set. In fact, in a comparison among populations, the \log_{10} ovule production

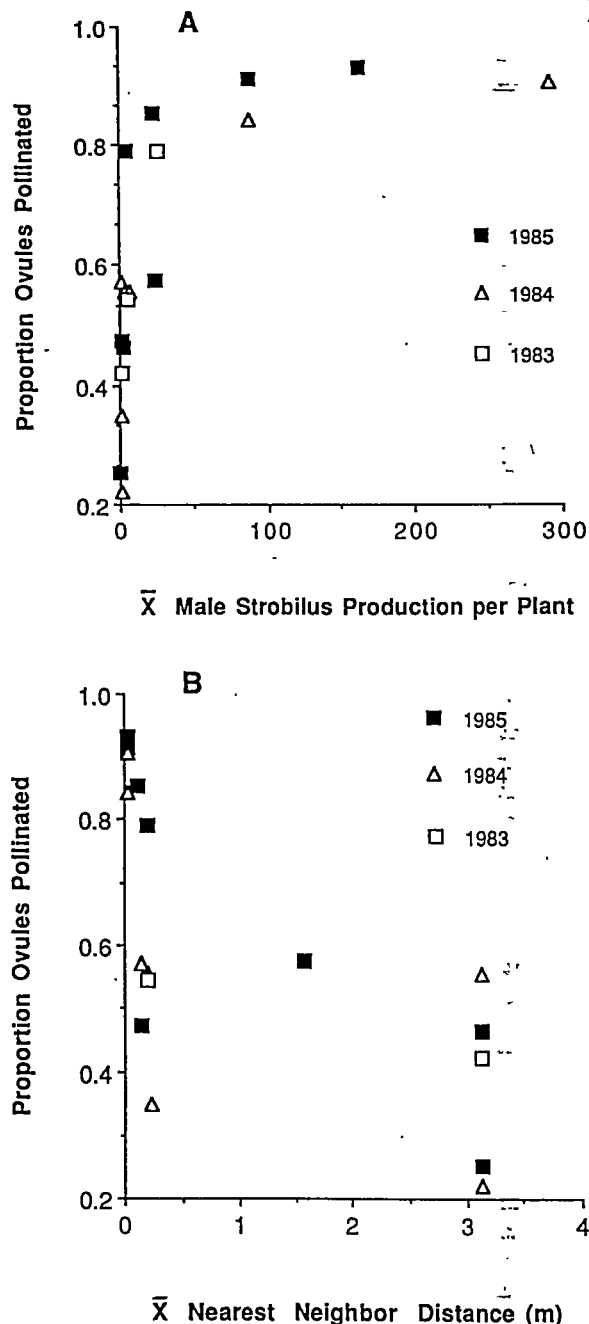


FIG. 1. Plot of pollination success (proportion of ovules fertilized) vs. (A) mean male strobilus production and (B) mean nearest neighbor distance of different *Taxus canadensis* populations.

is strongly correlated with both \log_{10} male strobilus production and pollination success (Table 2). When adjusting for male strobilus production, however, ovule production does not significantly explain additional variation in pollination success. The reverse is not true; male strobilus production adds significantly to the regression when adjusting for ovule production. Ovule production is significantly negatively correlated with

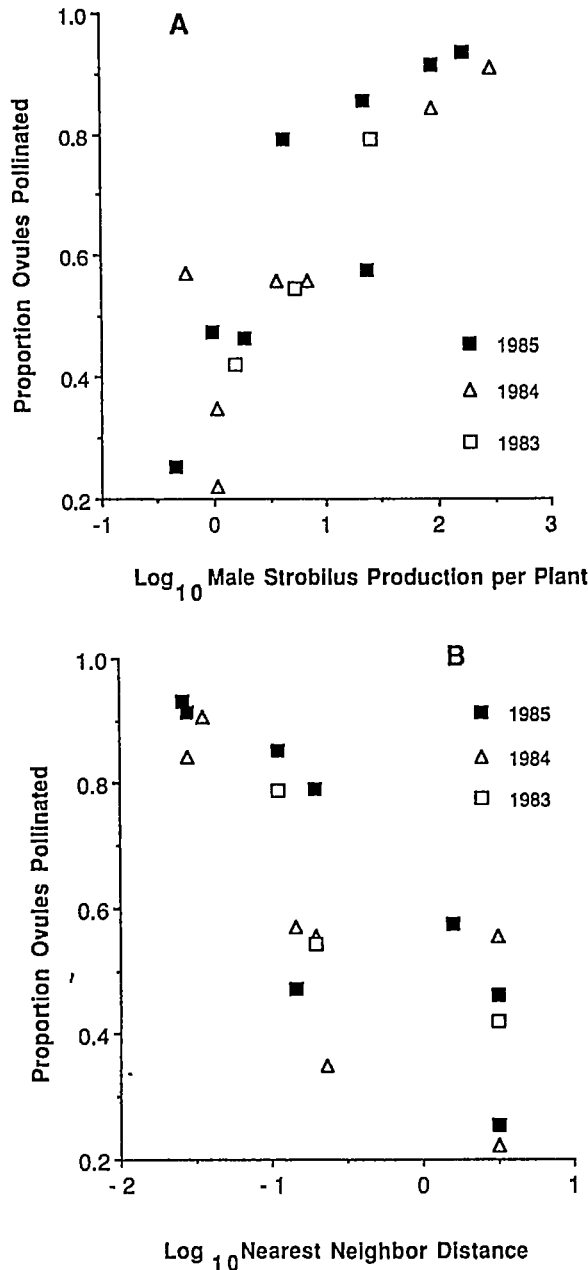


FIG. 2. Plot of pollination success vs. (A) \log_{10} male strobilus production and (B) \log_{10} nearest neighbor distance. Nearest neighbor distance is measured in metres. The regression equation for part A is given in Table 3a.

tion in natural populations of a wind-pollinated species. As expected, pollination success in *T. canadensis* populations is positively correlated with pollen production and negatively correlated with plant spacing. The similarity in the patterns of pollination success in different years and the significance of these patterns even when data are pooled from geographically separated populations is striking. If, for example, pollen production decreased in a population in one year, this was reflected in reduced pollination success in that population. Variables such as spring weather conditions apparently had little influence on pollen dispersal and pollination (see also Sarvas 1962, Matthews 1963). Others have noted that the morphology of wind-pollinated flowers ensures that pollen release generally occurs under optimal conditions for pollen transport (e.g., Bianchi et al. 1959).

The use of spacing as a measure of abundance emphasizes the leptokurtic character of pollen dispersal and implies that the pollination dynamics of a wind-pollinated plant is dependent on its nearest neighbor. Expressing abundance as plant density may be a more appropriate measure, as it emphasizes that the pollen reaching a plant has an areal or diffuse origin rather than a point origin (Levin and Kerster 1974). In the current study, I do not have the data to resolve this issue adequately.

Mean nearest neighbor distance can be converted to density (Southwood 1978). Using the latter variable in the regression will not affect the magnitude of the regression coefficient, but the sign of the coefficient obviously will be reversed. Nevertheless, the average distance between plants does accurately describe pollen availability for the average plant in a population, particularly when combined with mean pollen production. In particular, the two variables interact to influence pollination efficiency. For example, plant spacing on Basswood and Rocky Island are identical (Table 1), but the higher pollen production of Rocky Island corresponds to higher pollination success for *T. canadensis* individuals in that population. In contrast, Stockton Island and Outer Island have similar levels of pollen

TABLE 2. Matrix of regression coefficients for \log_{10} male and \log_{10} female strobilus production, \log_{10} nearest neighbor distance, pollination success, and seed set. All regressions are significant at $P < .05$ with $n = 18$.

Variable	Variable				Seed set
	\log_{10} male	\log_{10} female	\log_{10} nearest	Pollination success	
\log_{10} male	...				
\log_{10} female	.945	...			
\log_{10} nearest	-.702	-.631	...		
Pollination success	.872	.789	-.810	...	
Seed set	.558	.569	-.499	.713	...

seed set when the latter is adjusted for pollination success (Table 3d). In populations with equivalent pollination success, those populations that, on average, have fewer ovules per plant will have higher seed set.

DISCUSSION

This is the first study that quantitatively relates pollination efficiency to plant spacing and pollen produc-

TABLE 3. Summary of regression equations for pollination success and proportion seed set. Eq. 3a corresponds to the plot in Fig. 2B.

a)	$Y = 0.42 + 0.23X_1; r^2 = 0.75$
	Y = pollination success (percent ovules pollinated)
	$X_1 = \log_{10}$ mean male strobilus production per ramet
b)	$Y = 0.41 + 0.16X_1 - 0.12X_2; r^2 = 0.86$
	Y = pollination success
	$X_1 = \log_{10}$ mean male strobilus production per ramet
	$X_2 = \log_{10}$ mean nearest neighbor distance (measured in metres)
c)	$Y = 0.22 + 0.08X_1; r^2 = 0.31$
	Y = proportion ovules setting seed
	$X_1 = \log_{10}$ mean male strobilus production per ramet
d)	$Y = -0.03 + 0.57X_1 - 0.008X_2; r^2 = 0.71$
	Y = proportion ovules setting seed
	$X_1 = \log_{10}$ mean male strobilus production per ramet
	$X_2 = \log_{10}$ mean nearest neighbor distance (measured in metres)

production, but the greater spacing between plants on Stockton results in lower pollination success.

Seed set (in comparison to pollination success) is not as well correlated with pollen production or plant spacing, possibly reflecting the greater variety of factors influencing seed set. For example, inbreeding depression resulting from increased self-fertilization in low-density populations of wind-pollinated species (e.g., Farris and Mitton 1984) could account for the reduced seed set in low-density *T. canadensis* populations. *T. canadensis*, however, appears to be highly self-fertile (Allison 1987).

Rodent predation on developing seeds may reduce seed set in *T. canadensis*. I frequently observed empty husks of developing seeds on the forest floor, and small seed receptacles bearing tooth marks were often left on the plant, indicating that developing seeds had been removed. The intensity of seed predation on *T. canadensis* varies annually and among populations (T. D. Allison, *personal observation*).

Differences in resource availability may also influence patterns of seed set observed among the different sites. The interaction between resource availability and pollen availability as an influence on seed set is suggested by the equation in Table 3d, which combines pollination success and ovule production as variables determining seed set. When pollination success (influenced by pollen availability) in two populations is equivalent, populations with high ovule production per plant will have lower seed set than populations with low average ovule production per plant. This suggests resource limitation of seed production (Stephenson 1980). Within *Taxus* populations, however, the relationship between ovule number and seed set was weak and frequently not statistically significant. Although resources may influence seed set in *T. canadensis*, the majority of variation observed in seed set among sites (51%) can be explained by differences in mean pollination success. The latter, in turn, is strongly correlated with pollen production and plant spacing.

The regression equations can be used to estimate pollination success and seed set in other *T. canadensis* populations. To test the regression model, I used data on male strobilus production, nearest neighbor distance, and pollination success collected in 1985 from Oak Island of the Apostle Islands. These data were *not* used in building the original regressions. *T. canadensis* plants on Oak Island are small and, on average, produce few male strobili. I substituted the following values into the equation of Table 3b: \log_{10} no. of male strobili produced per ramet = 0.47; \log_{10} of the nearest neighbor distance (measured in metres) = -0.07. The predicted pollination success for Oak Island based on these parameters is 0.494; the observed value was 0.485. The extremely high predictability (98%) of the equation in this particular instance may be fortuitous. The results suggests, however, that the relationship between pollination success, plant spacing, and male strobilus production in *T. canadensis* is strong and may be usefully applied to estimating the importance of pollen availability as a regulator of pollination success and seed set in *T. canadensis* populations throughout the species' range.

The regulation of seed set by pollen availability in plant populations is widely debated, although most models of plant sexual reproduction assume that resources and not pollen limit seed set (Willson and Burley 1983, Lloyd 1984, but see Bierzychudek 1981). In fact, the relationships described in this paper were possible due to the wide natural variation in pollen availability, a result of the differences in plant density and pollen production recorded in the various populations of *T. canadensis*. The wide variation in plant density and pollen production that I measured is due principally to the deer history of the Apostle Islands. Several islands currently have deer or had deer in the past. Other islands never had deer. The yew populations on islands that have deer now or had deer in the past consist of widely spaced plants that produce little pollen and have low levels of pollination success and seed set. Hand-pollination significantly increased seed set in these populations, indicating that seed production was pollen limited (Allison 1987).

All of these relationships are based on population means; mean pollen production per plant and mean nearest neighbor distance estimate the average amount of pollen produced at an average distance from the average plant. There is considerable variation in pollination efficiency among plants within populations, however, indicating that pollen availability is not the same for all plants. Greatest variation among plants is recorded in populations with low mean pollination success. In part, this is a statistical artifact related to the nature of percentage data, but in these populations some individuals have high levels of pollination and seed set.

Although the pollen cloud is derived from the entire population, a variety of factors could result in local variation in the density of the pollen cloud reaching a

plant. Characteristics of a plant's nearest neighbors, e.g., their distance and pollen production, or the amount of pollen produced by the plant, if self-fertile, could be important. For example, *T. canadensis* is self-fertile, and I observed a weak, but significant relationship between a plant's pollination success and its pollen production in *some* but not all, Apostle Islands populations (maximum $r = 0.25$). On Rocky Island, however, pollination success of individual plants is not significantly correlated with nearest neighbor distance or the pollen production of the plant's nearest neighbor. This indicates that determination of the factors influencing pollen availability for individual wind-pollinated plants is not simple. Chance, in particular, may play a large role.

The variation in the pollen availability within a population has important consequences for our attempts to model sexual allocation in plants. For example, wide variation in gender has been observed among individuals of plant populations (e.g., Primack and Lloyd 1980). Typically, such variation is assumed to reflect the influence of plant status (i.e., the size, age, and overall resource budget of the plant; Lloyd and Bawa [1984]) and not pollen availability on plant reproductive success. There is growing evidence, however, that pollen availability varies among populations of a species (this study; Worthen and Stiles 1988). Pollen availability may also vary among individuals within a population, limiting seed set in some plants while resources may limit seed set in others. Variations in reproductive success and sex expression among plants could result from variations in resource and pollen availability.

The equations described here (Table 3) may provide a quantitative basis for studying changes in sex expression in response to changes in pollen availability. For example, from a plant's perspective, the equation estimating pollination success (Table 3b) also estimates the probability of one of the plant's ovules being pollinated (e.g., for Oak Island, 0.494, see above). This probability increases as pollen availability increases, indicating that a plant's gain in female fitness is partly influenced by pollen availability. Female flowers or structures (i.e., ovules) function as pollen collectors in wind-pollinated plants. Increasing the number of ovules when pollen availability and the probability of pollination is low ensures that a minimum number of ovules will be pollinated. At low levels of pollen availability, greater fitness gains for a wind-pollinated plant may be achieved by increased allocation to ovules (female function) rather than to pollen (male function). Further work in wind-pollinated species is required to determine the importance of pollen availability to seed production and plant sex expression.

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