

## Wind of change: new insights on the ecology and evolution of pollination and mating in wind-pollinated plants

Jannice Friedman\* and Spencer C. H. Barrett

Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks St, Toronto, Ontario, M5S 3B2, Canada

Received: 13 November 2008 Returned for revision: 17 December 2008 Accepted: 9 January 2009 Published electronically: 14 February 2009

• *Background* The rich literature that characterizes the field of pollination biology has focused largely on animal-pollinated plants. At least 10% of angiosperms are wind pollinated, and this mode of pollination has evolved on multiple occasions among unrelated lineages, and hence this discrepancy in research interest is surprising. Here, the evolution and functional ecology of pollination and mating in wind-pollinated plants are discussed, a theoretical framework for modelling the selection of wind pollination is outlined, and pollen capture and the occurrence of pollen limitation in diverse wind-pollinated herbs are investigated experimentally.

• *Scope and Conclusions* Wind pollination may commonly evolve to provide reproductive assurance when pollinators are scarce. Evidence is presented that pollen limitation in wind-pollinated plants may not be as common as it is in animal-pollinated species. The studies of pollen capture in wind-pollinated herbs demonstrate that pollen transfer efficiency is not substantially lower than in animal-pollinated plants as is often assumed. These findings challenge the explanation that the evolution of few ovules in wind-pollinated flowers is associated with low pollen loads. Floral and inflorescence architecture is crucial to pollination and mating because of the aerodynamics of wind pollination. Evidence is provided for the importance of plant height, floral position, and stamen and stigma characteristics in promoting effective pollen dispersal and capture. Finally, it is proposed that geitonogamous selfing may alleviate pollen limitation in many wind-pollinated plants with unisexual flowers.

**Key words:** Wind pollination, reproductive assurance, pollen limitation, geitonogamy, sex allocation, inflorescence architecture, mating systems.

### INTRODUCTION

*As a large quantity of pollen is wasted by anemophilous plants, it is surprising that so many vigorous species of this kind abounding with individuals should still exist in any part of the world; for if they had been rendered entomophilous, their pollen would have been transported by the aid of the senses and appetites of insects with incomparably greater safety than by the wind. . . . It seems at first sight a still more surprising fact that plants, after having been once rendered entomophilous, should ever again have become anemophilous.*

Charles Darwin (1876, p. 409)

Wind pollination (anemophily) is a derived condition in flowering plants and has arisen independently in numerous families. Charles Darwin was perplexed by the evolution of this seemingly inefficient pollination mechanism from animal pollination, and yet this transition is commonplace among angiosperm families. Wind pollination has evolved at least 65 times from animal-pollinated ancestors, and approx. 10% of angiosperm species rely on wind pollination (Linder, 1998; Ackerman, 2000). Phylogenetic analyses indicate that wind pollination evolves more often in certain clades, most probably because they have morphological features conducive to wind pollination. For example, traits such as small, unisexual flowers and dry pollen may facilitate transitions to wind pollination (Linder, 1998; Friedman and

Barrett, 2008). However, in comparison with other angiosperm reproductive transitions (e.g. the evolution of selfing from outcrossing and dioecy from hermaphroditism), remarkably little is known about the microevolutionary forces responsible for the evolution of wind pollination, and the paucity of plant groups showing intraspecific variation in pollination mode, including animal and wind pollination, has impeded experimental investigations. Our knowledge of the reproductive ecology of most wind-pollinated plants is quite rudimentary, and the functional relationships between pollination and mating are poorly understood.

Previous reviews on wind pollination largely focused on morphological traits that facilitate pollen release and capture (Whitehead, 1969; Regal 1982; Niklas, 1985; Ackerman 2000), characters that facilitate the evolution of wind pollination (Linder, 1998) and the prevalence of mixed wind and animal pollination – ambophily (Culley *et al.*, 2002). The same suite of reproductive traits is commonly associated with anemophily in many unrelated families and comprises the wind pollination syndrome (Faegri and van der Pijl, 1979). The utility of pollination syndromes in animal-pollinated plants has been questioned (Waser *et al.*, 1996), although their reality in many groups is surely beyond doubt (Fenster *et al.*, 2004). The traits typically associated with wind pollination (Table 1) are well established and tend to be less variable, and perhaps for this reason the notion of a ‘wind pollination syndrome’ has not attracted much scepticism.

Our review provides an overview of current understanding of key processes in the pollination and mating of anemophilous

\* For correspondence. E-mail jannice.friedman@utoronto.ca

TABLE 1. Some characters typically associated with wind vs. animal pollination

Wind pollination	Animal pollination
Many flowers	Few flowers
Small or absent petals	Large petals
Floral colour greenish or whitish	Floral colours contrasting, bicoloured
Nectaries absent	Nectaries present
Flowers unscented	Flowers scented
Styles feathery	Styles solid
Ovules per flower few or one	Ovules per flower many
Pollen size less variable	Pollen size highly variable
Pollen grains many	Pollen grains few
Pollen ornamentation absent	Pollen ornamentation present
Protogyny	Adichogamous or protandrous
Unisexual flowers	Hermaphrodite flowers
Synchronous flowering	Less synchronous flowering
Open habitats	Closed habitats
Temperate distribution	Tropical or temperate distribution
High conspecific density	Low conspecific density
Higher gene flow	Lower gene flow
Lower net speciation rates	Higher net speciation rates

There are numerous exceptions to these associations, but many of the traits listed for wind pollination collectively describe the wind-pollination syndrome.

plants, and challenges some traditionally held assumptions, which may have biased understanding of the functional biology of wind pollination. Contrasts are drawn with knowledge of similar processes in animal-pollinated plants and important areas that lack empirical data or theory are highlighted. We begin by discussing the conditions that may favour the evolution of wind pollination, focusing on the role of pollinator loss, with wind pollination providing a reliable alternative. We then consider some of the demographic and genetic consequences of wind pollination, including the effects of wind pollination on effective population size and gene flow. Having established a framework for understanding the evolution of wind pollination and its ecological consequences, we then turn our attention to particular features of wind-pollinated species that are fundamental to pollination and mating. Current theory and empirical investigations on sex allocation in wind-pollinated species are reviewed, and novel perspectives on the role of floral morphology and inflorescence architecture in pollen dispersal are provided. Finally, we conclude by discussing how strategies that promote outcrossing in animal-pollinated species are implemented in wind-pollinated plants.

## THE EVOLUTION OF WIND POLLINATION AND ITS ECOLOGICAL AND DEMOGRAPHIC CONSEQUENCES

Two principal questions concerning the evolution of wind pollination from animal-pollinated ancestors that have defied simple answers are: (1) what are the selective mechanisms driving the evolution of wind pollination? and (2) which evolutionary pathways are involved in the transition? There is remarkably little concrete information about either of these issues, although it may be easier to speculate on the selective conditions under which wind pollination evolves. Several

review papers have speculated on environmental circumstances favouring the evolution of wind pollination (Regal, 1982; Whitehead, 1983; Cox, 1991; Culley *et al.*, 2002), but there has been no rigorous treatment of the issue.

### Theoretical considerations

There is a rich theoretical literature on reproductive transitions in the angiosperms, such as the evolution of selfing (e.g. Uyenoyama *et al.*, 1993) and the evolution of gender strategies (e.g. Charlesworth, 1999). However, remarkably, there has been no theory developed for the evolution of wind pollination. Theoretical approaches for understanding the evolution of wind pollination might include ESS models based on sex allocation and gain curves, classical population genetic approaches, or simulation models that consider the timing and effectiveness of pollen dispersal for animal vs. wind pollination under various demographic scenarios.

A large body of theory investigates evolutionary strategies for dividing resources among female and male function in plants for various life history, reproductive and ecological situations (e.g. Charlesworth and Charlesworth, 1981; Charnov, 1982; Lloyd, 1984). The transition from animal to wind pollination could be explored similarly with models that seek the ESS allocation to female and male function and pollinator attraction, which is not needed for wind pollination. Contrasting allocation scenarios might affect female and male fertilities differently, depending on gain curves and the effectiveness of animal vs. wind pollination. Here, we briefly outline a modeling framework that could be elaborated further.

Consider a hermaphroditic plant species that is primarily animal pollinated, but wind coincidentally disperses some fraction of its pollen. The fixed pool of resources that individual plants invest in flowering is divided proportionally among primary female ( $F$ ) function, primary male ( $M$ ) function and pollinator attraction ( $A$ ), with the constraint that  $F + M + A = 1$ . The quantity of pollen delivered and removed by animals varies positively with investment in attraction, whereas the success of wind pollination depends only on investment in primary sex function and the effectiveness of wind as a vector ( $\gamma$ ). The final model would consider two dispersal phenotypes, a common type and a rare invader, and then find the allocation pattern that cannot be invaded by any alternative pattern. Each phenotype would have its own version of eqns (1) and (2) below for female and male fitness components, respectively. Here, we present equations for the common type. The female component of fitness is proportional to resources invested in ovules ( $F$ ) multiplied by the fraction of ovules that are fertilized, which depends on the amount of pollen delivered by both insects and wind:

$$w_f \propto F[\pi_a(A^{k_1}) + \pi_w(\gamma^{k_2})] \quad (1)$$

where  $A = 1 - F - M$ , and  $\pi_a$  and  $\pi_w$  are the amounts of pollen delivered by insects and wind respectively, and are functions of  $A$  and  $\gamma$ . Equation 1 holds when seed production is pollen limited, otherwise  $w_f \propto F$ . The male component of fitness is proportional to the resources invested in pollen ( $M$ ), the pollen removed by insects ( $p$ ), which depends on a

plant's attractiveness, and the pollen removed by wind:

$$w_m \propto M \left\{ p(A)^{k_3} + \left[ 1 - p(A) \right]^{k_4} \gamma \right\} \quad (2)$$

where  $A = 1 - F - M$ . Using this approach one could identify the pollination conditions specified by exponents  $k_1, k_2, k_3$  and  $k_4$  that select for variants with reduced allocation to attraction, which instead rely more on wind pollination. The model above is for illustrative purposes only, and one would need to insert specific functions for  $\pi_a(A^{k_1})$ ,  $\pi_w(\gamma^{k_2})$  and  $p(A)$ , and account for competition of pollen from different dispersal phenotypes for ovule fertilization. In addition to identifying conditions that might select for wind pollination, this approach could provide insight on the stability of ambophily.

#### Ecological context for the evolution of wind pollination

The evolution of wind pollination in animal-pollinated lineages is thought to occur when physical and biological conditions render biotic pollination less reliable (Whitehead, 1969; Regal, 1982; Cox, 1991). Under such conditions it might be advantageous for individuals to decrease the proportion of pollen dispersed by animals, and increase the proportion dispersed by wind. Wind pollination might evolve when pollinators are scarce, absent or deliver poor quality pollen (Weller *et al.*, 1998; Goodwillie, 1999), such as when plants colonize areas with low insect abundance (Berry and Calvo, 1989; Gomez and Zamora, 1996). In these situations, plants may use a combination of animal and wind pollination, either sequentially or simultaneously (reviewed in Culley *et al.*, 2002). However, it is unclear whether ambophily is an evolutionarily stable strategy selected for its flexibility, or is simply an intermediate condition during the transition to complete wind pollination. More work is needed on ambophily to establish its frequency and evolutionary relationships with animal and wind pollination.

The evolution of wind pollination will be favoured in taxa that possess morphological traits that fulfil the aerodynamic requirements of pollen dispersal and capture. Plants with small flowers, exerted stamens and short or no corollas may be more likely to evolve wind pollination, because pollen dispersal and capture are not impeded by large and/or complex perianth structures. Plants with these features are usually unshowy and pollinated by generalist pollinators, which may often deliver poor quality pollen because of their local foraging behaviour (Charlesworth, 1993; Bawa, 1994; but see Renner and Feil, 1993). Genera with both animal- and wind-pollinated species, such as *Schiedea* and *Thalictrum*, are instructive in this regard because the animal-pollinated species have small relatively inconspicuous flowers, which are visited by generalist pollinators. The open, exposed morphology of flowers in these groups probably facilitated the evolution of wind pollination (Kaplan and Mulcahy, 1971; Weller *et al.*, 2006).

The most common explanation for why wind pollination evolves from animal pollination is that it is favoured by selection when pollinators are unreliable. This implies that populations receiving unsatisfactory pollinator service become

pollen limited, and wind pollination evolves because it provides reproductive assurance. However, selection for reproductive assurance is thought to be one of the major factors in the evolution of self-fertilization in animal-pollinated hermaphrodite plants (Eckert *et al.*, 2006). Indeed, Darwin believed that reproductive assurance was the chief reason for the evolution of selfing in plants (Darwin, 1876). Interestingly, the concept of reproductive assurance has seldom been extended to consider wind-pollinated plants.

We conducted a large-scale comparative analysis and found that wind pollination evolves more often in animal-pollinated lineages with unisexual flowers (Friedman and Barrett, 2008). In lineages with unisexual flowers the evolution of selfing through autonomous self-pollination would be unlikely and wind pollination may replace selfing as a mechanism providing reproductive assurance. According to this hypothesis, insufficient pollinator service resulting in pollen limitation could elicit two quite different evolutionary transitions, depending on the floral condition of ancestral populations. In populations with hermaphroditic flowers, autonomous self-pollination would relieve pollen limitation, resulting in the evolution of selfing. In contrast, in populations with unisexual flowers, wind pollination may serve the same role by increasing cross-pollination. A similar scenario may have occurred in *Schiedea* in which dichinous species suffer from pollinator limitation and the origin of wind pollination is evident (Weller *et al.*, 1998). Whether transitions from animal to wind pollination are commonly driven by pollinator limitation is not known. Unfortunately, the lack of species with both animal- and wind-pollinated populations has impeded empirical investigation.

#### Pollen limitation and pollen dispersal

The idea that wind pollination evolves as a means of reproductive assurance implies that pollen limitation may be infrequent for wind-pollinated plants. Unfortunately, despite a burgeoning literature for animal-pollinated species (Burd, 1994; Larson and Barrett, 2000; Ashman *et al.*, 2004), information on the prevalence of pollen-limited reproduction in wind-pollinated groups is sparse. Recently, there have been several studies showing pollen limitation in wind-pollinated trees in fragmented habitats (Fox, 1992; Knapp *et al.*, 2001; Totland and Sottocornola, 2001; Sork *et al.*, 2002; Koenig and Ashley, 2003), but we have almost no information for herbaceous plants (but see Davis, 2004; Davis *et al.*, 2004).

To investigate this issue, we studied ten herbaceous species, comprising eight monoecious *Carex* species and two dioecious species (*Rumex acetosella* and *Thalictrum dioicum*) growing at the Koffler Scientific Reserve, Ontario, Canada. We tested whether female fertility in populations was pollen limited by comparing seed set in open-pollinated plants with those that received supplemental pollen. The experiments revealed that only one of the ten species showed significantly greater seed set when flowers received supplemental pollen (Fig. 1). The rarity of pollen limitation in these species suggests that pollen loads are sufficient to ensure full seed set. Further work is needed on a diversity of wind-pollinated taxa to assess the frequency of pollen limitation in comparison with animal-pollinated plants where it has proven to be surprisingly

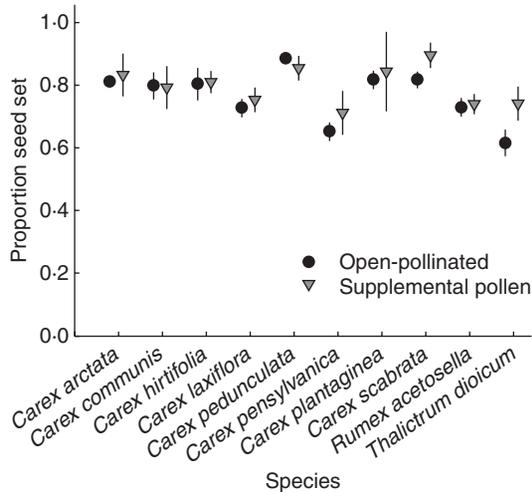


FIG. 1. Pollen limitation is infrequent in wind-pollinated plants. The data show seed set ( $\pm$  s.e.) for ten species that were open-pollinated or received supplemental pollen by hand pollination. All species were studied at the Koffler Scientific Reserve, (44°03'N, 79°29'W) Ontario, Canada in their natural habitats during summer 2004 and 2005. Values presented are the mean of 20 individuals for each treatment. Seed set was measured as the proportion seed set/spike for the *Carex* species, and seed set/plant for *R. acetosella* and *T. dioicum*. All species are uniovulate, making classification of successful seed production straightforward. *Carex scabrata* is the only species for which there was a significant difference between the pollination treatments (intact mean = 0.82, s.e. = 0.02; supplemental mean = 0.89, s.e. = 0.04;  $F_{1,33} = 11.33$ ,  $P < 0.001$ ).

common, occurring in 62 % (Burd 1994) and 73 % (Ashman *et al.*, 2004) of the studies investigated. If wind pollination does evolve primarily as a mechanism of reproductive assurance, we predict that pollen limitation will be less common than it appears to be in animal-pollinated plants.

Fundamental to any consideration of pollen limitation is the density of conspecific plants and pollen transport distances. Wind-dispersed pollen has a leptokurtic distribution from point sources (Bateman, 1947; Gleaves, 1973; Levin and Kerster, 1974), so that the seed set of recipients should decrease rapidly with distance from the pollen donor. However, few studies have examined the role of density in governing pollen limitation in wind-pollinated plants. Although large population sizes and high densities often characterize populations of wind-pollinated species, several studies have demonstrated that mating is quite local and neighbourhood composition can have profound consequences. For example, pollination success in *Taxus* was negatively correlated with plant spacing (Allison, 1990), and in *Spartina alterniflora*, an invasive grass, the low-density leading edge of a local invasion suffered Allee effects (Davis *et al.*, 2004). In two dioecious *Thalictrum* species occurring at low density, increased distance to male plants reduced seed set (Steven and Waller, 2007); and in *Festuca pratensis* most pollen was deposited within 75 m of donors (Rognli *et al.*, 2000). Similarly, in dioecious *Rumex nivalis*, increasing distance between males resulted in reduced pollen loads and decreased seed set (Stehlik *et al.*, 2008). Trees in fragmented populations in anthropogenically disturbed habitats can have average pollen dispersal distances as low as 65 m (Knapp

*et al.*, 2001; Sork *et al.*, 2002). Thus, there is evidence that relatively small-scale variation in plant density can have consequences for pollination, but how commonly this translates into pollen limitation of seed set is unclear.

Both pollen dispersal and plant density can have consequences for the genetic structure of plant populations. Hamrick *et al.* (1979) reported that wind pollination was associated with higher levels of genetic diversity, larger effective neighbourhood sizes, reduced inbreeding and less genetic differentiation between populations than occurs in animal-pollinated plants. Similarly, Loveless and Hamrick (1984) proposed that because long-distance pollen dispersal and background pollen levels prevent genetic differentiation over large geographic areas, wind-pollinated species should have larger effective population sizes ( $N_e$ ) and reduced subdivision within populations. However, the allozyme data used in these comparative surveys were comprised of only two taxonomic groups – conifers and grasses – so generalization is problematic. The very short duration of pollen viability in many wind-pollinated species (Dafni and Firmage, 2000) may limit long-distance gene flow. As discussed above, the dispersal distance of most wind-borne pollen is surprisingly short and the overall significance of long-distance gene flow in wind-pollinated plants remains unclear.

Highly synchronous flowering and a short duration of anthesis can be viewed as strategies that limit the quantity of pollen that fails to reach stigmas in many wind-pollinated species. For example, wind-pollinated prairie species have narrower phenological curves than those that are insect pollinated, due either to shorter flowering times or to greater flowering synchrony (Rabinowitz *et al.*, 1981). While synchronous, predictable phenology favours intraspecific pollen transfer, it may also reduce the amounts of heterospecific pollen transfer among sympatric species. Grass species flower at distinctive times of the day for brief periods of 15–20 min (Gregory, 1973), and gene flow between two rice species, *Oryza sativa* and *O. glaberrima*, was partially reduced by diurnal differences in flowering (Sano, 1989). Although there is no evidence of seasonal partitioning of mating among species in anemophilous communities (Bolmgren *et al.*, 2003), wind-pollinated species may be able to discriminate between conspecific and heterospecific pollen prior to deposition on stigmas through different pollen behaviours in the aerodynamic environments generated around stigmas (Niklas and Buchmann, 1987; Linder and Midgley, 1996). If wind-pollinated species commonly limit their exposure to interspecific pollen by flowering at predictable times, or by preferentially capturing conspecific pollen, this would challenge the traditional view that pre-zygotic barriers to interspecific pollination are unlikely in wind-pollinated species (Grant, 1949).

## SEX ALLOCATION AND POLLEN DISPERSAL

### Male-biased sex allocation

Male-biased sex allocation commonly occurs in wind-pollinated species and is particularly associated with large plant size (McKone, 1987; Burd and Allen, 1988; Solomon, 1989; Aizen and Kenigsten, 1990; Ackerly and Jasienski, 1990; Fox, 1993;

Dajoz and Sandmeier, 1997; Pannell, 1997; McKone *et al.*, 1998). Male fitness is usually assumed to be an approximately linear function of resource investment into pollen production, because wind is unlikely to saturate with pollen (Charlesworth and Charlesworth, 1981; Charnov, 1982; Klinkhamer and de Jong, 1997) and indeed there is limited support for this (Schoen and Stewart, 1986). This pattern contrasts with the saturating gain curves generally assumed for animal-pollinated plants. However, male fitness may depend non-linearly on pollen dispersal, rather than linearly on pollen production (Burd and Allen, 1998). Larger plants are more effective at dispersing pollen, because they tend to be taller and release pollen at higher points. Pollen dispersal distances are greater when pollen is released at elevated heights; because wind speeds are higher, there is often less intervening vegetation, and pollen takes longer to settle out of the airstream (Levin and Kerster, 1974; Okubo and Levin, 1989). Thus, unlike animal-pollinated plants, size-dependent sex allocation should select for increasing maleness with height (Bickel and Freeman, 1993; de Jong and Klinkhamer, 2005).

Theoretical research on sex allocation in wind-pollinated plants has considered the conditions under which male-biased sex allocation is maintained. Sakai and Sakai (2003) found that the relative size of the pollen dispersal to seed dispersal area in large vs. small plants determines whether they should exhibit male-biased ESS sex allocation vs. female-biased sex allocation, respectively. Pollen transfer efficiency (the proportion of pollen captured) and competitive sharing among male flowers affects sex allocation, and more reproductive resources should select for increasing maleness (Masaka and Tanada, 2006). Thus, adaptive patterns of sex allocation should favour greater male function and particularly increased maleness in larger plants.

Fitness returns in wind-pollinated plants may depend more on relative plant height than absolute height. Smaller plants may perform better at capturing pollen, while larger plants are more effective at dispersing pollen to their neighbours. Size-dependent sex allocation occurs in monoecious *Ambrosia artemisiifolia*, where taller plants have relatively more male allocation than smaller plants (McKone and Tonkyn, 1986; Ackerly and Jasienski, 1990; Traveset, 1992; Lundholm and Aarssen, 1994). By using shading treatments to simulate the effect of neighbours, Paquin and Aarssen (2004) demonstrated that when size is constrained because of shading, a decrease in plant size is associated with a decrease in maleness and an increase in femaleness.

We investigated the effect of shading on plastic sex allocation and its influence on the expression of dichogamy in *A. artemisiifolia*. The results demonstrate that there is a trade-off in female and male function (Fig. 2). Plants in shade treatments were shorter, protogynous and produced more female flowers, whereas plants in sun treatments were taller, protandrous and produced more male flowers. Under field conditions, small plants often occur in shaded environments and relatively tall plants are more likely to grow in full sun. Using light intensity to perceive neighbourhood composition may enable plants to maximize their success as either pollen donors or recipients. For wind-pollinated plants, plastic sex allocation may give individuals the flexibility to alter gender expression

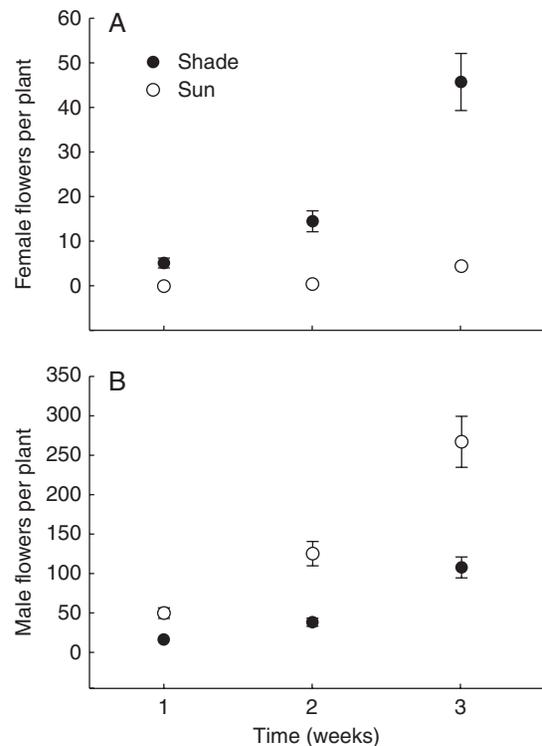


FIG. 2. Number of (A) female and (B) male flowers produced by *Ambrosia artemisiifolia* in shade vs. sun treatments for the first 3 weeks of flowering. Plants were grown in 4-inch (10-cm) diameter pots under uniform glasshouse conditions during July–August 2006 at the University of Toronto, Ontario from open-pollinated seed collected at the Koffler Scientific Reserve. The values presented are the means ( $\pm$  s.e.) for  $n = 77$  sun plants and  $n = 74$  shade plants. Plants in the shade treatment were placed under frames covered with black neutral-density shade cloth that reduced light levels by approx. 80%. The sun treatment involved ambient full sunlight.

to match neighbourhood conditions, thus optimizing fitness as maternal and paternal parents.

#### Pollen–ovule ratios and pollen transfer efficiency

Prodigious pollen production is a characteristic feature of the anemophilous syndrome, and pollen–ovule ratios are generally much higher than in animal-pollinated taxa (wind, median 22 150:1; animal, median 3450:1; Cruden, 1977, 2000). Cruden's explanation for this pattern focused on the 'efficiency' of the pollination system gauged as the likelihood of pollen arriving on stigmas. However, as pointed out by Charnov (1982), this explanation assumes that pollen is produced in just the right quantities to ensure ovule fertilization and equates plant reproductive success with seed production, thus ignoring male function. This view also assumes that much more pollen is wasted in anemophilous systems than with animal pollination. Indeed, the idea that wind pollination is an inefficient and wasteful system has pervaded the literature since Darwin (see quote at the beginning of this article; Proctor *et al.*, 1996; Ackerman, 2000). However, despite this widespread view, there have been no studies comparing pollen capture in animal- vs. wind-pollinated taxa.

To investigate pollen transfer efficiency in wind-pollinated plants, data were collected on the amount of pollen produced and the quantity of pollen captured by stigmas for 19 wind-pollinated herbaceous species. The species were located in their natural habitats at either the Koffler Scientific Reserve (44°03'N, 79°29'W, Ontario, Canada) or the Kananaskis Field Station (51°02'N, 115°03'W, Alberta, Canada). For each species, data were collected from 20 individuals and three flowers per plant. Mean pollen capture was 0.32% (range 0.01–1.19%) of the pollen produced (Fig. 3). Harder (2000) reported that for 24 animal-pollinated species with granular pollen the proportion of pollen captured ranged from 0.03 to 1.9%. Although our values are lower, they are within the same orders of magnitude and do not support the overall contention that pollen dispersal in wind-pollinated plants is considerably more wasteful than in animal-pollinated plants.

The timing and rate of arrival of pollen grains may affect opportunities for microgametophytic competition in wind-pollinated plants. If pollen arrives gradually, the first grains will probably be successful at fertilization, regardless of their competitive ability. However, anthesis in wind-pollinated plants tends to be highly synchronous within populations (Dowding, 1987), and in grasses flowering can be over in <5 h (Beddows, 1931). Thus, pollen grains may arrive synchronously and compete to fertilize ovules. Also, anemophilous pollen grains arrive independently and so may be drawn more evenly from potential sires than with animal pollination. The above considerations point to the possibility of intense

post-pollination competition in wind-pollinated plants leading to gametophytic selection, and this has the potential to result in greater progeny vigour (Mulcahy and Mulcahy, 1987). Thus, if wind-pollinated species do not generally exhibit substantially lower pollen transfer efficiencies in comparison with animal-pollinated species (Fig. 3), the copious pollen production of wind-pollinated taxa may instead reflect the intensity of post-pollination competition, rather than any general inferiority of the wind as a pollen vector.

#### Causes of low ovule number in wind-pollinated plants

There has been surprisingly little consideration of differences in ovule number between animal- vs. wind-pollinated plants despite their striking differences in pollen-ovule ratios. Low ovule number, including many taxa with uniovulate flowers (e.g. Cyperaceae, Juglandaceae, Poaceae), is a characteristic feature of wind-pollinated plants. Phylogenetic evidence indicates that a reduction in ovule number usually occurs after the evolution of anemophily (Linder, 1998; Friedman and Barrett, 2008). The most common explanation for this association is the small chance of stigmas capturing multiple pollen grains (Pohl, 1929; Dowding, 1987). Unlike animal-pollinated plants, where pollen grains commonly arrive in clumps, pollen of wind-dispersed species is usually transported as single units, so the chance of capturing each pollen grain is an independent event. However, stigmas of wind-pollinated plants often capture amounts of pollen that far exceeds ovule number. For example, in our study of 19 species (Fig. 3), mean stigmatic pollen load was  $34.1 \pm 3.8$  grains. Elsewhere pollen loads on open-pollinated stigmas of wind-pollinated taxa in Poaceae, Proteaceae, Ranunculaceae, Restionaceae and Rosaceae (mean pollen grains per ovule range from 3 to 100: Honig *et al.*, 1992; Linder and Midgley, 1996; Davis, 2004; Friedman and Harder, 2004) are inconsistent with the proposal that low pollen loads lead to decreased ovule number in wind-pollinated species.

Several morphological and aerodynamic features of wind-pollinated plants may favour few ovules or a single ovule per flower. The low cost of producing flowers in wind-pollinated plants may favour a packaging strategy with more flowers per plant each containing few ovules. Burd (1995) provides indirect support for this idea by showing theoretically that low floral costs generally favour fewer ovules per flower, although his model only considered animal-pollinated plants. Also, by producing more flowers with fewer ovules, the spatial dispersion of flowers on a plant may enlarge the volume of air sampled and increase the probability of capturing more pollen grains. A more mechanistic understanding of the functional association between wind pollination and low ovule number would be informative.

#### FLORAL AND INFLORESCENCE ARCHITECTURE

The floral morphology and inflorescence architecture of wind-pollinated plants largely reflect the aerodynamic requirements for successful pollen liberation from anthers and capture by stigmas. Fluid dynamic theory predicts that pollen removal is enhanced by traits that help move initially stationary pollen

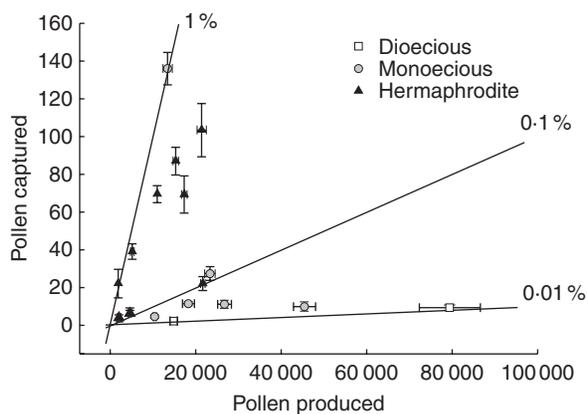


FIG. 3. Proportion of pollen produced that is captured by stigmas for 19 wind-pollinated species at Koffler Scientific Reserve, Ontario (summer 2004 and 2005) and Kananaskis Field Station, Alberta (summer 2001 and 2002). Species included: *Elymus repens*, *Ambrosia artemisiifolia*, *Bromus inermis*, *Carex communis*, *C. hirtifolia*, *C. pedunculata*, *C. plantagineae*, *C. stipata*, *Chenopodium album*, *Leymus innovatus*, *Festuca campestris*, *Anthoxanthum nitens*, *Phleum pratense*, *Plantago lanceolata*, *Rumex acetosella*, *R. crispus*, *Schizachne purpureascens*, *Scirpus microcarpus* and *Thalictrum dioicum*. The number of pollen grains in undehisced anthers was counted using an Elzone 5380 particle counter (Micromeritics Inc., Atlanta, GA), stigmatic pollen loads were assessed by staining stigmas with 1% basic fuschin, and pollen grains that had been deposited were counted under a compound microscope ( $\times 20$ ). Each species is categorized based on its sexual system (hermaphroditic flowers; monoecious, dioecious), and plotted values represent the mean of 20 individuals and three flowers each. The lines depict the percentage of pollen produced that was captured by stigmas, and provide a reference guide.

grains out of the boundary layer and into the airstream (Niklas, 1992). Because the speed of flow rises with increasing distance from an object, anthers experience higher wind speeds when they are suspended beyond the boundary layer of still air created by other floral organs. This physical constraint has led to the evolution of highly diverse floral and inflorescence morphologies that distinguish wind- from animal-pollinated plants (Fig. 4). The anthers of wind-pollinated species are typically extended on long flexible filaments, enabling them to move in the slightest breeze. For example, *Pennisetum clandestinum* (Fig. 4D) possesses extremely long filaments that project anthers away from the plant, whereas stigmas are deployed near to the ground. Also, wind speeds increase with distance from the ground, so pollen dispersal is more effective when male flowers are presented in upper portions of the plant, which also reduces interference by vegetative structures. This leads to the prediction that in monoecious species male flowers should be presented above female flowers (e.g. as in *Carex pedunculata*, Fig. 4A). Although the data are sparse, there appears to be some support for

these positional relationships (Freeman *et al.*, 1981; Bickel and Freeman, 1993; Fox, 1993).

To examine whether the position of a flower within an inflorescence affects pollen capture, data were collected on four herbaceous wind-pollinated species from four families (Fig. 5). Each species illustrates a different aspect of how architecture may influence pollen capture. In monoecious *C. pedunculata*, female flowers in upper positions of the inflorescence captured significantly more pollen than flowers at lower positions. Because male flowers are presented at the top of the inflorescence above female flowers, this pattern probably reflects increased self-pollen capture in upper female flowers since the species exhibits high selfing rates (Friedman and Barrett, 2009). Like other grasses with diffuse panicles, florets in upper positions in *Festuca campestris* capture more pollen (Fig. 5B) because they sweep through a larger volume of air during oscillation (Friedman and Harder, 2004). *Plantago lanceolata* is protogynous, flowers acropetally, and the scape elongates during flowering, so that female and male functions are separated in height. Thus, stigmas at the top of the

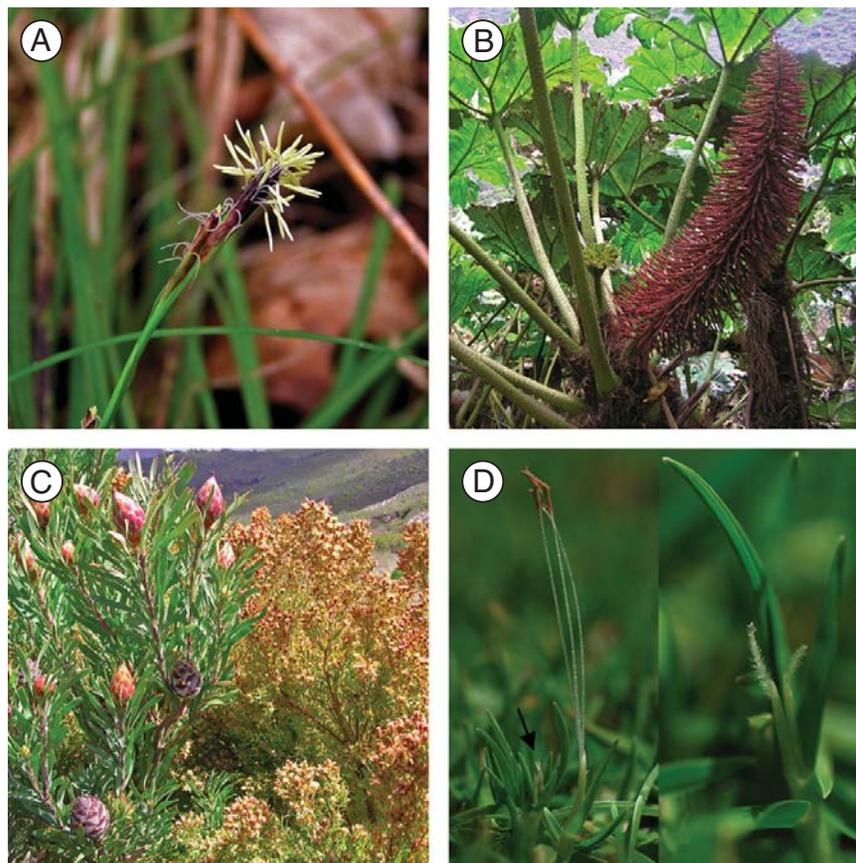


FIG. 4. Diverse inflorescence and floral morphology in four wind-pollinated species. (A) *Carex pedunculata* (Cyperaceae) in Ontario, Canada. Plants are monoecious and protogynous, with male flowers clustered at the top of the inflorescence and female flowers below. (B) Gynomonocious *Gunnera peltata* (Gunneraceae), Isla Más Afuera, Juan Fernandez Islands. Inflorescences in this species are very large and upright, perhaps to compensate for growing under extensive leaf canopies. *Gunnera* is frequently described as wind pollinated (e.g. Bernardello *et al.*, 2001), but to our knowledge this has not been confirmed through experimental studies. (C) Female (left side) and male (right side) individuals of *Leucadendron rubrum* (Proteaceae) in Cape Province, South Africa. The species is dioecious and has extreme sexual dimorphism between the sexes. (D) *Pennisetum clandestinum* (Poaceae) in Cape Province, South Africa illustrating striking differences in the functional deployment of stigmas and anthers. The panel on the left shows anthers extended on very long filaments, with the arrow pointing to the stigmas. The panel on the right is a close-up of the feathery stigmas presented at ground level. All images are by S.C.H.B., except (D), which is courtesy of L. D. Harder.

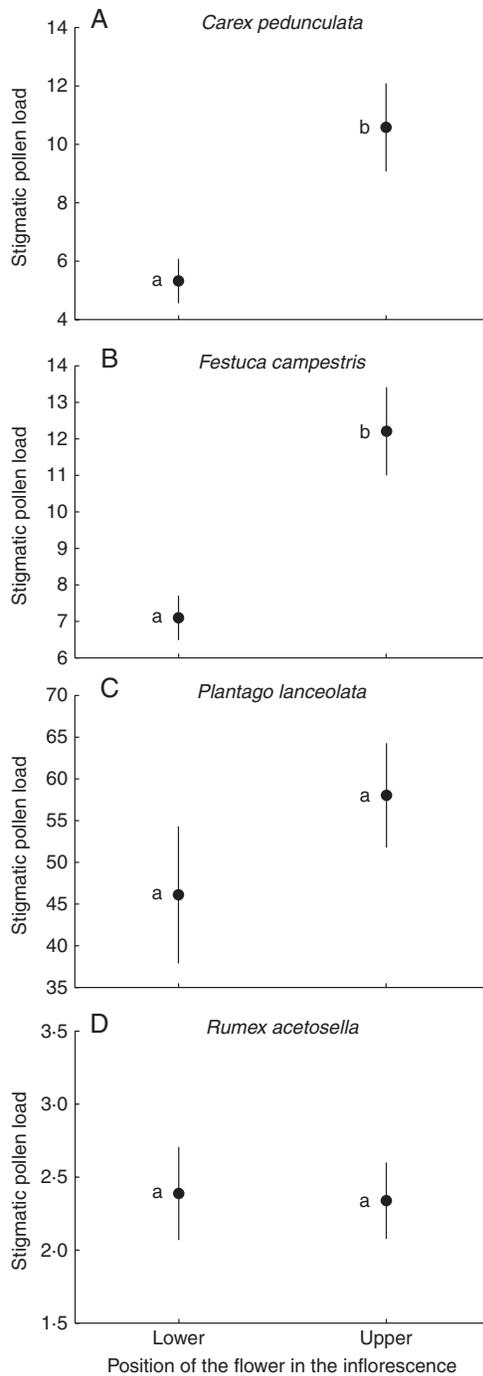


FIG. 5. Relationship between the position of flowers within an inflorescence and stigmatic pollen loads for four wind-pollinated herbaceous species at the Koffler Scientific Reserve (summer 2004 and 2005), Ontario and Kananaskis Field Station (summer 2001), Alberta. In both *Carex pedunculata* (Cyperaceae) and *Festuca campestris* (Poaceae), flowers in the upper positions of the inflorescence captured significantly more pollen than those in lower positions (*C. pedunculata*,  $t_{2675} = 3.43$ ,  $P = 0.01$ ; *F. campestris*,  $t_{2863} = 3.96$ ,  $P = 0.002$ ). In *Plantago lanceolata* (Plantaginaceae) and *Rumex acetosella* (Polygonaceae) there was no significant difference in pollen capture between flowers in the upper and lower positions (*P. lanceolata*,  $t_{2731} = 1.08$ ,  $P > 0.5$ ; *R. acetosella*,  $t_{2878} = 0.11$ ,  $P > 0.5$ ). All  $P$ -values are adjusted for multiple contrasts; different letters next to symbols indicate significant differences.

inflorescence have the potential to capture self-pollen from anthers below (Bos *et al.*, 1985; Young and Schmitt, 1995). Although in this species there was a trend for upper flowers to capture more pollen than lower flowers, the difference was not significant (Fig. 5C). Finally, there was no evidence of position effects in *R. acetosella* (Fig. 5D), probably because it is dioecious and female and male plants are approximately the same height. If pollen is homogeneously distributed in the airstream, then we expect flowers at different positions to capture equivalent amounts of pollen. These examples illustrate how architecture, sexual system and aerodynamics may interact to affect pollen capture in wind-pollinated plants.

Pollen capture in wind-pollinated plants is also dependent on the morphology of flowers. The feathery stigmas of many anemophilous species have higher collection efficiencies than solid stigmas, because they have smaller radii, and because they produce proportionally thinner boundary layers (Niklas, 1985). Furthermore, the reproductive morphology of wind-pollinated species creates a unique aerodynamic environment in the immediate vicinity of reproductive organs. Using wind-tunnel experiments, Niklas (1985) demonstrated that the morphology of ovulate organs influences the airflow through which pollen travels. Thus, pollen morphology and ovulate organs may act synergistically to generate aerodynamic environments that increase a species' efficiency of pollen capture (Niklas and Buchmann, 1987; Paw U and Hotton, 1989; Friedman and Harder, 2005). Linder and Midgley (1996) provided evidence for pollen discrimination by anemophilous species in a field study of four sympatric co-flowering species. They found high proportions of conspecific pollen on stigmas (range 40–80%) in comparison with pollen frequencies in the air. Whether this pollen filtering is a general phenomenon for sympatric wind-pollinated species remains to be determined; however, it does suggest that pollen capture may be a more refined process than a simple random sampling of the airstream and that pre-zygotic barriers to interspecific pollination may serve to reduce gamete wastage.

#### Pollen size evolution

Unlike animal-pollinated taxa (see Harder, 1998), the evolution of pollen size in wind-pollinated species depends strongly on pollen transport conditions. Pollen size in anemophilous plants probably reflects stabilizing selection that balances two conflicting demands (Whitehead, 1969; Niklas, 1985). Small pollen grains have low inertia, facilitating removal from anthers and low settling velocity, which allows pollen to travel farther before falling out of the airstream. On the other hand, large pollen grains have greater momentum, which increases the chance of breaking away from deflected streamlines to collide with stigmas. As a result of these influences, wind-pollinated species exhibit a smaller range of pollen sizes (17–58  $\mu\text{m}$ ) than animal-pollinated species (5–200  $\mu\text{m}$ ), although average pollen size does not differ greatly among these groups (Wodehouse, 1935), contrary to popular misconception. Aerodynamic constraints on pollen size are evident in *Plantago*, where species with chasmogamous (open) flowers have much less variable pollen sizes than species with cleistogamous (closed) flowers (Primack, 1978). Variation in pollen size among wind-

pollinated species can be predicted by the size of the structure (either flower or inflorescence) that interacts with the airstream (Paw U and Hotton, 1989; Friedman and Harder, 2005).

#### *Inflorescence architecture*

The packaging of flowers within inflorescences affects how female and male reproductive parts interact with airflow, thereby influencing pollination. For example, in grasses, where a striking diversity of inflorescence architectures occur, wind-tunnel experiments demonstrate a dichotomy in the mechanics of pollen receipt depending on whether species possess compact or diffuse panicles (Niklas, 1987). Compact panicles act as a bluff-bodied obstruction to airflow, so that much entrained pollen is deflected from windward stigmas and is instead captured by sedimentation from eddies on the leeward side of the inflorescence. In contrast, diffuse panicles disrupt airflow less, so that most pollen collides with windward-facing stigmas. Manipulative field experiments on grasses with compact and diffuse panicles demonstrate that the oscillation of grass inflorescences has contrasting effects on pollen removal and receipt (Friedman and Harder, 2004). Specifically, immobilization of culms by tethering in three species with compact panicles reduced pollen removal, but did not affect pollen receipt. In contrast, immobilization did not affect pollen removal from two species with diffuse panicles, but reduced pollen receipt. Together, these studies demonstrate that compact and diffuse inflorescences function differently to effect pollination. Studies comparing inflorescence architecture of plants growing in high-wind (e.g. open habitats) vs. low-wind (e.g. forests) conditions would be informative in this regard.

There is growing evidence that inflorescence architecture in wind-pollinated plants has been shaped by selection for efficient pollen dispersal and capture; however, many unresolved questions remain. It is likely that there is also selection on inflorescence architectural traits for characteristics related to seed dispersal. For example, the position of flowers within inflorescences may affect seed provisioning by the maternal plant. If seeds are wind dispersed, selection may act on traits that facilitate dispersal. Teasing apart the gender role and life history stage on which selection acts in hermaphroditic wind-pollinated species is likely to be tricky. However, comparing plant and inflorescence architectures between females and males in wind-pollinated dioecious species can circumvent this difficulty. In such cases the architecture of male plants should largely be selected for efficient pollen dispersal, whereas female plants will be influenced by selection pressures for pollen capture and seed dispersal. This should lead to greater levels of dimorphism in wind-pollinated dioecious species than in animal-pollinated species where too much morphological divergence may influence pollinator behaviour and interfere with successful cross-pollination (Vamosi and Otto, 2002). *Leucadendron rubrum* provides a spectacular example of the extreme sexual dimorphism that can arise in a wind-pollinated species because of these contrasting selection pressures (Fig. 4C). To what extent selection acting on architectural traits related to pollen dispersal, pollen capture and seed dispersal oppose one another is unknown, but

could be evaluated in groups that possess both hermaphroditic and dioecious species.

#### STRATEGIES THAT PROMOTE OUTCROSSING

Plants are sessile and therefore require pollen vectors for cross-pollination. Natural selection shapes the interactions with pollen vectors so that pollen is dispersed effectively among conspecifics. In animal-pollinated species these interactions have given rise to the great structural diversity of flowers and inflorescences. Reproductive structures function to manipulate animal foraging in a predictable manner, promoting pollen dispersal and reducing the incidence of self-pollination. We expect that the flowers and inflorescences of wind-pollinated plants are also under similar selective pressures, although precisely how floral and inflorescence traits influence pollination and mating has received scant attention in the literature.

#### *Prevalence of mixed mating*

One of the most recognized features of mating in wind-pollinated plants is the apparent low incidence of mixed mating leading to a bimodal distribution of outcrossing rates (Schemske and Lande, 1985; Aide, 1986; Barrett and Eckert, 1990; Goodwillie *et al.*, 2005), with species more frequently either predominantly selfing or outcrossing. However, the reported distribution of outcrossing rates for wind-pollinated plants should be viewed with some caution (and see Iqic and Kohn, 2006). In the most recent compilation (Goodwillie *et al.*, 2005), all but 18 of the 76 wind-pollinated species belong to just two families (Poaceae and Pinaceae), and clearly further effort is required to broaden taxonomic representation. Nonetheless, if we assume that the apparent trend is real, it is worth considering what factors might contribute to a lower incidence of mixed mating in wind-pollinated plants compared with those that are animal pollinated.

Paucity of mixed mating may reflect different selective pressures in wind-pollinated species including a less stochastic pollination environment (Aide, 1986; Vogler and Kalisz, 2001; Goodwillie *et al.*, 2005). This implies that wind is a more predictable vector of pollen than animals and, provided population densities are sufficient, flowers should receive adequate outcross pollen. However, empirical data to support this idea are scant and the occurrence in herbaceous wind-pollinated lineages (e.g. grasses, sedges) of many predominantly selfing species indicates that pollen dispersal is not always predictable.

In our survey of pollen capture in wind-pollinated plants there was a tendency for higher pollen capture in hermaphrodite vs. dioecious species, and between monoecious species vs. those with perfect flowers (Fig. 3). Although sample sizes in our study are small, this order of increasing pollen load is consistent with the likelihood of self-pollen capture. We caution, however, that a large number of the hermaphrodite species in our survey were grasses (Poaceae) and most of the monoecious species were sedges (*Carex*). Although the lack of phylogenetic independence precludes us from making statistical comparisons among sexual systems, the

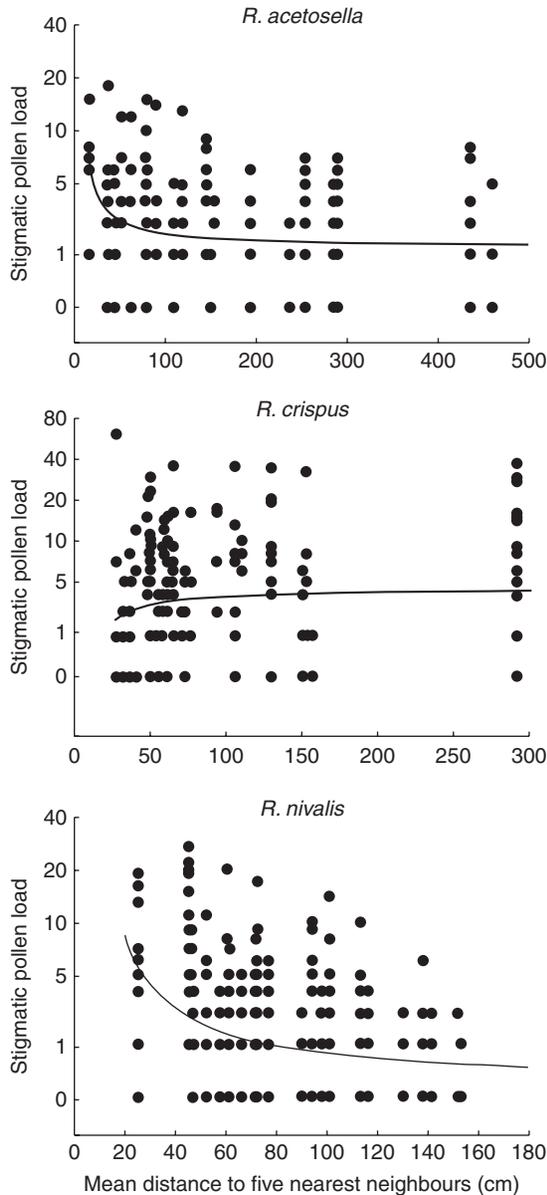


FIG. 6. Relationship between mean distance to the five nearest neighbours and stigmatic pollen load for three *Rumex* species. Both of the dioecious species, *R. acetosella* and *R. nivalis*, captured significantly more pollen when neighbours were close (*R. acetosella*,  $t_{117} = 2.66$ ,  $P < 0.01$ ; *R. nivalis*,  $t_{53.4} = 3.06$ ,  $P < 0.005$ ), while the relationship is not significant for the hermaphrodite species, *R. crispus* ( $t_{97.8} = 1.46$ ,  $P = 0.15$ ). The equations for the relationship between pollen receipt and distance to neighbours are: *R. acetosella*,  $y = 16.32x^{-1} + 0.78$ ; *R. crispus*,  $y = -14.06x^{-1} + 1.67$ ; *R. nivalis*,  $y = 27.45x^{-1} + 0.56$ . *Rumex nivalis* was investigated during summer 2004 at Davos, Switzerland (46°41'N, 9°48'E) and *R. acetosella* and *R. crispus* during summer 2005 at Koffler Scientific Reserve (44°03'N, 79°29'W).

trend is interesting and should motivate further studies. It is possible that high levels of geitonogamous selfing are inevitable for many wind-pollinated plants, especially those of large size with many flowers in anthesis at the same time. Indeed, selection against this form of selfing may explain the common association between dioecy and wind pollination,

and the frequent occurrence of self-incompatibility in wind-pollinated groups such as Poaceae.

#### Sexual strategies, pollen capture and mating

To investigate the effect of the sexual system on pollen capture and its interaction with plant density, three wind-pollinated *Rumex* species were investigated. Two species, *R. acetosella* and *R. nivalis*, are dioecious, and *R. crispus* is hermaphroditic. For each species stigmas were collected from at least three flowers on 20 plants and the distance to the nearest five pollen-producing neighbours was measured. A significant relationship between pollen load and mean distance to neighbours was evident in both dioecious species, with more pollen captured on plants that had close neighbours (Fig. 6A, C). There was no relationship between plant density and pollen loads in hermaphroditic *R. crispus* (Fig. 6B), and in this species self-pollination may buffer plants against the effects of low density. Although *R. crispus* is protandrous, there is considerable overlap in female and male function within an inflorescence, and hence this form of dichogamy appears to be largely ineffective in promoting outcrossing (Bertin, 1993; Routley *et al.*, 2004).

There are strong associations between anemophily and protogyny (Bertin, 1993; Sargent and Otto, 2004), and transitions from biotic to abiotic pollination are more likely among protogynous species than among protandrous species (Sargent and Otto, 2004). These patterns may occur because following a switch to wind pollination protogynous species are less likely to suffer from increased self-fertilization (Lloyd and Webb, 1986; Bertin and Newman, 1993; Sargent and Otto, 2004). Protogyny is associated with self-compatibility, and protandry with self-incompatibility more often than expected under a random model (Bertin, 1993; Routley *et al.*, 2004). This finding is consistent with the inbreeding avoidance hypothesis for the evolution of protogyny (Lloyd and Webb, 1986). The associations between protogyny and anemophily and between protogyny and self-compatibility suggest that protogyny may be an effective outcrossing mechanism in many anemophilous species.

A widely recognized feature of wind pollination is the higher frequency of unisexual flowers in wind-pollinated vs. animal-pollinated species (Bawa, 1980; Charlesworth, 1993; Renner and Ricklefs, 1995; Vamosi *et al.*, 2003). There is no comprehensive mechanistic explanation for this association, although some conceptual arguments are compelling (Charlesworth, 1993). Several hypotheses have been proposed, including a reduction in shared fixed costs of floral display and pollinator rewards between female and male flowers (Lloyd, 1982), a more linear male gain curve (Charnov *et al.*, 1976) and the prevention of intrafloral self-fertilization (Lloyd and Webb, 1986; Charlesworth, 1993).

Although protogyny and unisexual flowers may limit self-fertilization in some wind-pollinated groups, our own investigations indicate that this is not the case in some *Carex* species (Friedman and Barrett, 2009). Emasculation experiments and estimates of mating patterns using genetic markers in seven monoecious, protogynous species demonstrated that geitonogamous self-fertilization predominated. Indeed, based on our studies, we proposed that unlike animal-

pollinated species, where geitonogamy is rarely adaptive (Lloyd, 1992), geitonogamy in wind-pollinated herbs with unisexual flowers may often provide reproductive assurance when ecological conditions limit outcross pollen dispersal. In the *Carex* we investigated, low wind speeds in the woodland understorey occupied by all seven species and the small stature of plants make this seem quite likely.

## CONCLUSIONS

Many issues need to be addressed regarding evolution and adaptation in wind-pollinated plants. This review has largely focused on functional questions related to sex allocation, inflorescence design and mating strategies, highlighting areas that need future work. In comparison with animal-pollinated plants, there is a paucity of basic information about the reproductive biology of wind-pollinated plants. Indeed, in some groups routinely described as wind pollinated (e.g. *Gunnera*, see Fig. 4B), experimental evidence is needed to confirm the role of wind in pollen transport. Much more quantitative data on pollen dispersal, pollen limitation and mating patterns are required before generalizations can be made concerning the efficacy of wind pollination in comparison with animal pollination. Three areas that are in particular need of future attention are: (1) theoretical investigations of the evolution of wind pollination; (2) measurement of fitness returns for male allocation strategies; and (3) studies of mating systems in wind-pollinated plants, particularly modes of selfing and patterns of paternity. Future mechanistic studies that extend the seminal work of Niklas (1985, 1987; Niklas and Buchmann, 1987) linking reproductive morphology and plant architecture to the aerodynamics of pollen release and pollen capture, and efforts to link pollen dispersal and mating through the use of genetic markers, have the potential to reveal complex and fascinating new details on the reproductive biology of wind-pollinated plants.

## ACKNOWLEDGEMENTS

We thank Jeff Karron, Randy Mitchell and Rebecca Irwin for the opportunity to contribute to this volume. Thanks also to Lawrence Harder for permission to use his image of *Pennisetum clandestinum* and for insightful discussions on various aspects of wind pollination, and Livia Wanntorp for information on *Gunnera*. This research was supported by the Natural Sciences and Engineering Research Council of Canada, through a Canada Graduate Scholarship (J.F.), and funding from Discovery Grants and the Canada Research Chair's Program (S.C.H.B.)

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