

SEX AMONG THE FLOWERS: THE DISTRIBUTION OF PLANT MATING SYSTEMS

DONNA W. VOGLER^{1,2} AND SUSAN KALISZ^{3,4}*Department of Biological Sciences, The University of Pittsburgh, Pittsburgh, Pennsylvania 15260*¹*E-mail: voglerdw@oneonta.edu*³*E-mail: kalisz@pitt.edu*

Abstract.—Previous reviews of plant outcrossing rate survey data have agreed that predominant selfing and predominant outcrossing are alternative stable states of mating system evolution. We reanalyzed the most recent data and plot outcrossing rates as a continuous variable rather than as a class variable. Wind-pollinated species are indeed bimodal. However, the shape of the distributions for animal-pollinated species reveals that intermediate rates of outcrossing are common (49% of species fall between 20% and 80% outcrossing). Consequently, we suggest that mating system is best considered a continuous rather than a discrete character of plant populations.

Key words.—Intermediate outcrossing, mating systems, mixed mating, outcrossing rates, selfing rates, *t*-values.

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Three major surveys of plant outcrossing rate (*t*) data have been published (Schemske and Lande 1986; Barrett and Eckert 1990; Barrett, Worley and Harder 1996) and have examined how closely the data fit the bimodal distribution of *t* predicted by Lande and Schemske's (1985) model. These surveys divide *t* estimates into five equal classes (*t* = 0–20, 21–40, 41–60, 61–80, and 81–100) and use a categorical χ^2 analysis to test a null hypothesis of equal distribution across classes. Previous surveys all concluded that the deficiency of species in the intermediate classes (i.e., 21–40, 41–60, 61–80) supports the idea that predominant selfing (*t* < 0.20) and predominant outcrossing (*t* > 0.80) are alternative stable endpoints of mating system evolution (e.g., Lande and Schemske 1985; Barrett and Eckert 1990; Barrett et al. 1996; Charlesworth and Charlesworth 1987).

However, the grouping of data into classes is an important decision that may affect the interpretation of results for any categorical analysis. In the earliest survey of plant outcrossing rates the relatively large bin size of 20% increments of *t* was likely statistically necessary given the limited data available (i.e., *n* = 55 total published outcrossing rates available to Schemske and Lande 1985). However, "When the sample size is small or the class intervals are wide, the general impression one obtains of the frequency distribution may depend in part on exactly how the class limits are defined. Shifting the class limits may remove the appearance of bimodality or change the apparent location of the mode." Sokal and Rolf (1995, p. 25.).

Despite the fact that we now have fivefold more data, Schemske and Lande's (1985) original broad categories remain the standard in plant mating systems literature. We believe that the continued use of broad outcrossing rate classes, and the lack of resolution associated with large class sizes has contributed to the general acceptance of selfing and outcrossing as two, relatively symmetrical and evolutionarily stable states. Similarly, the related ideas, the rarity of inter-

mediate outcrossing rates, or even where to define the limits of selfing and outcrossing are also likely to be influenced by this original histogram. For example, Barrett and Eckert (1990) considered species with *t* estimates less than 20% as selfing, whereas the inbreeding depression study of Husband and Schemske (1996) designated selfing species as those with any *t* estimate lower than 45%.

Using the most recent plant *t* estimates (data kindly provided by S. C. H. Barrett and C. G. Eckert), we applied three graphical approaches to examine the distribution of average *t* estimate among species. We treat wind-pollinated species and animal-pollinated species separately, as in other surveys (Aide 1986; Barrett and Eckert 1990). In the first graphs (Figs. 1a, 2a), *t* is divided into the usual 0.20 increments, although here we include a sixth category for species with *t* estimates greater than 1.0. The second graph (Figs. 1b, 2b) is similar, but here we use classes of 0.05 increments. In the third graph (Figs. 1c, 2c), we rank-ordered the *t* estimate data, determined the rank as a cumulative percentile value for each data point, then graphed cumulative percentile versus ranked *t* estimate. Using cumulative percentile values allows distributions of the ranked *t* estimate data for animal- and wind-pollinated species to be compared directly.

All graphs indicate a discontinuous distribution of *t* for wind-pollinated species (Fig. 1), which is in agreement with other workers (Aide 1986; Barrett and Eckert 1990). That is, wind-pollinated species are either highly selfing or highly outcrossing and intermediate *t* values are rare. By contrast, animal-pollinated species exhibit a bimodal, but continuous distribution of *t* estimates (Figs. 2b 2c).

Moreover, the finer scale graphs (Figs. 1b,c, 2b,c) reveal several trends not apparent in the histograms using the larger bin size (Figs. 1a, 2a). In particular, the selfing and outcrossing ends are not symmetric for either wind- or animal-pollinated species. At the selfing end, species are clustered in the lowest bin (*t* ≤ 0.10) for both wind- and animal-pollinated species. This similar lower bound (< 0.1) for highly selfing species of both pollination modes could be due to common selective or genetic factors acting in both groups. Alternately, the common lower bound could be due to properties of the

² Present address: Biology Department, State University of New York at Oneonta, Oneonta, New York 13820.

⁴ Corresponding author.

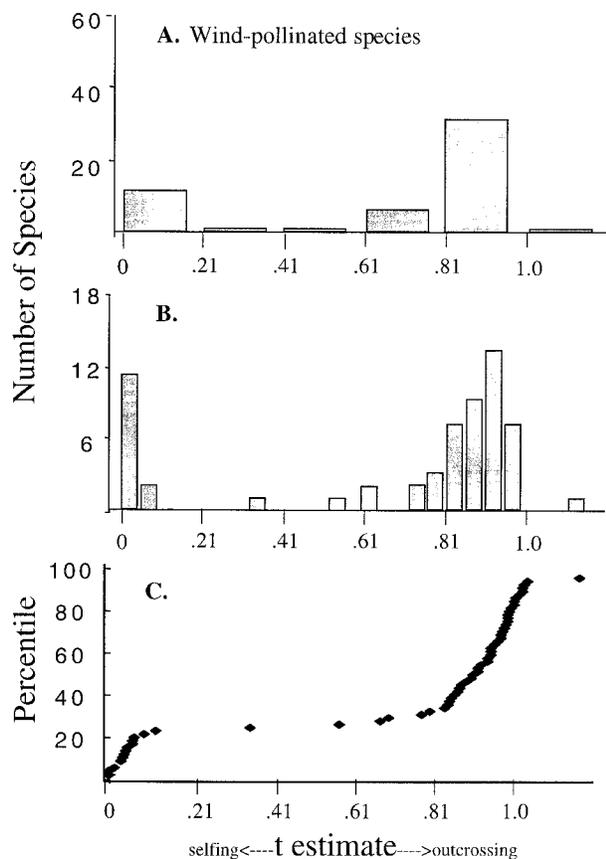


FIG. 1. Distribution of t estimates for $n = 59$ wind-pollinated plant species presented in three graphical forms. (A) Frequency histogram with data classes of 0.20 intervals. (B) Frequency histogram with data classes of 0.05 intervals. (C) Plot of percentile vs. ranked t estimate data.

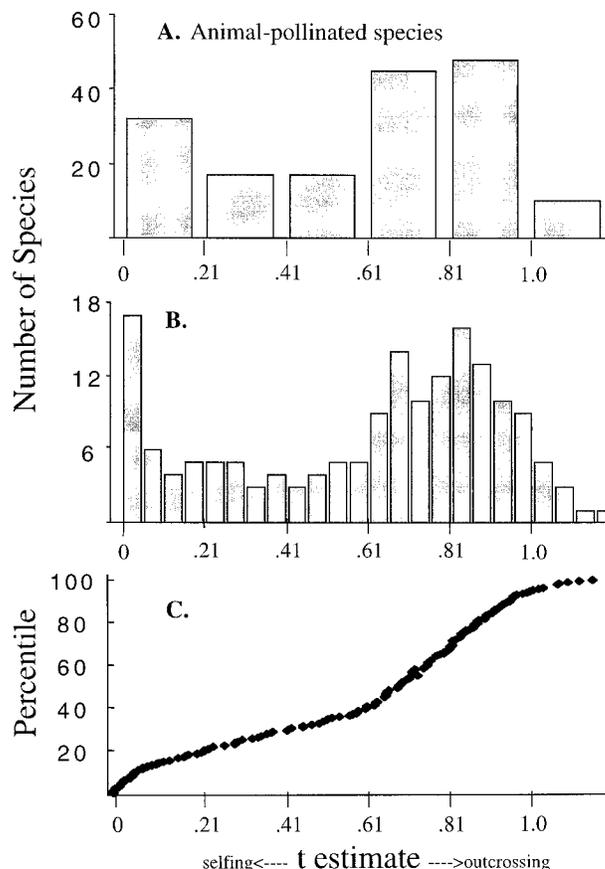


FIG. 2. Distribution of t estimates for $n = 169$ animal-pollinated plant species presented in three graphical forms. (A) Frequency histogram with data classes of 0.20 intervals. (B) Frequency histogram with data classes of 0.05 intervals. (C) Plot of percentile versus ranked t -estimate data.

estimator itself, since low t values (higher selfing rates) have lower associated standard errors than do high t values (D. Schoen, pers. comm.).

The distribution of outcrossing rates and the high outcrossing ends are broader than the selfing end of the distribution for both pollination modes, but differ dramatically between wind- and animal-pollinated species. This is seen in the fine scale histograms (Figs. 1b, 2b) but is even more obvious in the ranked distributions (Figs. 1c, 2c). The high outcrossing end of the distribution for wind-pollinated species spans 80–100%. In contrast for animal-pollinated species, the high outcrossing span is twice as wide and continuous, with many species of intermediate t values. The 82/169 species (49%) falling above 20% t and below 80% t for animal-pollinated species contrasts sharply with the 6/59 species (10%) falling in the gap between the selfing and outcrossing ends for wind-pollinated species.

The differences between the two distributions (Figs. 1c, 2c) at intermediate t values are especially interesting, since the common factors that generate intermediate t values (i.e., spatial aggregation of plants within populations and mating with related plants (e.g., Uyenoyama and Waller 1991; Uyenoyama et al. 1993; Harder and Barrett 1995)) are equally likely to occur in wind- or animal-pollinated species. One

contributing factor could be that the presence of wind is a relative constant in natural populations, whereas pollinator population abundance and visitation rates are highly variable (Horovitz and Harding 1972; reviewed by Burd 1994). This pollinator unpredictability could select for the capacity for both self- and outcross- pollination for each flower (Baker 1955; Schoen and Brown 1991; Lloyd 1979, 1988, 1992; Schoen et al. 1996), but only in the animal-pollinated species. Clearly, the broader range of outcrossing for animal-pollinated species revealed in this analysis (Fig. 2c) suggests that biotic pollen vectors add a layer of complexity in the evolution of outcrossing rates not seen in wind-pollinated species.

Graphing outcrossing rate data as a continuous variable highlights regions of the distribution of evolutionary interest not obvious in previous histograms with few classes. The graphs emphasize the discrete nature of outcrossing rate when it truly exists (i.e., for wind-pollinated species) and reveal that intermediate outcrossing rates predominate for animal-pollinated species. The shapes of the distributions for the two pollination groups also indicate regions where important ecological and/or genetic processes related to plant mating may be acting in common (e.g., selfing end) or differently (e.g., outcrossing end). Deeper insights into the evolutionary driv-

ers of plant mating systems are likely to be revealed by models and experiments combining both ecological and genetic/phylogenetic factors (e.g., Waller, 1986; Uyenoyama, et al. 1993; Schoen et al. 1996; Johnston 1998). Because these graphs reveal that intermediate t rates are so prevalent in natural populations, it is likely that the “well-trod evolutionary pathway” between outcrossing and selfing proposed by Stebbins (1974) may be of special interest for animal-pollinated species.

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