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Abiotic Pollination: An Evolutionary Escape for Animal-Pollinated Angiosperms [and Discussion]

Paul Alan Cox and P. J. Grubb

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Abiotic pollination: an evolutionary escape for animal-pollinated angiosperms

PAUL ALAN COX

Department of Botany & Range Science, Brigham Young University, Provo, Utah 84602, U.S.A.

SUMMARY

Early botanists considered abiotic pollination to be primitive in angiosperms. But we now deduce from studies of palaeoecology and of extant 'primitive' angiosperms that animal pollination was concomitant with the rise of the angiosperms. Recent studies of wind and water pollination in angiosperms also show these systems to be highly sophisticated. If entomophily contributed to the rise of the early angiosperms, why should many of their descendants have later evolved abiotic pollination systems?

Although entomophily was initially advantageous to the early angiosperms, abiotic pollination systems may be superior in areas of low species diversity, newly colonized habitats, and places with extremely short growing seasons or other adverse climatic conditions. Abiotically pollinated plants are not constrained by the range of animal pollinators, and as a result are spectacularly successful in long-distance dispersal. Abiotic pollination also offers an escape from deleterious sexual selection and from dependency on pollinators that are climatically limited in their distribution in space or time and vulnerable to extinction. Because evolution of abiotic pollination frequently leads to dicliny or dichogamy, it is largely irreversible. This evolutionary irreversibility coupled with lowered rates of extinction and speciation give wind- or water-pollinated taxa unique phylogenetic profiles.

> 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 have again become anemophilous.
>
> (Darwin 1876, p. 407)

1. INTRODUCTION: IS ENTOMOPHILY A PRIMITIVE CHARACTER IN ANGIOSPERMS?

In *The effects of cross and self fertilization in the vegetable kingdom*, Charles Darwin struggled with the implausibility of entomophilous plants ever undergoing retrograde evolution to a more primitive condition: anemophily. Yet even though Darwin knew of a few probable cases of reversion such as *Poterium sanguisorba* (Rosaceae), in his time this mystery was not regarded as particularly pressing as only a few species were believed to have so reverted.

This lack of interest in the evolution of abiotic pollination systems in angiosperms in the late 19th century is hardly surprising: at the time, abiotic pollination was unquestionably regarded as primitive. In the evolutionary scheme proposed by Axell (1869) wind-pollinated species were considered to be the most imperfect and primitive phanerogams because of their immense waste of pollen. Delpino (1868, 1869) added an even lower rung to the evolutionary ladder: hydrophily, a somewhat surprising denigration given the previous biological and theological significance accorded to water pollination (Darwin 1790–1791; Paley 1802; Cox 1988*a*).

This belief in the inherent primitiveness of abiotic pollination was promulgated by Müller (1873) in his influential *Die Befruchtung der Blumen durch Insekten*:

> Finally from the wind-pollinated angiosperms, entomophilous flowers arose, as insects came first accidentally and afterwards regularly to seek their food on flowers, and as natural selection fostered and perfected every change which favored insect visits and thereby aided cross-fertilization... The transition from wind pollination to insect pollination and the first traces of adaptation to insects, could only be due to the influence of quite short-lipped insects with feebly developed color sense.
>
> (Müller 1881, pp. 593–594)

That these hierarchical schemes were regarded as orthodox was underscored by Darwin's laudatory preface to the English version of Müller (Müller 1883). Müller's ranking of pollination types was later adopted by Verhoeff (1894) and Knuth (1898).

Today, this mystery is far greater than in Darwin's time, for recent research has shown that the early

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angiosperms were not wind pollinated, as Darwin and his contemporaries assumed, but instead insect pollinated. This contemporary view comes not only from pollination biology (Meeuse 1961; 1984; Proctor & Yeo 1973; Fægri & Van der Pijl 1979; Thien *et al.* 1985) but from paleobotany and systematics (Doyle 1978; Crane *et al.* 1986; Crepet & Friis 1987; Doyle & Donoghue 1987).

Key to this understanding has been evidence that the first angiosperms and their sister groups were probably entomophilous. Friis & Crepet (1987) argue that the hermaphroditic reproductive structures of the Bennettitalean genera *Williamsoniella* and *Wielandiella* were functionally analogous to a magnolialean flower, with beetles and possibly dipterans as the putative pollinators. Pollen evidence, however, is more equivocal (Retallack & Dilcher 1981).

Friis & Crepet (1987) propose *Illicium* (Illiaceae–Magnoliidae) pollination by flies and beetles (Thien *et al.* 1983) as a modern analogue of early angiosperm pollination. Other possible modern analogues include *Zygogynum* (Winteraceae), *Drimys* (Winteraceae) and *Degeneria* (Degeneriaceae), all of which are pollinated by flies and beetles (Thien 1980; Thien *et al.* 1985; Miller 1989).

Although reconstruction of ancient pollination ecologies from fossils and modern analogues is admittedly uncertain, there now appears to be little argument concerning the primitiveness of entomophily in angiosperms, although some of the early angiosperms may have utilized both insects and the wind as pollen vectors (Dilcher 1979; Retallack & Dilcher 1981). This conclusion, if true, dramatically increases the difficulty of Darwin's mystery: the evolution of abiotic pollination must now be explained in not only a few specialized species, but rather in all anemophilous and hydrophilous angiosperms.

2. POSSIBLE TRANSITIONS BETWEEN ANEMOPHILY AND ENTOMOPHILY

What are some of the possible reasons that anemophily might evolve in an entomophilous species? This question can be divided into two separate issues: (i) the possible evolutionary pathways by which abiotic pollination could be derived from entomophily, and (ii) the evolutionary forces that could favour such a transition.

Obvious candidates for such a change are species that use a combination of biotic and abiotic pollen vectors. In these species strict entomophily and anemophily appear to be but two endpoints on a spectrum, with some species using both vectors sequentially whereas other species use them simultaneously. For example, the flowers of *Bartsia* and *Lathraea* (Scrophulariaceae) and many Ericaceae, such as *Calluna vulgaris* and *Erica carnea*, when first opened, have their pollen dispersed only by insects. Later, though, when the filaments elongate and the anthers are exerted beyond the corolla mouth, the pollen is carried by the wind to other flowers (von Marilaun 1895). A similar mechanism exists in *Cyclamen* with the oily pollenkitt which serves to adhere the pollen to insects reportedly vanishing as the flowers progress in age (Hilldebrand 1897).

Plants with simultaneous entomophily and anemophily are also known. Many species of the otherwise anemophilous genus *Luzula* (Juncaceae) such as *L. lutea*, *L. nivea* and *L. lactea* produce brilliantly coloured flowers with brightly coloured pseudo-nectaries; in these species pollen is dispersed by both insects and the wind (Buchenau 1871; Knuth 1898). Insects also visit otherwise anemophilous taxa such as *Plantago lanceolata* and *P. media* (Plantaginaceae), species of the genus *Tilia* (Tiliaceae) and a nectarless species of *Helianthemum* (Cistaceae) (Clifford 1962; Fægri & van der Pijl 1973; Proctor & Yeo 1973; Primack 1978).

Tilia is worthy of further note as Pohl (1937*b*) found that *Tilia* has a pollen:ovule ratio well within the range of entomophilous species. Yet the intensity of *Tilia* pollen rain throughout Britain is very high, with up to 83.6 grains cm^{-3} year^{-1} in Cambridge (Hyde 1950). The British pollen rain is also rich in other predominantly entomophilous species such as *Salix* and *Sambucus*.

In some genera there is variation among the species in the relative allocation to anemophily or entomophily. For example *Acer* (Aceraceae) species differ in pollenkitt, and have corresponding differences in pollination syndrome (Hesse 1979). *Acer negundo* (Aceraceae) is strictly anemophilous, *A. campestre*, *A. opalus*, and *A. pseudoplatanus* use a combination of pollination vectors, whereas *A. platanoides* is entomophilous. Similar variation occurs in *Thalictrum* (Ranunculaceae). Most species are visited by insects, but *T. polygonum* and *T. flavum* use both insects and the wind as pollen vectors, whereas *T. dioicum* and *T. minor* are strictly anemophilous, bearing traces of their entomophilous ancestry (Müller 1883; Proctor & Yeo 1973; Melampy & Hayworth 1980).

It appears, therefore, that several entomophilous species have either some component of anemophilous pollination or are potentially anemophilous, even if their wind-dispersed pollen is not efficacious in fertilization. Inefficacy of wind-borne pollen probably indicates a female floral or stigmatic morphology that is aerodynamically inappropriate for pollen reception. The evolution of anemophily in such taxa would therefore require development of appropriate aerodynamic surfaces for pollen capture.

Are there cases where the converse is true, i.e. where the aerodynamic surfaces for pollen capture are present, but where the adaptations necessary for wind-borne pollen have not yet evolved? One such example occurs in the Pandanaceae, which has tristichous phyllotaxy as a synapomorphy uniting the family. In *Pandanus* this phyllotactic pattern functions to position the floral bracts beneath the pistillate inflorescence in such a way as to impart the aerodynamic characteristics necessary for pollen capture by the stigmatic surfaces (Cox 1985, 1990).

However, similar flow patterns are also produced by the tristichous bracts of pistillate inflorescences of the vertebrate-pollinated species *Freycinetia reineckei* (Pandanaceae). But in the case of *Freycinetia*, tristichous phyllotaxis appears as a preadaption to anemophily because its pollen is covered with a sticky, lipid-rich pollenkitt, which effectively prevents wind dispersal. Thus the tristichous arrangement of floral bracts in *Freycinetia* could prove functional for wind pollination only with a loss of pollenkitt and some changes, such as lengthening of the internode, in the staminate inflorescence. None of these changes would be dependent on major alteration in structural gene sequences, but would require only subtle difference in the timing of regulatory gene activity. A process similar to this may have allowed wind pollination in *Pandanus* to evolve from vertebrate-pollinated ancestors (Cox 1990).

Similar evolutionary lability between anemophily and entomophily as a result of developmental timing is apparent in the mangrove family Rhizophoraceae. *Ceriops decandra*, which is insect pollinated, and *Rhizophora mangle*, which is wind pollinated but has relic nectaries, have strikingly similar floral ontogenies (Juncosa & Tomlinson 1987). Judging from the Pandanaceae and the Rhizophoraceae, the evolutionary gap between anemophily and entomophily, measured in the amount of necessary structural genetic change, may be small indeed. This realization leads to a new question: are all plant species equally likely to evolve abiotic pollination systems, even if these systems have selective advantage?

It seems unlikely that a species with a sympetalous corolla and anthers basifixed to the corolla throat could easily evolve anemophily because of inherent difficulty in pollen dispersal. But a species with exerted stamens, and short or no corolla would be a more likely candidate. Fægri & van der Pijl (1973) suggest that just such a reduction of tepals in brush blossoms can facilitate anemophily and offer a putative transition series in *Thalictrum*. In hydrophilous species, floral appendages can play an important role unrelated to their ancestral function of pollinator attraction. In both *Vallisneria* and *Enhalus* (Hydrocharitaceae) the staminate flowers are carried on the water surface by the reflexed petals, and fall into the depressions created by the long, floating petals of the pistillate flowers (Cox 1988*a*). The staminate flowers of the related seagrass genus *Halophila* still bear long petals underwater, although these do not appear to be functional in pollination.

3. IS ENTOMOPHILY ALWAYS BENEFICIAL?

The idea that abiotic pollination systems are inherently primitive is no longer tenable: recent research has highlighted the sophisticated mechanisms used for pollen dispersal and capture in anemophilous and hydrophilous angiosperms (Whitehead 1983; Niklas & Buchmann 1985; Cox 1988*a*). For example Typhaceae, which used to be considered the most primitive monocotyledonous family (Engler & Gilg 1924), has a wind-pollination system that is remarkably sophisticated and successful. Wind-dispersed tetrads of *Typha latifolia* pollen frequently grow pollen tubes from the stigma of one flower to the stigma of an adjacent flower (Nicholls & Cook 1986). Resultant seed is set high; although in the field only one third of the stigmas are pollinated, remarkably over two thirds of the uniovulate flowers set seed (Krattinger 1978). Similarly, the seagrass genera *Amphibolis* and *Thalassodendron*, once believed to be the most primitive seagrasses (Hartog 1970), have recently been found to have intricate pollination mechanism involving tidally synchronized release of submarine male flowers, rapid expulsion of noodle-like pollen on the water surface, and formation of floating search vehicles of high efficiency (Cox & Knox 1989; Cox 1991).

At the community level, abiotic pollination systems do not appear to be as inefficient or wasteful as might have been previously assumed. In this symposium, Midgley & Bond report that wind-pollinated taxa are as speciose as animal-pollinated taxa in the Cape flora, and do not appear to be at a reproductive disadvantage. The number of cases in which anemophilous species clearly have entomophilous ancestry also argues against a global disadvantage for wind-pollinated species. Under what conditions, then, might anemophily be advantageous?

To answer, it is necessary to consider the conditions under which insect pollination is disadvantageous. This may seem an odd question, as it has been argued by many authors (and summarized in this symposium by Crepet *et al.*) that insects and insect pollination have played a pivotal role in the evolution of angiosperms, with many of the reproductive structures of angiosperms evolving in response to insect pollination. Yet perhaps evolutionary importance is not always synonymous with evolutionary beneficence.

Is it possible, for example, that tightly coevolved plant–pollinator relations such as those involving figs and fig wasps, or yuccas and yucca moths, may not represent an evolutionary achievement, but rather an evolutionary dead-end?

4. POSSIBLE MECHANISMS DRIVING THE EVOLUTION OF ABIOTIC POLLINATION SYSTEMS FROM ENTOMOPHILOUS SYSTEMS

Under what conditions could anemophily possibly evolve from entomophily? In an ecological sense, if we consider a plant such as a *Tilia* or *Plantago* species which uses both biotic and abiotic vectors for pollination, we might ask under what conditions would it be advantageous for individuals to decrease the proportion of pollen dispersed by animal vectors, and to increase the proportion of pollen dispersed by abiotic vectors. In an evolutionary sense we can examine the conditions that might cause anemophily to become an evolutionary stable strategy (ESS) such that a wind-pollinated population would be invulnerable to invasion by an insect pollinated mutant.

The following are examples of circumstances that could favour abiotic pollination as an ESS.

(*a*) *Range expansion or colonization ability*

Raven (1977) has argued that entomophily allowed the angiosperms to persist as widely dispersed populations, particularly in tropical ecosystems where accurate pollination transfer between widely spaced individuals is important. However this advantage is likely to hold only at intermediate scales of distance, and rapidly vanishes in the case of long-distance dispersal, where the migration ability of an entomophilous plant is ultimately constrained by the range of its pollinators.

Even on a local scale, entomophilous plants that colonize microsites unattractive to pollinators may have reduced success (Watson 1969; Handel 1983). But clearer distinctions emerge on large geographical scales, because differences in long-distance dispersal ability and colonization appear to be closely tied to modes of pollination. *Pandanus* (Pandanaceae), with its anemophilous pollination system, can colonize any appropriate island regardless of the island's faunal composition. This anemophily, coupled with facultative apomixis, has given it a range throughout the Pacific and Indian oceans that is much larger than the related vertebrate pollinated genus *Freycinetia*, and vastly larger than the related entomophilous genus *Sararanga* (Cox 1985, 1990).

The facilitation of long-distance dispersal by abiotic pollination has been very important in seagrasses. Even though only 12 genera exist, there are few coastlines or islands with appropriate substrates that have not been successfully colonized by these hydrophilous monocotyledons. Of the temperate genera, *Zostera* (Zosteraceae) has a strikingly large distribution, being found along the coasts of southeastern Africa, Europe, Australia, New Zealand, eastern Asia, and both coasts of North America. A tropical genus, *Halophila*, is found throughout the Indian Ocean, South Pacific, Caribbean, and west tropical Atlantic (den Hartog 1970). Although the seagrasses are capable of clonal growth, recent research has highlighted their high levels of sexual reproduction and resultant genetic diversity (Cox 1988*a*; Cox *et al.* 1991). Dependency on specific animal-pollination vectors would have greatly limited the ability of both Pandanaceae and the seagrasses to colonize new areas, particularly oceanic islands.

(*b*) *Pollinator extinction*

The spectre of extinction frequently haunts plant species dependent on highly specific pollinators: if the pollinator goes extinct, their own survival is threatened. However, confirmed reports of plant extinctions linked to pollinator losses are few, because the pollination biologies of rare species are little studied and the extinction processes are likely rapid. In Hawaii, the extinction of indigenous avian pollinators imperiled *Freycinetia arborea* until a new pollinator was inadvertently introduced (Cox 1983). In the western United States the overwhelming majority of rare or endangered plants are entomophilous while very few are anemophilous (Harper 1979); Clearly anemophilous taxa are rarely forced to face the loss of their pollen vector. However, although I suggest that extinction rates should be lower in anemophilous taxa, Eriksson & Bremer (1991) find that the R value (speciation rate minus the extinction rate) is significantly higher for animal-pollinated than for abiotically pollinated species, a result similar to that of Niklas *et al.* (1985). Although this may constitute a contradiction to my hypothesis, these higher R values may merely reflect the higher speciation rates of entomophilous taxa.

(*c*) *Deleterious sexual selection*

Under sexual selection, small increases in male reproductive effort can result in disproportionately large increases in reproductive success (Willson 1979), far in excess of what could be obtained through investment in abiotic pollination (figure 1). However, sexual selection can rapidly drive phenotypic evolution to the point where even large investments in male reproductive functions result in only marginal increments of reproductive success.

Consider, for example, pollination in the Madagascar orchid *Angraecum*. In 1862 Darwin predicted that *A. sesquipedale*, which has a 22 cm long spur concealing nectar, would be found to be pollinated by a giant hawkmoth with a 22 cm long proboscis. Just such a hawkmoth, *Xanthopan morgani praedicta*, was discovered over 40 years later (Rothschild & Jordan 1903). The existence of these long corolla spurs (up to 30 cm in *A. sesquipedale* and *A. sororium*) and interminable moth proboscii, may in fact, represent a case of coevolution out of control. Nilsson (1985, 1987) suggests a process of remorseless selection for increasing tongue length in the moths, because even slightly shorter-proboscis moths are unable to reach the nectar in the longest spurs. But the flowers also have remorseless selection for increasing spur length, as flowers with slightly shorter spurs are unable adequately to position their pollinaria on the moths with the longest proboscis. As result, each round of selection requires the orchid to pay a higher price for pollination.

Sexual selection can therefore alter relative advantages of abiotic and biotic pollination by changing the expected return on male reproductive effort (figure 1). As sexual selection advances, abiotic pollination provides a more favourable return on male reproductive investment, although in many cases (such as *Angraecum*) switching to abiotic pollination may be morphologically impossible.

(*d*) *Low community diversity*

In Utah and Idaho, dominant, overstory plant species are typically anemophilous, whereas species with low frequency and dominance values are usually entomophilous (Ostler & Harper 1978). This prevalence of anemophilous species in temperate regions, and their relative absence from tropical regions, has long been noted (Whitehead 1983). Clearly the structural and microclimatic features of moist tropical forests may impede wind pollination, whereas those of the wind-swept arid regions may favour it. But I suggest that the tremendous differences in species diversity between the tropics and temperate areas may also play an important role.

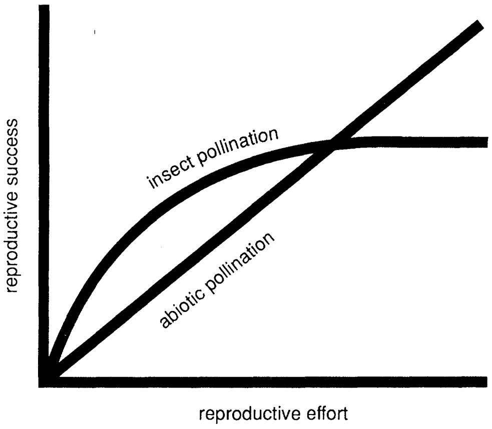

Figure 1. Effects of sexual selection.

Even though anemophilous species can aerodynamically partition the wind, selectively capturing their own grains based on size and velocity (Buchman *et al.* 1989), there might be a limit to the number of species that can effectively divide the wind between themselves. Furthermore, as species diversity increases, population densities must of necessity decrease, also lowering the proportion of self-pollen landing on stigmas. But although some theoretical upper limit on the number of wind-pollinated species in a community may exist, there probably is a lower limit to the number of entomophilous species that can occupy a plant community. For unless an entomophilous species has an extremely smeared phenology, it is in a sense dependent on other flowering species that maintain its pollinators when it itself is not in flower. Thus in communities of extremely low species diversity abiotic pollination systems may be favoured.

(*e*) *Outbreeding in founder populations*

Even though most wind-borne pollen travels short distances, a small amount is dispersed further away (Whitehead 1983). Even long-distance pollination is possible, with significant quantities of *Nothofagus* (Fagaceae) pollen travelling over 5000 km from South America to Tristan da Cuhna in the middle of the Atlantic (Proctor & Yeo 1973). Although the extremely short viability of hydrophilous pollen, measured in hours, makes fertilization at long distances unlikely, the much longer viability of anemophilous pollen makes long-distance pollination, however rare, a distinct possibility. Such long-distance pollination may be important in maintaining a modicum of seed set in small isolated populations of self-incompatible, dichogamous, or diclinous populations at the extension of the species range, and may also play an important genetic role (see §4*h*).

(*f*) *Phenological and developmental flexibility*

Another reason that anemophilous taxa are successful in temperate areas may be that they are not phenologically constrained in the same manner that entomophilous taxa are. Selection drives flowering times of entomophilous taxa to be closely tied to periods of maximal pollinator activity, in many cases effectively excluding early season and late-season flowering. Highly synchronous phenologies may also be more difficult to achieve in entomophilous taxa either because of the need to avoid pollinator satiation or because of the necessity to maintain trap-lining pollinators. Hence in entomophilous taxa there may be potential conflicts between flowering times optimized for pollination success and flowering times optimized for fruit development.

Lack of dependency on biotic vectors may, conversely, allow anemophilous taxa to have longer developmental periods for fruits, to have highly synchronous flowering bouts when favoured by climatic conditions, or even to have a highly smeared flowering phenology if bet hedging is in order. The ability precisely to calibrate flowering with fruiting times may give anemophilous taxa a tremendous advantage in areas with short growing seasons or adverse climates.

(*g*) *Phenological synchrony with abiotic phenomena*

As mentioned above, abiotic pollination systems might allow for better synchrony with abiotic phenomena. This capability may be of importance in fine-tuning flowering times for solar-linked phenomena, such as the change of seasons in temperate and arctic climates. But even in these areas there is a rough correlation between onset of pollinator activity and change of the solar calendar. No such correlation exists between pollinator activity and lunar-linked phenomena such as tides, and the ability to synchronize flowering with tides is crucial in the seagrasses. For many seagrasses, surface pollination is possible only during low spring tides and flowering times are tightly synchronized with these periods (Cox 1988*a*, 1991; Cox & Knox 1989). Even submarine-pollinated plants show phenologies synchronized with the tides (Cox & Tomlinson 1988; Cox *et al.* 1990).

(*h*) *Changed population structure*

Abiotically pollinated plants are more likely to be able to persist as pioneering populations in new habitats because they are not constrained by pollinator ranges. They can also set seed and maintain limited genetic contact with parent populations as a result of long-distance pollination. However, except for freshwater hydrophilous plants growing in ponds, small pioneering populations of entomophilous plants are more likely to be reproductively isolated, leading to higher speciation rates. The ability of anemophilous species to undergo dramatic range expansions, persisting as groups of geographically dispersed subpopulations that still maintain limited genetic contact with another, dramatically reduces the likelihood of extinction due to local environmental perturbations. This maintains a broad ecological amplitude for anemophilous species, allowing results of successful genetic experiments to be rapidly communicated throughout the range of the species.

(*i*) *Phenotypic plasticity*

The increased ecological amplitude of anemophilous plants allows them to have greater colonization ability, particularly in early successional stages. Thus rather than being micro-site specialists, anemophilous species can utilize more generalized, *r*-type strategies. This inherent phenotypic plasticity allows anemophilous species to adapt more rapidly to changing abiotic environments. The indiscriminate nature of the wind also may give anemophilous species more opportunities for interspecific and even intergeneric hybridization. Anemophily may give better chances for autopolyploid experiments to succeed, particularly in the colonization of newly opened habitats such as in the genus *Atriplex* (Chenopodiaceae), where autopolyploids invaded new habitats opened with the rapid Pleistocene recession of Lake Bonneville (Stutz & Sanderson 1979).

5. ANEMOPHILY IN ANGIOSPERMS: A CASE OF IRREVERSIBLE EVOLUTION?

Crepet (1981) has hypothesized that wind pollination in angiosperms may have evolved in seasonally dry tropical environments before the mid-cretaceous before the evolution of the bees (Willemstein 1987). Competition for pollinators in beetle-pollinated taxa favoured the evolution of wind pollination, with these anemophilous tropical taxa later invading more temperate areas. But if this is the case, why does abiotic pollination appear to be a one-way evolutionary street? Why have not anemophilous taxa reverted to entomophily with changing conditions?

Much of the reason, I suspect, has to do with the strong need for anemophilous plants to separate male and female sexual functions in either time or space. Entomophilous hermaphrodites use the same floral displays, odours, and pollinator rewards to disperse as well as to attract pollen. But in wind- or water-pollinated taxa, the mechanisms for pollen dispersal tend to interfere with the mechanisms for pollen capture, and hence dimorphic flowers tend to predominate. For example, 75% of seagrass genera are dioecious, and this separation of the sexes is likely maintained because of potential mechanical interference between the sexes (Cox 1988*a*, *b*). The frequency of dicliny is also high in wind-pollinated taxa. Even those abiotically pollinated species with monomorphic flowers tend to be strongly dichogamous, effectively separating male and female functions in time.

This strong selection for physical separation of male and female reproductive functions in abiotically pollinated taxa may lead to what Bull & Charnov (1985) term 'irreversible evolution'. Their concept is similar to the evolutionary 'blind alleys' and 'traps' articulated by Simpson (1953). In short, although anemophily can often rapidly evolve in an entomophilous taxon, the evolution of entomophily in an anemophilous taxon is very rare, particularly in dioecious taxa.

For entomophily to be an ESS the population must be vulnerable to invasion by an entomophilous mutant. Let us consider the case of a dimorphic anemophilous population invaded by an entomophilous mutant; i.e. a mutant plant that suddenly starts attracting insects through the production of nectar, showy floral displays, or other contrivances. If the mutant is male, it must sire more ovules than anemophilous males for the invasion to succeed. However, because the other females in the population lack pollinator attractants, insect-dispersed pollen would be at a disadvantage compared to wind-dispersed pollen, as female plants already have the aerodynamic mechanisms necessary for pollen capture. On the other hand, if the mutant is female and effective at attracting insects, the insect visitors would not be likely to bring pollen from the unattractive, nectarless males unless they were pollen robbers. In either case it is difficult to imagine what would attract the insects to the nectarless flowers of the other sex, and hence pollen flux would probably be far lower for the entomophilous males or females. However, for the invasion to succeed, male progeny of the mutant must successfully disperse more pollen than anemophilous males, and female progeny must set more seed than anemophilous females, all in the absence of nectar rewards. Hence the interference between male and female functions in anemophilous taxa ultimately leads to dicliny or dichogamy, making the evolution of anemophily largely irreversible.

6. CONCLUSIONS

> Such cases, however, are intelligible, as almost all plants require to be occasionally intercrossed; and if any entomophilous species ceased to be visited by insects, it would probably perish unless it were rendered anemophilous... The same result would follow to a certainty, if winged insects ceased to exist in any district, or became very rare. (Darwin 1876, pp. 407–408)

In dealing with the few known cases of evolutionary 'reversion' to anemophily Darwin suggested one possible factor favouring anemophily: the vulnerability of entomophilous species to pollinator extinction. Darwin's list has here been modestly expanded, but these few emendations scarcely seem adequate to deal with the current problem. Moreover, much like Gödel's theorem, the technique of analysis used in this essay, relying heavily on ecological correlation, points to its own inadequacy. If speciation and extinction rates are themselves skewed by abiotic pollination, then species correlations are themselves invalid (Cox 1990). What is needed is painstaking phylogenetic analysis to determine the precise clades in which abiotic pollination evolved. Although a few attempts have been made along these lines (Cox 1990), a broader phylogenetic approach is needed to reveal the underlying patterns.

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Discussion

P. J. GRUBB (*Botany School, University of Cambridge, U.K.*). None of Professor Cox's nine conditions favouring wind pollination over insect pollination seems to cover explicitly the preponderance of wind pollination in the trees of cool temperate deciduous forests, the grasses that dominate the steppes and the shrubs that dominate cold semi-deserts. Is it unreasonable to suggest that the major factor here has been the unreliability of insect populations in spring resulting from the effects of the winter cold?

P. A. COX. Professor Grubb is correct in suggesting that unpredictable mortality of insect pollinators in cool temperate areas may favour wind-pollinated species. This idea extends my evolutionary arguments concerning pollinator extinction to an ecological arena of greater testability: possible higher variance in the reproductive success of entomophilous species as compared with anemophilous species due solely to fluctuations in pollinator populations.