A PHYLOGENETIC ANALYSIS OF THE EVOLUTION OF WIND POLLINATION IN THE ANGIOSPERMS

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Wind pollination is predominantly a derived condition in angiosperms and is thought to evolve in response to ecological conditions that render animal pollination less advantageous. However, the specific ecological and evolutionary mechanisms responsible for transitions from animal to wind pollination are poorly understood in comparison with other major reproductive transitions in angiosperms, including the evolution of selfing from outcrossing and dioecy from hermaphroditism. To investigate correlations between wind pollination and a range of characters including habitat type, sexual system, floral display size, floral showiness, and ovule number, we used a large-scale molecular phylogeny of the angiosperms and maximum likelihood methods to infer historical patterns of evolution. This approach enabled us to detect correlated evolution and the order of trait acquisition between pollination mode and each of nine characters. Log likelihood ratio tests supported a model of correlated evolution for wind pollination and habitat type, floral sexuality, sexual system, flower size, flower showiness, presence versus absence of nectar, and ovule number. In contrast, wind pollination and geographical distribution and number of flowers per inflorescence evolve independently. We found that in wind-pollinated taxa, nectar is lost more often and ovule number is reduced to one. We also found that wind pollination evolves more frequently in lineages already possessing unisexual flowers and/or unisexual plants. An understanding of the ecological and life-history context in which wind pollination originates is fundamental to further investigation of the microevolutionary forces causing transitions from animal to wind pollination.

Keywords: anemophily, comparative analysis, correlated evolution, ecological correlates, morphological correlates, pollination.

Introduction

Wind pollination (anemophily) has evolved at least 65 times in the angiosperms from biotically pollinated ancestors (Linder 1998). A recent survey estimates that abiotic pollination occurs in at least 18% of angiosperm families (Ackerman 2000), with wind pollination more commonly represented than water pollination. The evolution of wind pollination is thought to occur when environmental conditions render biotic pollination less advantageous (Regal 1982; Cox 1991). For example, a decline in pollinator abundance or changes in the abiotic environment limiting pollinator activity have been invoked to explain why wind pollination has evolved in particular taxa (Berry and Calvo 1989; Weller et al. 1998; Goodwillie 1999). However, the specific ecological mechanisms causing transitions from animal to wind pollination have not been investigated in detail, and, in comparison with other reproductive transitions (e.g., the evolution of selfing from outcrossing and dioecy from hermaphroditism), little is known about the microevolutionary forces responsible for the evolution of wind pollination.

Comparative evidence clearly indicates that wind pollination evolves more frequently in certain clades (Ackerman 2000). As families and genera often share traits as a result of

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common ancestry, mapping traits onto phylogenetic trees is our best option for testing correlated evolution without bias from phylogenetic relationships (Felsenstein 1985; Donoghue 1989; Harvey and Pagel 1991). Taking phylogenetic relationships into account, we were interested in finding evidence for the existence of correlations between anemophily and specific morphological and ecological traits and determining the putative evolutionary pathways leading to these associations. Linder (1998) first examined morphological traits and their associations with wind pollination in a comparative context. However, his study was limited to families of the lower rosids and commelinoid monocots and used the concentrated-changes test (Maddison 1990), which is less powerful than current phylogenetic comparative methods (see Schluter et al. 1997; Pagel 1999), to investigate correlations. The recent advent of maximum likelihood phylogenetic comparative methods (Harvey and Pagel 1991; Pagel 1994; Freckleton et al. 2002) provides an opportunity to investigate correlations among life-history traits and ecology and biogeography and to examine the evolutionary history of reproductive associations (e.g., dioecy: Vamosi et al. 2003; dichogamy and self-incompatibility: Routley et al. 2004; protogyny and pollination mode: Sargent and Otto 2004). We were interested in examining the relations between wind pollination and a range of characters that have been proposed to be associated with this condition. We now briefly review the traits chosen and the functional arguments that have been proposed to explain their correlations with anemophily.

Regions of higher latitude, arid temperate environments, open vegetation, and island floras have the highest representation of wind-pollinated plants (Whitehead 1968; Regal 1982). The physical and aerodynamic requirements for successful wind pollination may explain these ecological and geographical correlates. However, it is unclear whether these associations are robust to phylogenetic considerations and whether wind pollination is more likely to originate under these conditions or is simply easier to maintain.

One of the more widely recognized features of wind pollination is the higher frequency of unisexual flowers in wind-pollinated species than in animal-pollinated species (Bawa 1980; Renner and Ricklefs 1995). Several hypotheses for this have been proposed, including a reduction in shared fixed costs between female and male flowers (Lloyd 1982), a more linear male gain curve (Charnov et al. 1976), and limiting self-fertilization because of the unavoidable geitonogamy that seems likely in wind-pollinated plants (Lloyd and Webb 1986; Charlesworth 1993). Some of these explanations are specific to dioecy, while others can be extended to dicliny (unisexual flowers) in general. These hypotheses imply that wind pollination precedes the evolution of unisexual flowers. This particular order of transition is supported in the Poaceae (Malcomber and Kellogg 2006) and *Fraxinus* (Wallander 2001); however, the opposite order appears to occur in *Leucadendron* (Midgley 1987; Hattingh and Giliomee 1989), *Thalictrum* (Kaplan and Mulcahy 1971) and possibly in *Schiedea* (Weller et al. 1998). Therefore, establishing the relative frequency of the two polarities that lead to a correlation between dicliny and anemophily is critical to understanding the functional basis of the correlation.

An association between wind pollination and low ovule number was reported by Linder (1998) in his comparative analysis of the evolution of anemophily. Wind-pollinated flowers have been presumed to produce only single ovules because of the small chance of multiple pollen grains landing on each stigma (Pohl 1929; Dowding 1987). Unlike in animal-pollinated plants, where pollen grains arrive in clumps, the pollen of wind-dispersed species is usually transported as single units, so that the chance of capturing each pollen grain is an independent event. These arguments imply that a reduction in ovule number occurs after the evolution of wind pollination, a sequence supported by the results of Linder (1998).

A suite of morphological traits is commonly associated with wind pollination and constitutes the anemophilous syndrome (Faegri and van der Pijl 1979). Many of the traits can be explained by functional arguments and the aerodynamic requirements for wind pollination. However, it is unclear whether these traits facilitate the evolution of wind pollination or evolve after the origin of wind pollination in particular lineages. In general, wind-pollinated plants have small flowers with highly reduced or no perianth parts. Nectaries are usually absent or nonfunctional (Faegri and van der Pijl 1979). The presence of complex, large, showy flowers may act as a constraint to the evolution of wind pollination, and it appears that nectaries are typically lost after the evolution of wind pollination (Linder 1998). Plants that already have small simple flowers may be more suitable for transporting and capturing some portion of their pollen by wind because the stigmas and anthers are likely to be exposed to air currents (Culley et al.

2002). Plants with a mixed pollination strategy involving both animal and wind pollination (ambophily) tend to have small unshowy flowers (e.g., *Piper* spp.: De Figueiredo and Sazima 2000; *Salix* spp.: Tamura and Kudo 2000; Karrenberg et al. 2002). Similarly, plants that use pollen as a reward (rather than nectar) may produce more pollen and be at a selective advantage if conditions change to favor wind pollination. However, it is not always clear whether wind pollination evolves more frequently in lineages that have small inconspicuous flowers and no nectar or whether these traits are lost after the evolution of wind pollination because of energetic reasons associated with a loss of function.

Here, we use a recent molecular phylogeny of the angiosperms (Soltis et al. 2000) to investigate evidence for correlations between anemophily and specific morphological and ecological traits and to evaluate the evolutionary pathways leading to these associations. Specifically, we investigated whether associations occur between wind pollination and (1) biogeographical and ecological traits, including temperate distributions and open habitat types; (2) sexual traits, including unisexual flowers (dicliny) and plants (dioecy) and low ovule numbers; and (3) a reduction in floral characteristics, including flower size and showiness. In cases where we detected associations, we then investigated the order of transition between the traits using tests of contingent evolution to assess the evolutionary pathways involved. This information enabled us to evaluate several potential hypotheses that have been proposed to explain the evolution of wind pollination from animal pollination.

Methods

Character Coding and Phylogenetic Data

We use the "B series" tree and branch lengths of the molecular phylogeny of angiosperms by Soltis et al. (2000). This tree is based on 567 taxa and three gene sequences (18s rDNA, *rbc*L, and *atp*B). For each species included in the phylogeny, we assigned states for the following 10 characters: pollination mode (animal or wind), floral sexuality (hermaphroditic or unisexual flowers), sexual system (cosexual or dioecious populations), ovules (one or more than one), flower size (small [<1 cm] or medium to large [>1 cm]), flower showiness (showy or plain [green, white, yellow-green]), number of flowers per inflorescence (few [<5] or many [>5]), nectar (present or absent), habitat type (open or closed), and geographical distribution (temperate or tropical).

We obtained information on these character states from Kubitzki (1993, 1998*a*, 1998*b*, 2003, 2004), Mabberley (1997), Hutchinson (1964), the database generously provided by Jana Vamosi (used in Vamosi et al. 2003), a variety of online floras, and extensive literature surveys (list of all sources available from the first author). All states were coded as binary characters. The Soltis et al. (2000) study depicts the relationships of genera, although the original phylogeny was estimated using representative species for each genus. We used these species for our character coding. When information was unavailable for a particular species, we used the most common state (>50%) for the members of the genus. We obtained information for all 560 angiosperm species in the phylogeny, of which 68 are wind pollinated.

Testing for Correlated Evolution and Directionality

To test for correlated evolution between wind pollination and alternative character states, we used BayesTraits (Pagel and Meade 2006). We implemented the BayesDiscrete module, which investigates correlated evolution between pairs of discrete binary traits. The program fits continuous-time Markov models to the discrete character data and allows the trait to change states over infinitesimally small intervals of time. The model estimates transition rates and the likelihood associated with different states at each node of the tree and calculates transition probabilities across all possible character states at each node, eliminating the need to assign ancestral states. We used the branch scaling parameter κ, suggested by Pagel (1994), which adjusted the weight of branch lengths in the model and allowed it to take its maximum likelihood value. In all cases, $\kappa < 1$, which reduces the length of longer branches more than shorter ones.

BayesDiscrete tests for correlated evolution in two binary traits by comparing the fit (log likelihood) of two of these continuous-time Markov models. The first is a model in which two traits (e.g., wind pollination and nectar) evolve independently on the tree. This creates two rate coefficients per trait. The other model allows the traits to evolve in a correlated fashion such that the rate of change in one trait depends on the background state of the other. The dependent model has four states, one for each combination of the two binary traits (0, 0; 0, 1; 1, 0; 1, 1; see fig. 1). To determine whether wind pollination is correlated with a trait, we compared the likelihood estimate of the independent model ($L(I)$) to the likelihood estimate of the dependent model ($L(D)$). Because likelihood ratios approximate a χ^2 distribution, support for correlated evolution is indicated when $L(D)$ is significantly greater than $L(I)$, which can be tested by comparing $-2[L(D) - L(I)]$ to a χ^2 distribution with 4 degrees of freedom.

We determined the statistical significance of each of the estimated parameters in the dependent model by restricting individual transition parameters to zero and recalculating the likelihood ratio of the model. We then compared the restricted seven-parameter model to the unrestricted dependent model with a 1-df χ^2 test. A significant likelihood ratio indicates that the transition rate is significantly different from zero. Finally, we tested specific hypotheses about contingent evolution by restricting two of the rates to being equal (e.g., unisexual flowers evolve equally in animal- and wind-pollinated lineages: $q_{12} = q_{34}$). This seven-parameter restricted model can be compared to the full dependent model using the likelihood ratio test, $-2[L(D) - L(q_{12} = q_{34})]$ with a 1-df χ^2 test. A significant likelihood ratio indicates that the parameters are significantly different from one another, demonstrating that the state of trait X influences the direction of evolution of trait Y (Pagel 1994). Because we performed multiple tests, we adjusted the α level using Bonferroni correction.

Results

Traits Correlated with Wind Pollination

We first examined whether traits were associated with pollination mode regardless of phylogenetic considerations. We found that all of the floral characteristics we investigated
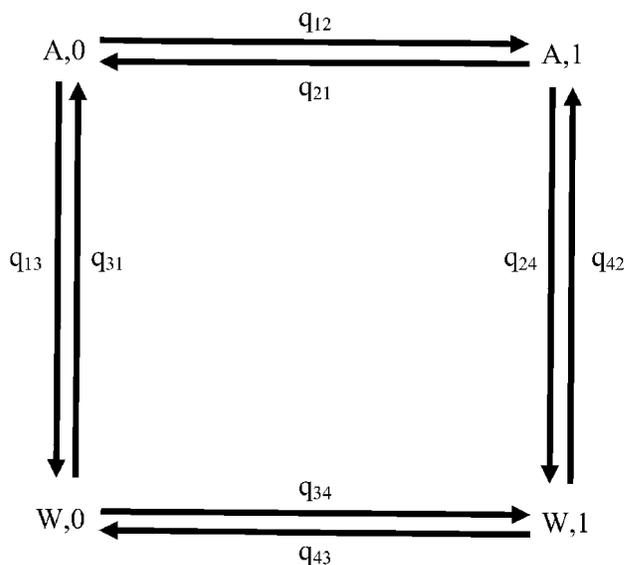
Trait	States
Pollination mode	A=animal, W=wind
Geographical distribution	0=tropical, 1=temperate
Habitat type	0=closed, 1=open
Floral sexuality	0=hermaphrodite, 1=unisexual
Sexual system	0=cosexual, 1=dioecious
Ovules	0=more than one, 1=one
Number of flowers	0=few, 1=several to many
Flower size	0=medium to large, 1=small
Flower showiness	0=showy, 1=plain
Nectar	0=present, 1=absent

Fig. 1 Rate parameters for the eight possible transitions between pollination mode and the binary characters under a model of dependent evolution. The code for pollination mode and states for the nine characters are provided above. The values of 0 and 1 do not necessarily indicate hypotheses about ancestral conditions.

were highly correlated with pollination mode while none of the ecological traits were correlated with pollination mode (table 1). When considering phylogenetic relationships, the results of the maximum likelihood analyses and the likelihood ratio tests indicated that wind pollination evolves in a correlated fashion with habitat type, floral sexuality, sexual system, ovule number, flower size, flower showiness, and nectar presence or absence (table 2). Wind pollination and geographical distribution and number of flowers per inflorescence evolve independently (table 2). To investigate these associations further and to determine the direction and order of transitions underlying correlated evolution, we tested specific hypotheses about each association.

Ecological Traits

Our results indicated that pollination mode and habitat type (closed habitats or open habitats) do not evolve independently. A model of correlated evolution fit the data better,

Table 1

Distribution of Species among the Pollination Modes and States of the Nine Characters Used in This Study

Trait and state	Pollination mode		χ^{2a}
	Animal	Wind	
Geographical distribution:			
Tropical	293	33	2.98
Temperate	199	35	
Habitat type:			
Closed	238	26	2.47
Open	254	42	
Floral sexuality:			
Hermaphrodite	394	18	88.31***
Unisexual	98	50	
Sexual system:			
Cosexual	440	38	53.80***
Dioecious	52	30	
Number of ovules:			
More than one	385	33	27.89***
One	107	35	
Number of flowers:			
Few	143	11	4.98*
Several to many	349	57	
Flower size:			
Medium to large	177	4	24.73***
Small	315	64	
Flower showiness:			
Showy	325	11	61.94***
Plain	167	57	
Nectar:			
Present	398	7	148.76***
Absent	94	61	

[a] χ^2 tests determine whether there is an association between pollination mode and the distribution of species among the two states of each trait.

* $P < 0.05$.

*** $P < 0.0001$.

and the transition rates predicted that wind pollination and open habitats are positively associated (table 2). Furthermore, wind pollination was more often lost in closed habitats (table 2). We were unable to reject the hypothesis that geographical distribution (tropical or temperate) and pollination mode evolved independently.

Floral Traits

Pollination mode and flower size (small or large) do not evolve independently. The transition rates we obtained predict that wind pollination and small flowers are positively correlated (table 2). Although none of the contingent-changes tests were significant, the transition rates indicate that wind pollination evolves more often in small-flowered lineages and once established is seldom lost. Similarly, flower showiness (showy or plain) and pollination vector do not evolve independently. The model of correlated evolution fit the data significantly better than the model of independent evolution, and transition rates predicted that plain flowers and wind pollination are positively associated. In contrast, we cannot reject the hypothesis that pollination mode and flower number (few or many) evolve independently. Finally, nectar (presence

or absence) and pollination mode evolve in a dependent way. Transition rates predict that an absence of nectar and wind pollination are positively correlated. The correlation arises because nectar is lost significantly more often in wind-pollinated clades (table 2).

Sexual Traits

Pollination mode and both floral sexuality and sexual system do not evolve independently. In both cases, a model of correlated evolution fit the data better than a model of independent evolution (table 2). Individual transition rates predicted that wind pollination and unisexual flowers are positively correlated. Furthermore, the contingent-change tests reveal that wind pollination evolves more often in clades with unisexual flowers (usually in species with either monoecious or dioecious sexual systems; table 2). To assess whether the presence of dioecious species is driving this association, we removed all dioecious species from the data set and reran the analysis. Again, we found that the model of correlated evolution fit the data better and that the transition rates predicted that wind pollination and monoecy are associated (data not shown). None of the contingent-changes tests were significant, possibly due to a lack of power, although the trend suggested that wind pollination evolves more often in monoecious lineages (data not shown). With respect to the correlation between dioecy and pollination mode, individual transition rates predicted that wind pollination and dioecy are positively associated. Furthermore, the contingent-change tests indicated that wind pollination evolves more often in dioecious clades (table 2).

Our analysis indicated that ovular condition (single ovule vs. multiple ovules) and pollination mode evolved in a dependent way. The transition rates revealed that single ovules and wind pollination are positively correlated (table 2). Furthermore, the contingent-change tests indicated that single ovules evolve from multiple ovules more often in wind-pollinated clades (table 2).

Discussion

The results of our phylogenetic analysis indicate that wind pollination evolves in a correlated way with open habitats, unisexual flowers, dioecy, the uniovulate condition, small plain flowers, and a lack of nectar. In contrast, wind pollination and geographical distribution and the number of flowers per inflorescence evolve independently. Although several of these associations have been examined previously (e.g., Regal 1982; Linder 1998; Vamosi et al. 2003), our study is the first to investigate correlations across the angiosperm phylogeny. Furthermore, in several cases we were able to detect contingent evolution and identify the most common background on which the evolution of a trait occurs. We now discuss potential adaptive explanations for the associations that our comparative analyses have revealed and comment on some of the limitations of using large-scale phylogenies for this type of analysis. Finally, we discuss unresolved questions and propose several future avenues of research that might be profitably pursued.

Ecological Traits

We found no evidence for correlated evolution between geographical distribution and wind pollination. This result may

Table 2

Likelihood Ratio Values for Tests of Correlated Evolution between Pollination Modes and Ecological and Morphological Traits for 560 Species Using the BayesTraits Program and the Phylogeny of Soltis et al. (2000)

Trait	Likelihood ratio of dependent vs. independent model	Trait (state 1) evolves more often in wind-pollinated clades	Wind pollination evolves more often in clades with trait (state 1)	Wind pollination lost more often in clades with opposite trait (state 0)	Opposite trait (state 0) evolves more often in animal-pollinated clades
Geographical distribution	6.92	1.06	2.43	.10	2.34
Habitat	14.85[**]	.53	2.50	7.37[*]	.06
Floral sexuality	58.32[***]	.27	13.63[***]	.78	6.15
Sexual system	53.35[***]	.62	19.30[***]	7.92[*]	9.62[**]
Ovules	21.43[***]	6.79[*]	.13	1.50	1.47
Number of flowers	8.20	2.32	.00	2.34	2.22
Flower size	34.83[***]	.82	1.04	5.55	2.03
Flower showiness	55.63[***]	.34	.42	5.69	2.93
Nectar	132.14[***]	15.44[***]	6.09	10.31[**]	1.26

Note. Likelihood ratio values are for tests of four hypotheses, which are not mutually exclusive, about contingent evolution.

[*] $P < 0.05$.

[**] $P < 0.01$.

[***] $P < 0.0001$.

at first appear to challenge many observations of the higher frequency of wind-pollinated species in temperate regions (e.g., Regal 1982; but see Bawa et al. 1985; Bullock 1994). However, in our study we were specifically interested in the correlated evolution of wind pollination, not in the frequency of wind pollination in contrasting geographical regions. For example, the high abundance of anemophily in temperate regions found by Regal (1982) may largely reflect the predominance of Poales (grasses, sedges, rushes, etc.) and Fagales (beeches, oaks, etc.) in many ecosystems. In our data set, each of these groups was represented by a single evolutionary transition. Although there is a greater abundance of wind-pollinated versus animal-pollinated plants in many temperate ecosystems, our analysis provides no evidence that ecological conditions in temperate regions preferentially select for the evolution of wind pollination from animal pollination, or that wind-pollinated plants have migrated from tropical to temperate regions because of more favorable environments.

The aerodynamic requirements for wind pollination occur in habitats with open vegetation that allow for moderate wind speeds (Whitehead 1983; Niklas 1985; Dowding 1987). Although the finding of independent evolution between pollination mode and geographical region (temperate or tropical) may seem to contradict this, we did not limit our coding of tropical regions to tropical forests but included species from other tropical ecosystems including savannas and grasslands. However, we specifically tested the effect of vegetation structure by looking for correlated evolution with open versus closed habitats because plant size and density are likely to influence the efficacy of pollen dispersal in wind-pollinated plants. We found that open habitats and wind pollination evolve in a dependent way and are positively associated. In addition, wind pollination was lost more often when it occurred in closed habitats.

These results suggest that there may be constraints on the origin of wind pollination in closed habitats and that wind-pollinated plants are more likely to persist in open habitats.

Support for this idea is indicated by the frequency with which plants in closed forests in tropical regions use a mixture of wind and insect pollination (e.g., Piperaceae: De Figueiredo and Sazima 2000; Arecaceae: Uhl and Moore 1977; Listabarth 1993; Berry and Gorchov 2004). Additionally, although we did not test for the effect of altitude (due to insufficient data), increasing altitudinal gradients are often coupled with a decrease in vegetative cover. Several studies have shown that altitudinal gradients, which impact both the pollinator community and habitat type, can select for wind pollination (Berry and Calvo 1989; Gomez and Zamora 1996). Our findings suggest that most wind-pollinated species are likely to be limited in distribution by the structure of the surrounding vegetation, including the seasonal phase of canopy cover.

Floral Traits

Not unexpectedly, we found strong evidence that nectar and pollination mode evolve in a correlated manner. Our results indicate that nectar is lost more often in wind-pollinated clades, as one might expect on energetic grounds. However, our results also suggest that the presence of nectar in animal-pollinated species does not act as a constraint to the evolution of wind pollination. It has been proposed that wind pollination evolves more readily in nectarless lineages in which pollen is used as reward for pollinators (e.g., *Thalictrum*: Kaplan and Mulcahy 1971). Although this may be true in particular cases, we found no evidence that nectar generally limits possibilities for transitions to anemophily. In contrast, although the pattern was less clear, it appears that large showy flowers may constrain the evolution of wind pollination. We found that wind pollination evolves more often in taxa with small unshowy flowers. Linder (1998) proposed that wind pollination evolved more often in animal-pollinated groups with poorly developed or undifferentiated perianths, such as the magnoliids, caryophyllids, and rosids, and rarely in groups with zygomorphic flowers. Our data support this

proposal. Finally, we found no evidence for correlated evolution between the number of flowers per inflorescence and wind pollination. Weller et al. (2006) reported that the number of flowers, per se, in *Schiedea* was less important for wind pollination in comparison with inflorescence condensation, a composite measure of the number of flowers and the length of the inflorescence. Hence, inflorescence architecture probably plays a more important role in the evolution of wind-pollinated plants than the number of flowers produced within an inflorescence.

A strong association between wind pollination and reduced floral morphology is apparent throughout the literature. However, it is unclear whether this association arises as an adaptation to wind pollination or because large complex flowers constrain the evolution of wind pollination. Our results suggest that large flowers act as a constraint to the evolution of wind pollination, perhaps because they limit the exposure of anthers and stigmas to the airstream. However, there is no a priori expectation for why colorful flowers should also constrain the evolution of wind pollination. Therefore, it is possible that these associations arise because wind pollination evolves more often in species that are pollinated by generalist insects, including flies and small pollen-collecting bees, which are often associated with plants that have small white or pale-colored unshowy flowers. This is supported by the observation that most ambophilous taxa are pollinated by generalist pollinators (e.g., *Salix*: Peeters and Totland 1999; Tamura and Kudo 2000; *Piper*: De Figueiredo and Sazima 2000; *Linanthus*: Goodwillie 1999; *Thalictrum*: Kaplan and Mulcahy 1971; *Schiedea*: Weller et al. 1998, 2006). These patterns suggest that the evolution of wind pollination occurs in lineages with reduced floral morphology. Subsequent selection against attractive structures would then intensify the correlation with wind pollination.

Sexual Traits

Our finding that wind pollination is strongly correlated with dicliny and dioecy is in accord with several previous studies (e.g., Bawa 1980; Charlesworth 1993; Renner and Ricklefs 1995; Vamosi et al. 2003). There is no comprehensive mechanistic explanation for the association between wind pollination and unisexual flowers, although some conceptual arguments are compelling (see Charlesworth 1993). In hermaphrodite animal-pollinated plants, female and male functions usually share the costs of floral display and pollinator rewards (Lloyd 1982). Pollinators perform two services in one visit, delivering pollen to the stigma and picking up pollen from anthers. However, in wind-pollinated plants, the removal and capture of pollen are independent events, and different structural requirements are necessary for optimal pollen dispersal and pollen capture (Niklas 1985; Friedman and Harder 2004). Indeed, spatial interference between female and male structures in a flower may be directly disadvantageous and explain the high incidence of dichogamy and herkogamy in wind-pollinated species (Lloyd and Webb 1986; Webb and Lloyd 1986). Nonetheless, geitonogamous selfing may be inevitable for wind-pollinated plants, resulting in strong selection for dioecy as a mechanism of inbreeding avoidance. Benefits of sexual segregation, such as flexibility for altering male and female investment and differential positioning of

flowers for optimal pollen dispersal versus capture, are likely to be important in the evolution of unisexual flowers. Mechanistic studies examining the benefits of unisexual flowers in wind-pollinated species are necessary for understanding the selective factors responsible for this frequent association.

An important finding of our study concerns the order of transitions involving dicliny and wind pollination. We found that wind pollination evolves more often after the establishment of dicliny in unrelated lineages. This pattern was evident for species with unisexual flowers and also for those that were purely dioecious. This is the first time this pattern has been identified in a large-scale comparative analysis and is important because case studies of particular taxa provide conflicting scenarios. For example, it has been reported that dicliny precedes wind pollination in *Leucadendron* (Proteaceae: Midgley 1987) and *Thalictrum* (Ranunculaceae: Kaplan and Mulcahy 1971), whereas the opposite order apparently occurs in the Poaceae (e.g., *Buchloe*, *Distichlis*, *Scleropogon*, *Spinifex*: Connor 1979 and references therein) and in *Fraxinus* (Oleaceae: Wallander 2001), where wind pollination has originated at least three times, with dioecy evolving from androdioecy after wind pollination on at least three occasions. There are likely to be different selective factors favoring unisexual flowers depending on the ecological conditions, but our finding that wind pollination evolves more often in diclinous lineages suggests a common functional basis for this association.

Here we outline an evolutionary scenario for why wind pollination evolves more often in diclinous lineages. Dioecy is correlated with small unshowy flowers (Vamosi et al. 2003) that are usually pollinated by generalist pollinators (Charlesworth 1993; Bawa 1994). The floral morphology of these plants may make the evolution of wind pollination an especially feasible option because pollen dispersal and capture are not impeded by large or complex perianths. If pollinators become scarce or ineffective, reducing fertility as a result of pollen limitation, diclinous species may evolve wind pollination to ensure more effective pollen dispersal between plants (reviewed in Culley et al. 2002). These same ecological conditions commonly promote the evolution of selfing as a mechanism of reproductive assurance (reviewed in Eckert et al. 2006). However, the presence of unisexual flowers would in most lineages preclude the evolution of selfing through autonomous self-pollination (but see Ågren and Schemske 1993). According to this hypothesis, insufficient pollinator service resulting in pollen limitation could elicit two quite different evolutionary transitions in pollination systems, 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 the proficiency of cross-pollen dispersal. Thus, similar ecological conditions and selective agents could result in two very different evolutionary outcomes due to contrasting ancestral traits.

Several studies provide support for a scenario in which wind pollination evolves in dioecious lineages as a response to pollinator scarcity. Weller et al. (1998) report that some diclinous species of *Schiedea* (Caryophyllaceae) suffer from pollinator limitation, with the evolution of wind pollination

a common outcome. In *Leucadendron*, the genus is exclusively dioecious, and the vast majority of species is animal pollinated. However, there are at least four independent transitions from animal pollination to wind pollination (Midgley 1987; Hattingh and Giliomee 1989; Barker et al. 2004). *Leucadendron* is endemic to the fynbos shrublands of the Cape Floristic Region of South Africa, where competition for pollinators may be intense and pollen limitation of seed set is commonplace (Steiner 1988; Johnson and Bond 1997). Whether transitions from animal pollination to wind pollination in *Leucadendron* are driven by pollen limitation and the requirements of more effective cross-pollination is not known. Our finding that wind pollination evolves more often in lineages with unisexual flowers suggests that wind pollination evolves to relieve pollinator limitation (but see Cox 1991 for alternative explanations), particularly because a reversion to perfect flowers and autonomous self-pollination would be highly unlikely.

A similar argument might suggest that wind pollination should evolve more frequently in self-incompatible lineages following pollinator loss. However, this transition may be rare because self-incompatibility can break down quite readily in some taxa (see Igic et al. 2008) and certainly occurs more easily than transitions from dioecy to hermaphroditism (Bull and Charnov 1985). In self-incompatible *Linanthus parviflorus*, the evolution of wind pollination offers reproductive assurance against unreliable pollinators (Goodwillie 1999). In other species of *Linanthus*, the breakdown of self-incompatibility and the evolution of self-fertilization provide reproductive assurance (Goodwillie 2001). It would be interesting to determine the ecological and life-history contexts in which these contrasting outcomes occur. The transition to wind pollination in self-incompatible lineages has also been reported in the genus *Espeletia* (Asteraceae: Berry and Calvo 1989). In species where the evolution of selfing is prevented due to strong incompatibility and limited genetic variation for self-compatibility, there may be selection for wind pollination when pollinators are scarce.

We found strong evidence for a reduction in ovule number to one after the evolution of wind pollination. This suggests that the uniovulate condition is an adaptation to wind pollination. Further evidence for this transition is in the Poales, where there have been repeated reductions from multiple ovules per carpel to solitary ovules (Linder 1998; Linder and Rudall 2005). The most common explanation for this association is that wind-pollinated plants are unlikely to capture sufficient pollen grains to fertilize many ovules. However, experimental studies involving the measurement of pollen loads of naturally pollinated taxa of Poaceae, Restionaceae, Rosaceae, and Proteaceae (Honig et al. 1992; Linder and Midgley 1996; Friedman and Harder 2004) found amounts of pollen on stigmas that far exceeded ovule number (mean pollen grains per ovule range from 3 to 100). It is therefore unlikely that pollen limitation alone is responsible for selection of decreased ovule number in wind-pollinated species.

Several morphological and aerodynamic features of wind-pollinated plants may favor an optimal strategy of few ovules per flower. The relatively low cost of producing flowers in wind-pollinated plants may favor a packaging strategy with few ovules per flower and more flowers per plant. The model developed by Burd (1995) provides support for this idea by showing that higher floral costs generally favor more ovules per flower, although his model only considered animal-pollinated plants. Also, because wind pollination is a stochastic process where plants may capture pollen from a variety of potential mates, uniovulate carpels may be a mechanism to increase pollen-tube competition. Finally, by producing more flowers with fewer ovules, the spatial separation of flowers may increase the volume of air sampled by a plant and the probability of capturing pollen grains. A more mechanistic understanding of the functional relation between wind pollination and ovule number would be informative.

Caveats and Future Research

There are other traits that may be correlated with wind pollination that would be interesting to investigate. For some of these traits, we attempted to include them in our analysis but were unable to compile sufficient data for all taxa. Most noticeable are those traits associated with pollen. Copious pollen production and smooth, dry, small pollen grains are commonly cited as attributes of anemophilous pollen (Faegri and van der Pijl 1979; Whitehead 1983; Proctor et al. 1996). Linder (2000) reported a correlation between pollen aperture type and wind pollination across angiosperm families, and he also proposed that circular apertures may be linked to speciation. Other attributes that could yield informative results include altitude, life form, and characteristics of stigmas.

Some of the traits associated with wind pollination may not be independent and could complicate some of the correlations we report. We are not aware of analytical methods to investigate correlated evolution for more than two traits simultaneously in a phylogenetic context. The effects of a third trait could best be examined by looking at correlated evolution within higher-level phylogenies that are variable in only the trait of interest. However, there are few clades that have the repeated evolution of wind pollination and adequate variation in ecological and morphological traits (but see Wallander 2001). In an effort to understand the associations between traits, we examined all pairwise intercorrelations between the traits in this study that evolve in a correlated way with wind pollination (21 different pairwise associations; results not shown). We found that many of the morphological traits evolve in a correlated way with one another but that habitat type did not evolve in a correlated way with any trait except the presence of nectar. Unfortunately, where we detected significant intercorrelations between traits (e.g., the positive association between unisexual flowers and single ovules, $P < 0.001$) we cannot determine whether this association is driving correlations with wind pollination or whether the association with wind pollination is causing the intercorrelation. Until multivariate methods become available, it is impossible to tease apart the relative contributions of different associations to the overall positive correlation of a trait with wind pollination.

A potential bias in the methodology using transition rates may occur when the character states at the tips of the phylogeny are unequal and are poor indicators of the stationary frequencies. This issue has been recently addressed in the context of ecological specialization of insects (Nosil and Mooers 2005), where it was shown that there can be false detection of higher transition rates to the more common state. Currently

implemented methods of character state reconstruction assume that the rate of character change is the same over the entire phylogeny, which is unlikely to be the case, particularly if the trait itself can influence speciation and/or extinction. However, because we found about equal occurrences of traits evolving before or after wind pollination (table 2) this problem is unlikely to be a major factor influencing our results.

A serious concern for comparative studies of reproductive transitions is the frequent use in the literature of floral characters to infer pollination mode. Here, we were looking for correlations between morphological traits and wind pollination. For some of the taxa included in our study, it is likely that their assignment as wind-pollinated species in the literature was based purely on morphological characters associated with the "anemophilous syndrome" (Faegri and van der Pijl 1979). Clearly, it is then circular to test for correlations with wind pollination. Definitively determining pollination mode in some groups (e.g., large tropical trees) can be time consuming. Pollinator exclusion experiments using bags are commonly employed, but this method is inherently flawed because it changes the aerodynamic environment around inflorescences. Studies have shown that the structure of the stigma and/or inflorescence can have significant consequences for pollen flow (Niklas 1987; Niklas and Buchmann 1987; Linder and Midgley 1996; Friedman and Harder 2005), and so bagging experiments may inadvertently limit pollen dispersal by wind. Unfortunately, without detailed field observations and experiments, it is difficult to know with certainty whether a plant is insect pollinated or wind pollinated or both.

Our study included only a few species per family and only one species per genus. As a result, many transitions occurring at higher taxonomic levels will be undetected in our analysis. For example, in the Poaceae, which are entirely wind pollinated, unisexuality has evolved multiple times, and evidence also suggests frequent reversions to hermaphroditism (Connor 1981; Malcomber and Kellogg 2006). However, neither of the species included in this study are dioecious (*Oryza sativa* and *Zea mays*), and so these transitions are not accounted for. Similarly, Dodd et al. (1999) report a single origin of wind pollination in the Fagales, a result that we also observed in our study. However, a phylogeny of the Fagaceae indicates that there may be multiple origins of wind pollination (Manos et al. 2001). Applying comparative approaches similar to those used here to well-resolved phylogenies of particular angiosperm clades should further distinguish traits that facilitate the evolution of wind pollination from those that are direct adaptations to wind pollination.

There are many fundamental questions about wind pollination that remain unresolved. For example, the comparative study by Dodd et al. (1999) showed that transitions between biotic and abiotic pollination are strongly asymmetric, so shifts from biotic to abiotic pollination happen much more frequently and are also correlated with a net decrease in speciation rate. However, there are important exceptions to this, including the Poaceae, which is highly species rich with over 10,000 species (Doust and Kellogg 2002), and the Fagales, which is a species-rich group of wind-pollinated trees but may in fact have relatively low rates of diversification (Magallón and Sanderson 2001). Our study indicates that wind pollination and geographical distribution do not evolve in a correlated way, although there may be much greater abundance of wind-pollinated plants in temperate regions (Regal 1982). It is possible that wind-pollinated lineages in temperate regions are more likely to persist and undergo speciation, a hypothesis we were unable to test with this data set.

The transition from animal pollination to wind pollination remains a central problem in plant evolutionary biology. Using phylogenetic evidence, our study demonstrated correlated evolution between wind pollination and a range of traits, including open habitats, unisexual flowers, dioecy, uniovules, small plain flowers, and a lack of nectar. For five of these traits (open habitats, unisexual flowers, dioecy, uniovules, and lack of nectar), we found evidence of contingent evolution, allowing us to make predictions about the mechanisms responsible for the associations. Our study raises novel predictions about the causes of correlations between wind pollination and unisexual flowers and between wind pollination and a reduction in ovule number. These ideas would benefit from further exploration. Studies that target specific groups and test mechanistic hypotheses are essential for understanding the functional basis for the evolution and maintenance of wind pollination.

Acknowledgments

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