Plant Syst Evol (2010) 286:191–197
DOI 10.1007/s00606-010-0299-9

ORIGINAL ARTICLE

Pollen and ovule production in wind-pollinated species with special reference to *Juncus*

Stefan G. Michalski · Walter Durka

Received: 13 August 2009 / Accepted: 21 April 2010

Abstract The reproductive biology of wind-pollinated species in terms of pollen and ovule production is rarely studied compared with zoophilous species, despite available hypotheses on the effect of growth form and life-history traits on reproductive investment. Here, we use published data and new data for species of *Juncus* and *Luzula* (Juncaceae) to test the hypotheses that, in wind-pollinated species, woody perennials should exhibit larger pollen–ovule (P/O) ratios than herbaceous species and that species with separate sexes have larger P/O ratios than homoecious species. In total, we report pollen and ovule production for 291 wind-pollinated species, including 19 *Juncus* and 5 *Luzula* species. Compared with other wind-pollinated species, *Juncus* exhibits unusually low P/O ratios (log P/O = 2.06 ± 0.46) because of high ovule production. We argue that the high ovule and seed production in *Juncus*, associated with frequent self-fertilization, may be beneficial in habitats preferred by the genus. In general, we found higher P/O ratios in woody perennials (log P/O = 4.37 ± 1.18) or in species with separate sexes (log P/O = 4.28 ± 1.12) than in herbaceous (log P/O = 3.51 ± 0.77) or homoecious (log P/O = 3.52 ± 0.80) species, respectively. However, when we analyzed woody perennials separately, we found no significant difference in P/O ratios between homoecious and nonhomoecious species. We argue that woody perennials, independent of dicliny, may be preferentially outcrossed and therefore exhibit decreased variation in mating systems compared with herbs. Because the degree of outcrossing correlates with P/O ratios, differences between homoecious and nonhomoecious woody perennials could be less pronounced.

Keywords *Juncus* · Juncaceae · Wind pollination · Pollen–ovule ratios · Mating system · Life history

Introduction

Wind pollination is known from at least 18% of all angiosperm families (Ackerman 2000) and has evolved repeatedly from biotically pollinated ancestors (Linder 1998). On the level of regions or communities, it is more common in higher latitudes and altitudes, in temperate forests and open grasslands (Regal 1982; Whitehead 1983). Certain climatic and ecological factors may favor the occurrence and evolution of anemophily, such as dry conditions, open vegetation, uncertainty of pollinators, and high density of conspecifics (Whitehead 1969; Stebbins 1970; Niklas 1985; Ackerman 2000; Culley et al. 2002). In contrast to the floral variability found in zoophilous taxa, anemophily seems to be evolutionarily connected to very similar morphological adaptations (Pohl 1929; Whitehead 1969; Friedman and Barrett 2008). Consequently, a number of traits associated with wind pollination constitute the anemophilous syndrome (Faegri and Van Der Pijl 1979; Ackerman 2000). For example, inflorescences of wind-pollinated species are often condensed and catkin-like, and their nectarless flowers are often unisexual with an absent or reduced perianth (Culley et al. 2002; Friedman and

---

Electronic supplementary material The online version of this article (doi:10.1007/s00606-010-0299-9) contains supplementary material, which is available to authorized users.

S. G. Michalski (✉) · W. Durka
Helmholtz Centre for Environmental Research UFZ,
Department of Community Ecology (BZF),
Theodor-Lieser-Strasse 4,
06120 Halle, Germany
e-mail: Stefan.Michalski@ufz.de

Barrett 2008). However, some wind-pollinated and evolutionarily very successful groups such as Poaceae and Juncaceae exhibit hermaphroditic flowers, challenging the hypothesis of an association between unisexuality and wind pollination (Charlesworth 1993).

Floral adaptation to anemophily is believed to include modifications of ovule and pollen production per flower. For example, in wind-pollinated flowers, ovule number is frequently reduced to one (Pohl 1929; Friedman and Barrett 2008), and several non-mutually exclusive explanations for this fact have been proposed. First, capturing sufficient pollen grains to fertilize many ovules is unlikely in a stochastic process such as wind pollination. Second, uniovulate carpels may increase male–male competition. Third, producing many spatially separated flowers with fewer ovules may facilitate occupation and sampling of an increased volume of air by a plant and thus may increase the probability of capturing pollen grains (Friedman and Barrett 2008). Also, relative to animal-pollinated species, higher pollen production of wind-pollinated species has been attributed to inefficient pollen transfer (e.g., Whitehead 1969; Faegri and Van Der Pijl 1979; Proctor et al. 1996). However, this argument has been challenged by the frequent evolution of wind pollination from animal-pollinated ancestors and by empirical studies (Honig et al. 1992; Harder 2000). Nevertheless, various reasons may account for increased pollen production in wind-pollinated species. First, although wind-dispersed pollen is not smaller in average diameter than animal-dispersed pollen (Wodehouse 1935; see data in Andrew 1984), it is possibly cheaper to produce because it contains less protein (Roulston et al. 2000). Second, at least for self-incompatible wind-pollinated species, the increase in male fitness gain with increased pollen production is not expected to be limited by the transfer capacity of the pollen vector. In contrast, in animal-pollinated species, the transfer capacity of pollinators is likely to limit male fitness gain from increased pollen production (Charnov 1979; Lloyd 1984; Harder and Thomson 1989).

Low ovule and high pollen production should result in higher pollen–ovule (P/O) ratios in wind-pollinated species compared with animal-pollinated species. Although Pohl (1937) concluded that P/O ratios were of similar magnitude, Cruden (2000) and Michalski and Durka (2009) found P/O ratios on average higher in wind-pollinated species. Nevertheless, relative to animal-pollinated species, information regarding the reproductive and floral biology in anemophilous species is scarce (Ackerman 2000), and the number of studies concerning ovule and pollen production in wind-pollinated species is quite low (Cruden 2000). Thus, based on more comprehensive data, hypotheses concerning wind-pollinated species could be evaluated with more explanatory power. In general, life form and pollination mode have been found to contribute significantly to variation in P/O ratios (Michalski and Durka 2009). However, because woody perennials might be, on average, larger than herbaceous plants, it was hypothesized that, especially in wind-pollinated species, several size effects could lead to increased floral male allocation, and thus higher P/O ratios, in woody perennials than in herbaceous plants (Michalski and Durka 2009). Also, Cruden (2000) hypothesized that, in wind-pollinated species with only homoecious, hermaphroditic flowers, P/O ratios were lower than in species with a monoecious or dioecious sexual system. He argued that, assuming equal densities for individuals of different sexual systems, in plants with separate sexes the average distance between putative mates is greater than in homoecious species and therefore more pollen needs to be produced to outweigh the greater transport loss.

In general, studies targeting specific groups have been stated as essential for understanding of the evolution and maintenance of wind pollination (Friedman and Barrett 2008). Herein we report pollen and ovule production per flower for several species of the hermaphroditic, wind-pollinated Juncaceae, with special reference to the genus *Juncus*. Despite its widespread occurrence in many wetland habitats, *Juncus* is a so far very little studied group. Since the studies of Buchenau (1890, 1892), its reproductive biology has been investigated in detail only rarely (e.g., Michalski and Durka 2007a; Michalski and Durka 2007b). *Juncus* species are known to produce numerous seeds per capsule (Kirschner et al. 2002) and, at the same time, pollen production seems quite low. For example, when pollen concentrations in the air were recorded for several sites in Great Britain or southwest Spain, pollen of Juncaceae was found far less frequently than any other anemophilous pollen type (Proctor et al. 1996; Rodriguez et al. 2007). More directly, for *Juncus pusillus* a conspicuous low pollen production has been reported (cited in Pohl 1937). In conclusion, *Juncus* species appear to exhibit low P/O ratios in comparison with other wind-pollinated species.

We relate ovule and pollen production of *Juncus* species to wind-pollinated angiosperm species in general and, using this comprehensive data set, test the following hypotheses on pollen and ovule production in wind-pollinated species:

1. Woody perennials exhibit, on average, higher P/O ratios than herbaceous species;
2. Dicliny affects variation in P/O ratios resulting in, on average, lower P/O ratios in homoecious than in monoecious or dioecious species.

Materials and methods

Pollen and ovule counts for species of Juncaceae and some other wind-pollinated species were obtained as described by Cruden (1977) and therefore, fresh flowers, flowers preserved in 70% ethanol or dried material were examined. Flowers were collected from raised plants (*Juncus valvatus*), from natural populations, or from plants grown in botanical gardens (Table 1). Anthers of flowers had not opened at the time of collection. *Juncus* and *Luzula* species release their pollen in tetrads, thus the number of tetrads per flower was determined and then multiplied by four to obtain the number of pollen grains per flower. For monoecious *Carex* species, all male and female flowers in an inflorescence were counted and the male/female ratio was computed. The mean number of pollen grains per staminate flower was obtained from six to ten flowers per inflorescence. Because female flowers in *Carex* bear only one ovule, a P/O ratio was then obtained at inflorescence level by multiplying the mean number of pollen grains per staminate flower by the male/female ratio. For monoecious *Quercus robur* the P/O ratio was obtained as for *Carex* but assuming six ovules per pistillate flower (Mogensen 1975).

Pollen and ovule production, and P/O ratios of other wind-pollinated species were compiled from original papers. P/O ratios for some species with hermaphroditic

Table 1 Pollen and ovule production for species of Juncaceae and some additional taxa

Species	Source	*N*	Pollen per flower ± SD	Ovules per flower ± SD	P/O ratio ± SD
Juncus acutiflorus Ehrh. ex Hoffm.	Rathenow, Germany	9	10,808 ± 666	28.1 ± 1.6	386 ± 35
Juncus alpinoarticulatus Chaix	La Fouly, Switzerland	8	3,771 ± 802	48.3 ± 10.6	79 ± 16
Juncus articulatus L.	Halle (Saale), Germany	11	4,516 ± 1,091	44.9 ± 7.2	103 ± 28
Juncus atratus Krock.	Parey, Germany	13	6,050 ± 1,723	43.8 ± 7.8	144 ± 54
Juncus bufonius L.*	Warnau, Germany	9	1,239 ± 881	74.8 ± 12.5	17 ± 10
Juncus bulbosus L.	Halle (Saale), Germany	7	7,784 ± 1,530	39.6 ± 7.5	204 ± 58
Juncus compressus Jacq.	Halle (Saale), Germany	5	15,504 ± 1,069	114.6 ± 8.0	136 ± 15
Juncus conglomeratus L.	Halle (Saale), Germany	10	4,175 ± 500	68.5 ± 15.0	63 ± 11
Juncus effusus L.	Halle (Saale), Germany	8	3,480 ± 515	74.0 ± 7.1	48 ± 10
Juncus ensifolius Wikstr.	Botanical Garden Regensburg, Germany	6	1,802 ± 324	49.0 ± 3.2	37 ± 5
Juncus filiformis L.	Dessau, Germany	12	7,894 ± 3,287	105.0 ± 22.5	83 ± 46
Juncus inflexus L.	Halle (Saale), Germany	6	10,262 ± 406	95.3 ± 19.1	111 ± 18
Juncus nodosus L.	Saskatoon, Canada	8	4,044 ± 362	29.6 ± 3.4	137 ± 14
Juncus squarrosus L.	Altenberg, Germany	10	28,656 ± 6,160	68.5 ± 4.9	420 ± 92
Juncus subnodulosus Schrank	Mose, Germany	8	14,052 ± 900	21.9 ± 3.7	661 ± 128
Juncus tenuis Willd.*	Halle (Saale), Germany	7	6,816 ± 1,078	192.4 ± 22.5	36 ± 5
Juncus torreyi Coville	Saskatoon, Canada	10	4,092 ± 432	34.8 ± 2.0	118 ± 14
Juncus trifidus L.	Innsbruck, Austria	10	19,848 ± 3,974	17.9 ± 4.2	1,157 ± 351
Juncus valvatus Link	Botanical Garden, Coimbra, Portugal	6	2,366 ± 107	46.0 ± 2.3	52 ± 4
Luzula campestris (L.) DC.	Halle (Saale), Germany	8	61,320 ± 30,257	3.0	20,440 ± 10,086
Luzula luzuloides (Lam.) Dandy & E. Willm.	Mansfeld, Germany	10	38,208 ± 8,661	3.0	12,736 ± 2,887
Luzula multiflora (Ehrh.) Lej.	Halle (Saale), Germany	8	10,215 ± 3,223	3.0	3,405 ± 1,074
Luzula nivea (Nathh.) DC.	Botanical Garden, Regensburg, Germany	10	34,584 ± 7,381	3.0	11,528 ± 2,460
Luzula pilosa (L.) Willd.	Dorndorf (Saale), Germany	10	22,728 ± 6,857	3.0	7,576 ± 2,286
Alopecurus pratensis L.	Halle (Saale), Germany	10	8,334 ± 1,308	1.0	8,334 ± 1,308
Anthoxanthum odoratum L.	Halle (Saale), Germany	10	10,440 ± 1,979	1.0	10,440 ± 1,979
Carex acuta L.	Halle (Saale), Germany	2	8,433 ± 1,535	1.0	11,432 ± 248
Carex disticha Huds.	Halle (Saale), Germany	4	5,464 ± 1,407	1.0	8,273 ± 3,246
Carex umbrosa Host	Halle (Saale), Germany	5	11,148 ± 1,341	1.0	17,019 ± 2,533
Quercus robur L.	Halle (Saale), Germany	1	19,432 ± 3,809	6.0	98,527

Asterisk indicates annual species

flowers could also be obtained from studies concerning pollen production only (e.g., Agnihotri and Singh 1975; Subba Reddi and Reddi 1986; Prieto-Baena et al. 2003). From these studies and for species with a known invariant number of ovules produced per flower, P/O ratios were derived assuming that individuals bear flowers all alike (e.g., Poaceae, Cyperaceae). If for one species data was obtained from multiple studies, values were averaged and than used for the analysis. For all species compiled, life form (herbaceous or woody perennial) and sexual system (homoecious or not) were recorded.

Because P/O ratios follow a log-normal distribution (see also Fig. 1) and to meet the assumptions of standard statistical tests, pollen number per flower and P/O ratios were log-transformed prior to all analyses. The full data set is available in the Electronic Supplementary Material.

Trait correlations among a set of species can be the result of either phenotypic convergence or phylogenetic constraints. Hence, in comparative analyses the phylogenetic relatedness among species investigated should be taken into account. However, in similar analyses comparing P/O ratios of taxa representing a wide range of phylogenetic diversity, results were not altered by correcting for phylogenetic relatedness (Götzenberger et al. 2006, 2007; Michalski and Durka 2009). Moreover, phylogenetic relationships within Poaceae, which makes up 50% of the data set, and other taxa are not fully resolved for many species, rendering any analyses less powerful. We therefore present phylogenetically uncorrected data only.

Results

We compiled pollen and ovule production per flower and P/O ratios for, in total, 290 wind-pollinated species from 40 families out of 46 published original papers and additional sources, as well as from our own counts, which are displayed in Table 1. We obtained data for 236 herbs and 54 woody perennials, of which 24 (10%) and 39 (72%) were nonhomoecious, i.e., monoecious or dioecious, respectively. Best represented families were Poaceae ($N = 144$), Juncaceae ($N = 24$), Amaranthaceae ($N = 14$), Cyperaceae ($N = 14$), and Potamogetonaceae ($N = 11$). Pollen production ranged from 61 grains per flower in *Vulpia myuros* to 5,256,000 in *Rhizophora apiculata*. Ovule production per flower varied between 1 (e.g., Poaceae) and 940 in *Marathrum rubrum*. P/O ratios ranged from 17 in *Juncus bufonius* to 9,411,475 in *Carya tomentosa*.

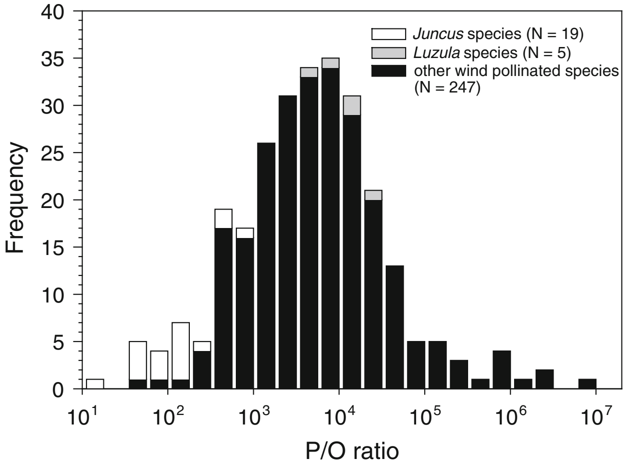

Fig. 1 Frequency distribution of P/O ratios for 271 wind-pollinated species

Pollen and ovule production in Juncaceae

For the 19 *Juncus* species investigated, pollen production per flower ranged from 1,239 to 28,656, and ovule production from 18 to 192. P/O ratios were in the range between 17 and 1,157 (Table 1). Comparing pollen and ovule numbers of *Juncus* species with that of other homoecious wind-pollinated herbs, no significant differences in pollen production per flower were found (Welch two-sample t test, $t = 0.91$, $df = 34.1$, $P = 0.37$). Nevertheless, ovule production was higher in *Juncus* species ($t = 5.28$, $df = 28.3$, $P < 0.001$), and consequently P/O ratios were significantly lower in *Juncus* ($t = 13.39$, $df = 24.9$, $P < 0.001$). Indeed, *Juncus* species had P/O ratios in the lower 28% percentile of all homoecious herbs (*Juncus*: mean log P/O ratio ± SD = 2.06 ± 0.46, $N = 19$; all other homoecious herbs: mean log P/O = 3.60 ± 0.62, $N = 193$). Among the *Juncus* species investigated, the two annual species, *J. bufonius* and *J. tenuis*, had the lowest P/O ratios. When compared with the closely related and also homoecious *Luzula* species, lower P/O ratios in *Juncus* were due to both a higher number of ovules per flower in *Juncus* (63.0 ± 41.7) than in *Luzula* (3), and also due to a lower pollen production per flower in *Juncus* (8,272 ± 7,027) than in *Luzula* (33,411 ± 19,075, Table 1).

Wind-pollinated species in general

On average, P/O ratios in homoecious species (mean log P/O = 3.52 ± 0.80) were lower than for species with separate sexes (log P/O = 4.28 ± 1.12; $t = -4.24$, $df = 51.8$, $P < 0.001$), even if *Juncus* species were excluded (data not shown). Pollen production per male flower was lower in homoecious species than in monoecious and dioecious species, but ovule production did not differ significantly between groups (data not shown). In general, herbaceous species (log P/O = 3.51 ± 0.77) exhibited lower P/O ratios than woody perennials (log P/O = 4.37 ± 1.18;

$t = -4.46$, $df = 49.2$, $P < 0.001$). Pollen production was higher in woody perennials; however, the number of ovules per flower was not significantly different between groups (data not shown).

Herbs and woody perennials were also analyzed separately for differences between homoecious species and species with separate sexes. Here, following the general trend, homoecious herbs exhibited lower P/O ratios ($t = -3.01$, $df = 16.8$, $P = 0.008$) and lower pollen production than monoecious or dioecious species ($t = -4.82$, $df = 25.9$, $P < 0.001$). Ovule production did not differ between groups (data not shown). Unexpectedly, for woody perennials, pollen production was larger in homoecious than in monoecious or dioecious species ($t = 2.40$, $df = 21.4$, $P = 0.03$); however, neither ovule production nor P/O ratios were significantly different ($P > 0.16$). The differences in pollen numbers were due to three *Rhizophora* species known to produce exceptionally large pollen quantities per flower (Tomlinson et al. 1979). When *Rhizophora* was excluded, the differences in woody perennials between homoecious and monoecious or dioecious species were nonsignificant ($P > 0.14$).

Discussion

Ovule and pollen production in Juncus

Among wind-pollinated taxa, *Juncus* species exhibit unusually low P/O ratios, representing the lower end of the distribution (Fig. 1). The low P/O ratios in *Juncus*, as compared with other wind-pollinated species, are the result of increased ovule production which is not compensated for by an increase in pollen production. High ovule production is unusual for wind-pollinated species, and thus fairly difficult to explain. The benefits of reduced number of ovules per flower when pollination is achieved by wind seem to be outweighed in *Juncus* by fitness gains through increased ovule and therefore seed production. For plants that colonize open, ruderal, and disturbed habitats, production of a large number of smaller seeds, associated with the ability for self-fertilization, is probably more beneficial than producing fewer, but larger and more competitive seeds (cf. Baker 1955; Mazer 1989; Westoby et al. 1996). Indeed, *Juncus* species generally grow in wetlands or open and disturbed habitats (Balslev 1996). Their small seeds are produced in large quantities (e.g., Moore and Burr 1948; Salisbury 1974) and have the potential for being easily dispersed by wind, animals or water (Richards and Clapham 1941; Alsleben et al. 2004). Also, many *Juncus* species are known to build up extensive and long-lasting seed banks (Thompson et al. 1997; Jensen 2004) that can help to maintain populations in temporally fluctuating environments. Thus, the increased ovule production in *Juncus* is possibly highly beneficial in its preferred habitats.

Nevertheless, for wind-pollinated species, producing numerous ovules per flower may hold the risk of severe pollen limitation. The ability for self-fertilization can reduce pollen limitation (Larson and Barrett 2000), and in fact, self-fertilization is described for several species of *Juncus* (Graebner 1934; Richards and Clapham 1941; Edgar 1964; Keighery 1985; Michalski and Durka 2007a) and was hypothesized to be the rule for the whole genus (Buchenau 1892). Also, a peculiar flowering phenology, synchronous pulsed flowering, has been described for some species (Buchenau 1892; Michalski and Durka 2007b), which may decrease pollen limitation and increase seed quality.

Self-fertilization can be associated with severe costs when selfed offspring suffer from inbreeding depression, as was demonstrated for *Juncus atratus* (Michalski and Durka 2007a). Reproductive assurance and reproductive compensation, the production of a greater number of ovules than mature seeds, and therefore the ability for selective abortion may favor increased selfing rates despite substantial inbreeding depression (Porcher and Lande 2005; Harder et al. 2008). However, neither mechanism has been experimentally demonstrated for *Juncus* species, although there is some evidence for reproductive compensation in *Juncus squarrosus*, which produces numerous ovules of which many fail to develop into seeds (Welch 1966). In conclusion, we hypothesize that high ovule production per flower in *Juncus*, as compared with other wind-pollinated species, is an adaptation to survival in disturbed habitats and accompanied by a high degree of self-fertilization.

P/O ratios have been found lower in species shedding their pollen in tetrads or larger units than in species with monads (Cruden 2000). It was hypothesized that low P/O ratios may evolve in species with aggregated pollen because of increased local mate competition if more sibling pollen grains reach individual stigmas than are needed to fertilize all available ovules (Harder and Johnson 2008). However, low P/O ratios in *Juncus* are unlikely to be related to the production of pollen tetrads, because members of the sister genus *Luzula*, which also produce tetrads, have much higher P/O ratios.

Ovule and pollen production in wind-pollinated species in relation to life form and sexual system

In general, we found P/O ratios to be lower in homoecious and herbaceous species than in nonhomoecious and woody perennials, respectively. This substantiates the results of earlier comparisons for wind-pollinated species with lower sample size (Cruden 2000; Michalski and Durka 2009).

Surprisingly, when looking in more detail, P/O ratios in woody perennials did not differ between homoecious and nonhomoecious species.

This finding may challenge the hypothesis that lower P/O ratios in homoecious compared with nonhomoecious species result from shorter distances between mates in the former (Cruden 2000). Because, in our analyses, monoecious and dioecious species were grouped together as nonhomoecious, it might be argued that the missing difference between the sexual systems is the result of monoecious species that may not in all cases show larger distances between mates (Cruden 2000). However, even if only homoecious and dioecious woody perennials were compared, no differences in P/O ratios could be found ($t = 0.53$, $df = 28.7$, $P = 0.60$). Thus, even though Cruden's consideration is not generally falsified, our results suggest that additional mechanisms are involved.

It has long been known that higher P/O ratios are, on average, related to higher degrees of outcrossing (Cruden 1977; Michalski and Durka 2009). This relationship is well understood in theory (Charnov 1979; Charlesworth and Charlesworth 1981). Furthermore, it has been hypothesized that the evolution of mating systems is not independent of life form, because in large-statured, woody perennials a larger lifetime mutational load may prevent selection for increased selfing (Scofield and Schultz 2006). This hypothesis is supported by empirical studies (Scofield and Schultz 2006; Michalski and Durka 2009). Hence, independent of the sexual system, in woody perennials adaptations for outcrossing should be predominant, possibly resulting in similar and relatively high P/O ratios. On the other hand, in mostly small-statured and short-lived herbs, homoecious species are likely to show the complete range of mating systems including self-fertilization, whereas nonhomoecious herbs are more likely to be predominantly outcrossed. In this group, dioecious species are necessarily outcrossed and, although in many monoecious species self-pollination is possible, they often exhibit some form of self-incompatibility mechanism (Proctor et al. 1996). Consequently, the average outcrossing rate in homoecious herbs is lower than in nonhomoecious herbs, and may correlate with differences in P/O ratios. Thus, we hypothesize that the observed difference between herbaceous and woody perennials with respect to P/O ratios and sexual system can be attributed to the influence of the mating system.

References

Ackerman JD (2000) Abiotic pollen and pollination: ecological, functional, and evolutionary perspectives. Plant Syst Evol 222:167–185

Agnihotri MS, Singh BP (1975) Pollen production and allergenic significance of some grasses around Lucknow. J Palyn 11:151–154

Alsleben K, Burkart M, Wichmann M (2004) Germination, establishment and spreading of *Juncus atratus*—a species adapted to disturbances. Verh Ges Ökol 34:243

Andrew R (1984) A practical pollen guide to the British flora. Quaternary Research Association, Cambridge

Baker HG (1955) Self-compatibility and establishment after 'long-distance' dispersal. Evolution 9:347–348

Balslev H (1996) Flora Neotropica: Juncaceae. The New York Botanical Garden, New York

Buchenau F (1890) Monographia Juncacearum. Bot Jahrb Syst 12:1–495

Buchenau F (1892) Ueber die Bestäubungs-Verhältnisse bei den Juncaceen. Jahrb Wiss Bot 24:363–424

Charlesworth D (1993) Why are unisexual flowers associated with wind pollination and unspecialized pollinators? Am Nat 141:481–490

Charlesworth D, Charlesworth B (1981) Allocation of resources to male and female functions in hermaphrodites. Biol J Linn Soc 15:57–74

Charnov EL (1979) Simultaneous hermaphroditism and sexual selection. Proc Natl Acad Sci USA 76:2480–2484

Cruden RW (1977) Pollen–ovule ratios: a conservative indicator of breeding systems in flowering plants. Evolution 31:32–46

Cruden RW (2000) Pollen grains: why so many? Plant Syst Evol 222:143–165

Culley TM, Weller SG, Sakai AK (2002) The evolution of wind pollination in angiosperms. Trends Ecol Evol 17:361–369

Edgar E (1964) The leafless species of *Juncus* in New Zealand. New Zeal J Bot 2:177–204

Faegri K, van der Pijl L (1979) The principles of pollination ecology. Pergamon, Oxford

Friedman J, Barrett SCH (2008) A phylogenetic analysis of the evolution of wind pollination in the angiosperms. Int J Plant Sci 169:49–58

Götzenberger L, Durka W, Kühn I, Klotz S (2006) The relationship between the pollen–ovule ratio and seed size: a comparative test of a sex allocation hypothesis. Evol Ecol Res 8:1101–1116

Götzenberger L, Durka W, Kühn I, Klotz S (2007) The relationship between the pollen–ovule ratio and pollen size: another comparative test of a sex allocation hypothesis. Evol Ecol Res 9:1145–1161

Graebner P (1934) Juncaceae. In: Kirchner O, Loew E, Schröter C, Wangerin W (eds) Lebensgeschichte der Blütenpflanzen Mitteleuropas, Band I, Abteilung 3. Eugen Ulmer, Stuttgart, pp 80–221

Harder LD (2000) Pollen dispersal and the floral diversity of monocotyledons. In: Wilson KL, Morrison DA (eds) Monocots: systematics and evolution. CSIRO, Melbourne, pp 243–257

Harder LD, Johnson SD (2008) Function and evolution of aggregated pollen in angiosperms. Int J Plant Sci 169:59–78

Harder LD, Thomson JD (1989) Evolutionary options for maximizing pollen dispersal of animal-pollinated plants. Am Nat 133:323–344

Harder LD, Richards SA, Routley MB (2008) Effects of reproductive compensation, gamete discounting and reproductive assurance on mating-system diversity in hermaphrodites. Evolution 62:157–172

Honig MA, Linder HP, Bond WJ (1992) Efficacy of wind pollination—pollen load size and natural microgametophyte populations in wind-pollinated *Staberoha banksii* (Restionaceae). Am J Bot 79:443–448

Jensen K (2004) Dormancy patterns, germination ecology, and seed-bank types of twenty temperate fen grassland species. Wetlands 24:152–166

Keighery GJ (1985) Breeding systems of the Wetsern Australian flora IV. *Juncus* and *Luzula* (Juncaceae). Bot Jahrb Syst 105:279–283

Kirschner J, Balslev H, Clemants SE, Ertter B, Alvarez MCFC, Hämet-Ahti L, Miyamoto F, Noltie HJ, Novara LJ, Novikov VS, Simonov SS, Snogerup S, Wilson KL (2002) Juncaceae 2: *Juncus* subg. *Juncus*, Species Plantarum: flora of the World Part 7. Australian Biological Resource Study, Canberra

Larson BMH, Barrett SCH (2000) A comparative analysis of pollen limitation in flowering plants. Biol J Linn Soc 69:503–520

Linder HP (1998) Morphology and the evolution of wind pollination. In: Owens SJ, Rudall PJ (eds) Reproductive Biology in systematics, conservation and economic botany. Royal Botanic Garden, Kew, pp 123–135

Lloyd DG (1984) Gender allocations in outcrossing cosexual plants. In: Dirzo R, Sarukhan J (eds) Perspectives on plant population ecology. Sinauer, Sunderland, pp 277–300

Mazer SJ (1989) Ecological, taxonomic, and life history correlates of seed mass among Indiana Dune angiosperms. Ecol Monogr 59:153–175

Michalski SG, Durka W (2007a) High selfing and high inbreeding depression in peripheral populations of *Juncus atratus*. Mol Ecol 16:4715–4727

Michalski SG, Durka W (2007b) Synchronous pulsed flowering: analysis of the flowering phenology in *Juncus* (Juncaceae). Ann Bot 100:1271–1285

Michalski SG, Durka W (2009) Pollination mode and life form strongly affect the relation between mating system and pollen to ovule ratios. New Phytol 183:470–479

Mogensen HL (1975) Ovule abortion in *Quercus* (Fagaceae). Am J Bot 62:160–165

Moore HI, Burr S (1948) The control of rushes on newly reseeded land in Yorkshire. Grass Forage Sci 3:283–290

Niklas KJ (1985) The aerodynamics of wind pollination. Bot Rev 51:328–386

Pohl F (1929) Beziehungen zwischen Pollenbeschaffenheit, Bestäubungsart und Fruchtknotenbau. Beih Bot Central 46:247–285

Pohl F (1937) Die Pollenerzeugung der Windblütler. Beih Bot Central 56:365–470

Porcher E, Lande R (2005) Reproductive compensation in the evolution of plant mating systems. New Phytol 166:673–684

Prieto-Baena JC, Hidalgo PJ, Dominguez E, Galan C (2003) Pollen production in the Poaceae family. Grana 42:153–160

Proctor M, Yeo P, Lack A (1996) The natural history of pollination. Timber, Portland

Regal PJ (1982) Pollination by wind and animals: ecology of geographic patterns. Annu Rev Ecol Syst 13:497–524

Richards PW, Clapham AR (1941) Biological flora of the British Isles—*Juncus* L. J Ecol 29:362–368

Rodriguez AFM, Palacios IS, Molina RT (2007) Cyperaceae and Juncaceae pollination measured in the air at two sites in SW Spain. Aerobiologia 23:259–270

Roulston TH, Cane JH, Buchmann SL (2000) What governs protein content of pollen: pollinator preferences, pollen–pistil interactions, or phylogeny? Ecol Monogr 70:617–643

Salisbury EJ (1974) The reproduction of *Juncus tenuis* (*Juncus macer*) and its dispersal. Trans Bot Soc Edinburgh 42:187–190

Scofield DG, Schultz ST (2006) Mitosis, stature and evolution of plant mating systems: low-Phi and high-Phi plants. Proc R Soc Lond B 273:275–282

Stebbins GL (1970) Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. Annu Rev Ecol Syst 1:307–326

Subba Reddi C, Reddi NS (1986) Pollen production in some anemophilous angiosperms. Grana 25:55–61

Thompson K, Bakker J, Bekker R (1997) The soil seed banks of North West Europe: methodology, density and longevity. Cambridge University Press, Cambridge

Tomlinson PB, Primack RB, Bunt JS (1979) Preliminary observations on floral biology in mangrove Rhizophoraceae. Biotropica 11:256–277

Welch D (1966) *Juncus squarrosus* L. J Ecol 54:535

Westoby M, Leishman M, Lord J (1996) Comparative ecology of seed size and dispersal. Philos Trans R Soc B 351:1309–1317

Whitehead DR (1969) Wind pollination in angiosperms: evolutionary and environmental considerations. Evolution 23:28–35

Whitehead DR (1983) Wind pollination: some ecological and evolutionary perspectives. In: Real L (ed) Pollination biology. Academic, Orlando, pp 97–108

Wodehouse RP (1935) Pollen grains. McGraw Hill, New York