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Seed dispersal in six species of terrestrial orchids in Biebrza National Park (NE Poland)

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Abstract

Knowledge about seed dispersal is required to explain problems in ecology, phylogeography, and conservation biology. Even though seed dispersal is a fundamental mechanism to understand problems at different levels of biological organization (individual, population, species, landscape), it remains one of the least recognized processes. Similar to other groups of plants, very little is known regarding patterns and distances of seed dispersal in orchids. Orchid seeds are generally assumed to be widely dispersed by wind because of their small size and low weight. Between 2006 and 2008, we conducted a field study of the distances at which orchid seeds are dispersed, and determined factors affecting dispersal. Investigations included 13 populations of six terrestrial orchid species – *Cypripedium calceolus*, *Cephalanthera rubra*, *Epipactis helleborine*, *Goodyera repens*, *Neottia ovata*, and *Platanthera bifolia*. To evaluate seed dispersal in orchid populations, 8.5-cm Petri dishes (traps) with self-adhesive paper were placed along transects, starting from a group of fruiting plants, which were considered to be the dispersal source. Seeds of the investigated orchid species were dispersed over relatively short distances. There were statistically significant negative correlations between seed density and distance from the fruiting plants. Seeds of species with taller fruiting shoots were dispersed farther than those with shorter ones ($R = 0.68$, $p < 0.05$). We discuss the causes and consequences of the dispersal patterns of orchid seeds.

Keywords

dispersal vector; long-distance dispersal; short-distance dispersal; terrestrial orchids

Introduction

Seed dispersal is essential for successful plant reproduction and adaptation, and research on the topic is required to explain problems in ecology, phylogeography, and conservation biology [1–6]. Firstly, studies on seed dispersal provide information about important aspects of species biology, which is indispensable to explain different ecological and evolutionary processes. Secondly, data about distances at which seeds are transported, along with knowledge of the distribution of individuals within one population and across populations of a given species within its geographical range, inform us of gene flow between different biological and ecological units [7–10]. At a time of fragmentation of natural environments and increasing biodiversity threats, knowledge of gene flow via seeds is crucial to determine the connectivity between populations of endangered

species. Generally, patterns and distances of seed dispersal are the most important factors shaping the structure of plant populations [2,11–14].

Even though seed dispersal is a fundamental mechanism to understand many problems at different levels (individual, population, species, landscape), it remains one of the least recognized processes. Most information is derived from mathematical models or experiments in special wind tunnels [3,6,15–20]. Data from field observations testing seed dispersal is very scarce, and mostly focused on seeds dispersed by animals, mainly in fleshy-fruited plants [21–25]. Genetic methods, based both on parentage analysis, fine-scale spatial genetic analysis and assignment tests, have also been used to assess the relative contributions of seed dispersal to gene flow [1,10,12,13,26–30]. We should remember that many genetic studies based on F_{st} (the standardized measure of the genetic variance among populations), although very valuable in explaining gene exchange, do not reflect actual seed dispersal. Firstly, these studies determine both recent and historical gene flow, and secondly, genetic estimates are not based on analyses of actual seed dispersal but more often on seedlings and/or adult plants presence. Thus, they show long-term dispersal (cumulative dispersal) and effective seed dispersal (dispersal of the seeds that develop into mature individuals) [1]. Therefore, both genetic and demographic data present seed dispersal based on spatial patterns of recruits vs. adults, and only partially document seed dispersal by showing seed deposition, including the availability of safe sites for germination. Concerning orchids, effective seed dispersal to a safe site indicates both seed arrival on the surface, and the presence of mycorrhizal fungi [13,31].

Commonly, seed dispersal is classified in terms of distance, and is described as either long- or short-distance dispersal. Many studies report that seed dispersal is usually very limited in space [2,3]. Short-distance dispersal (local dispersal) contributes to the maintenance of the local populations and enriches their genetic diversity, reducing their extinction risk, which is especially important when we consider the conservation of rare and endangered species [32–34]. Long-distance dispersal can occur accidentally, but is crucial for metapopulation dynamics [1,2,6,9]. Rare, stochastic events such as extreme climatic events are much more important in dispersal than formerly thought [3]. It enables gene exchange between populations, which usually increases genetic variation and simultaneously causes a homogenizing effect. Long-distance dispersal contributes to the emergence of new populations, thus influencing the geographical range of a particular species [3,4]. Moreover, long-distance dispersal events are also important in determining the selection of dispersal structures or adaptation to different environments [7,10,35].

Similar to other groups of plants, very little is known regarding patterns and distances of seed dispersal in orchids, which is not surprising because of their extremely small seeds. The lack of such information for one of the most endangered plant families is an important deficiency, because this parameter influences the persistence, dynamics, and evolution of orchid populations. Orchid seeds are generally assumed to be widely dispersed by wind because of their small size and low weight, in addition to their embryos occupying only a very small percentage of the space inside the testae (with an air content from 60 to above 90%) [36–38]. According to Gandawijaja and Arditti [39], these characteristics enabled orchids to reach Krakatau from Java (distance ca. 40 km) by air and to be among the first plants to colonize the island after the 1883 eruption. Besides seed properties, vegetation type, wind characteristics, and plant size are the most often considered factors influencing dispersal distance in species with dust seeds [16,40–42]. Although some authors have stated that information about long-distance dispersal over more than 10–15 km should be regarded as extremely rare [43], it is often reported in orchid literature [28,33,38]. Estimations of long-distance dispersal of orchid seeds have not been appropriately documented by empirical studies and often appear to be overestimated, affecting the interpretation of factors that shape the demographic and genetic structure of orchid populations. In many or even most of the papers concerning the genetic structure of orchids, high gene flow via seeds is one of the most common explanations for low population differentiation [28,33]. Such an interpretation of genetic data is mainly theoretical because there are no detailed investigations of the effect of long-distance dispersal on genetic diversity in orchids [1,44], excluding some examples [10]. Recently, a few authors have reported that gene flow in orchids via seeds appears to be restricted [16,27,41,45–48]. Tremblay and Ackerman

[49] hypothesized that limited gene flow among orchid populations is an important factor affecting the likelihood of genetic drift and selection at the population level, and may lead to differentiation and evolutionary diversification.

To our knowledge, studies on orchid seed dispersal via direct methods are very rare. Because of the limited information on orchid seed dispersal, and in the light of recent results, the main aim of the study was: (***i***) to investigate at which distances orchid seeds can be dispersed within populations and (***ii***) to determine the effect of certain factors (height of plants, weather conditions) on seed dispersal.

Material and methods

Field work was performed in Biebrza National Park (NE Poland). Investigations included 13 populations of six terrestrial orchid species – two populations of *Cypripedium calceolus*, *Neottia ovata*, and *Platanthera bifolia*, three populations of *Epipactis helleborine* and *Goodyera repens*, one population of *Cephalanthera rubra*. Most of populations were located in pine forests near Sośnia village (SOS) and fortification from the WWII (FORT) or hornbeam-oak forests growing on mineral islands among peat bogs named Oparzelisko (OPA), Pogorzały (POG), and Zabudnik (ZAB) (Tab. 1). One population of *C. calceolus* and *N. ovata* existed on small, deforested part (clearing) of hornbeam-oak forest on mineral island Zabudnik (ZAB). One *E. helleborine* population was located in meadow near Sośnia village (SOS). Excluding one *P. bifolia* population (POG), which was partially surrounded by sedges, cane, and young birches, remaining populations were located in places with short vegetation. Most populations existed in homogenous, flat areas, excluding one *G. repens* population, in which part of shoots was located at the base of small elevation, and others on its top.

Seed dispersal was monitored during fruiting seasons between 2006 and 2008 in different months depending on the species' fruiting period. Observations were conducted from the end of June to the middle of July for *N. ovata*, from the beginning of September to the beginning/middle of October for *C. rubra*, *G. repens*, *E. helleborine*, and *P. bifolia*, and from the first days of October to the middle of November for *C. calceolus*. To evaluate seed dispersal in orchid populations, 8.5-cm Petri dishes (traps) with self-adhesive paper were placed at the ground level, along transects, starting from a group of fruiting plants, which were considered to be the dispersal source. Dispersal sources were groups of plants (usually 1–3 shoots) located in places in which other shoots of the same species were lacking. In the first year of observation, the length of transects was 12–18 m, depending on field conditions. However, in the first year we noted that seeds were dispersed at shorter distances; therefore, in the following years, most transects were shortened to 10 m. For each population, in the majority of cases transects were arranged in four directions (max. seven directions) to check whether existing barriers (e.g., vegetation and topography) restricted seed dispersal. Moreover, general weather conditions (windy, rainy, and sunny) were noted to affect seed dispersal. Traps were placed along transects at regular intervals of 0.5 m. Additionally, we observed seed dispersal in detail up to 2 m in intervals of 0.2 m (these data were analyzed for *G. repens* only). Generally, traps were monitored at intervals of a few days. During field monitoring, traps containing seeds were collected and replaced by new ones. The Petri dishes with seeds were inspected under a microscope to record the number of seeds per dish. Fruiting shoots, which constituted dispersal sources, were measured to determine whether plant height influences the seed dispersal distances. To test the relationship between the distance from the dispersal source and the number of seeds dispersed in a particular species, we distinguished 12 distance classes. The seeds of *G. repens* were found at significantly shorter distances than in other species – up to 2.5 m. So, to observe a more accurate dispersal of *G. repens* seeds, we decided to remove *G. repens* from the whole data set and we analyzed it separately. Therefore, we divided the investigated populations into two groups. The first one contained only *G. repens*, and the second one included populations of the remaining species, where seeds dispersed at greater distances than 5 meters. In both groups, we considered the same number of classes (12), but different intervals. For *G. repens* the first 11 classes covered distances of up to 2.2 m at intervals of 0.2 m. The last distance class included all traps at a distance

Tab. 1 Seed distance dispersal in 13 populations of six orchid species in Biebrza National Park.

Species	Population/year	Type of vegetation	No. of used dishes / % of dishes without seeds	No. of trapped seeds	Max distance (m)	% of seeds 0–20 cm	% of seeds 0–50 cm	% of seeds 0–1 m	% of seeds 0–2 m	Seed Density × Distance (Spearman correlation)
Cephalanthera rubra	OPA/2007	Hornbeam-oak forest	146/55.0	322	5.0	54.9	67.4	78.3	91.3	−0.47**
Goodyera repens	SOS_1/2006	Pine forest	93/0.0	661	2.2	94.6	97.4	98.0	99.7	−0.43*
Goodyera repens	SOS_2/2007	Pine forest	275/80.0	630	2.0	89.4	93.0	97.0	100.0	−0.44**
Goodyera repens	SOS_2/2008	Pine forest	391/50.4	6413	0.8	86.4	98.3	100.0		−0.36**
Goodyera repens	FORT/2008	Pine forest	111/53.8	2063	0.8	94.8	99.1	100.0		−0.66**
Epipactis helleborine	POG/2006	Hornbeam-oak forest	210/11.4	2798	10.0	48.9	66.9	90.3	98.4	−0.49**
Epipactis helleborine	POG/2007	Hornbeam-oak forest	166/35.0	527	8.0	24.3	30.0	41.2	75.7	−0.66**
Epipactis helleborine	FORT/2007	Pine forest	279/26.2	4453	7.5	80.4	82.6	88.2	96.0	−0.38**
Epipactis helleborine	FORT/2008	Pine forest	257/71.0	2202	2.5	71.8	91.5	98.0	99.5	−0.69**
Epipactis helleborine	SOS/2008	Meadow	541/22.6	26771	15.5	50.0	79.8	96.4	98.0	−0.77**
Cypripedium calceolus	OPA/2007	Hornbeam-oak forest	277/79.4	250	5.0	55.0	67.4	78.3	91.3	−0.39**
Cypripedium calceolus	ZAB/2007	Clearing	213/62.4	251	9.2	70.0	76.2	90.0	92.5	−0.41**
Platanthera bifolia	POG/2007	Hornbeam-oak forest	158/1.9	2780	6.0	91.0	93.1	96.0	99.0	−0.85**
Platanthera bifolia	FORT/2007	Pine forest	259/17.8	5632	6.0	52.0	66.0	90.0	96.3	−0.70**
Neottia ovata	ZAB/2007	Clearing	226/14.6	2429	10.0	48.3	52.4	64.0	75.3	−0.37**
Neottia ovata	POG/2007	Hornbeam-oak forest	154/3.2	5595	9.0	67.0	78.6	88.1	95.4	−0.78**

Significance code: *** *p* < 0.001; ** *p* < 0.01; * *p* <0.05.

greater than 2.2 m. For populations of the other species, the first class covered distances up 0.2 m, the second from 0.2 m to 0.5 m, and classes 3–11 included distances from 0.5 to 5 m at intervals of 0.5 m. The last distance class in this case included all traps at distances greater than 5 m.

Because different numbers of traps were used in each interval, we converted the seed number data to densities data. We used the Kruskal–Wallis test (nonparametric ANOVA) implemented in R to test the differences between the densities in different distance classes. In the cases when the null hypothesis was rejected as a post hoc test, we used the Dunn test and the Conover–Iman test [50,51]. Spearman rank correlation was used to determine the relationship between trap distances and the densities of trapped seeds and height of plants. All figures were prepared using the statistical program R [52].

Results

Overall, seeds of the investigated orchid species were dispersed at relatively short distances (Fig. 1a–f, Tab. 1). However, depending on species, site, and year differences between distances were identified (Fig. 1, Tab. S1). The smallest maximum distances (2.2 m) were noted in *Goodyera repens* (Tab. 1). The maximum distance at which orchid seeds were trapped was 15.5 m in one population of *E. helleborine* in 2008 (Tab. 1). We noted similarities in seed dispersal distances of a given orchid species both in different populations and consecutive years, excluding *Cypripedium calceolus* (Fig. 1b). In all cases, the highest densities of seeds were observed near the dispersal sources (Fig. 1). We noted statistically significant differences between densities of seeds trapped at different distances (Tab. S1). In *G. repens*, statistically significant differences were only found in the SOS_2 and FORT populations in 2008 (Tab. S1). Excluding the *E. helleborine* population from POG in 2007, approximately 50% to above 90% of seeds were trapped near the fruiting plants (Class 1, Tab. 1). In most cases, over 90% to 100% of trapped seeds were noted up to a distance of 2 m (Tab. 1). Many dishes, especially at farther distances did not contain seeds.

There were statistically significant negative correlations between seed density and distance from the fruiting plants (Tab. 1, Spearman rank correlation). Analyzing seed dispersal temporally, we observed a specific dispersal phenology. In the case of *E. helleborine* and *C. calceolus*, dispersal times, including dispersal peak, overlapped, excluding the *E. helleborine* FORT population in 2007 (Fig. 2). The phenology of *G. repens* seed dispersal was more differentiated in particular populations and consecutive years (Fig. 2). Most orchid seeds were dispersed during sunny and windy days. Sometimes, over a few sunny and windy days, one half to above 90% of seeds were trapped (Fig. 2).

Seeds of species with taller fruiting shoots (for example *E. helleborine*) were dispersed farther than those with shorter ones, for example *G. repens* ($R = 0.68$, $p < 0.05$). Moreover, in species with lower shoots (*G. repens*) we noted a higher proportion of seeds near infructescences than in species with taller shoots ($R = -0.67$, $p = 0.05$).

Our results suggest the importance of physical barriers to seed dispersal. In the FORT population of *P. bifolia*, where fruiting plants grew along a moat (an element of fortification from the WWII), the number of seeds deposited in traps from transects located at the same level as plants was higher (1989) than in traps located along the transect connected to the top of the neighboring elevation (491).

Discussion

Factors influencing seed dispersal in orchids

Despite the great potential of the small, dust-like seeds of orchids to be dispersed long-distances by wind, the results of our experiments indicate a restricted dispersal in the representative species of this group. This result is consistent with the newest, but mainly fragmentary, information from other studies on orchids [41,45,48,53] . Machon et al.
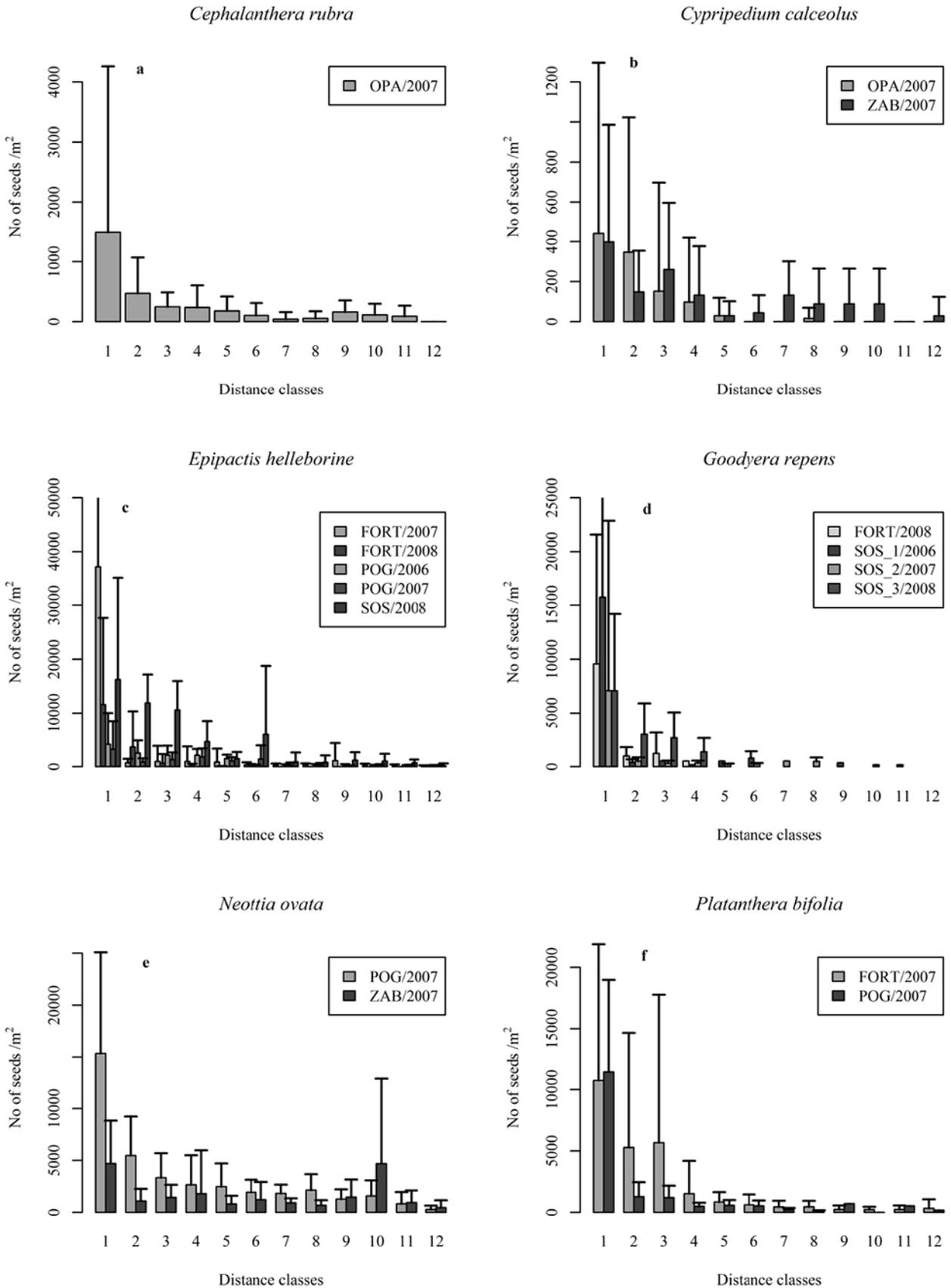
Fig. 1 Density of seeds in populations of six orchid species at different distances from dispersal sources. Error bars indicate standard deviation.
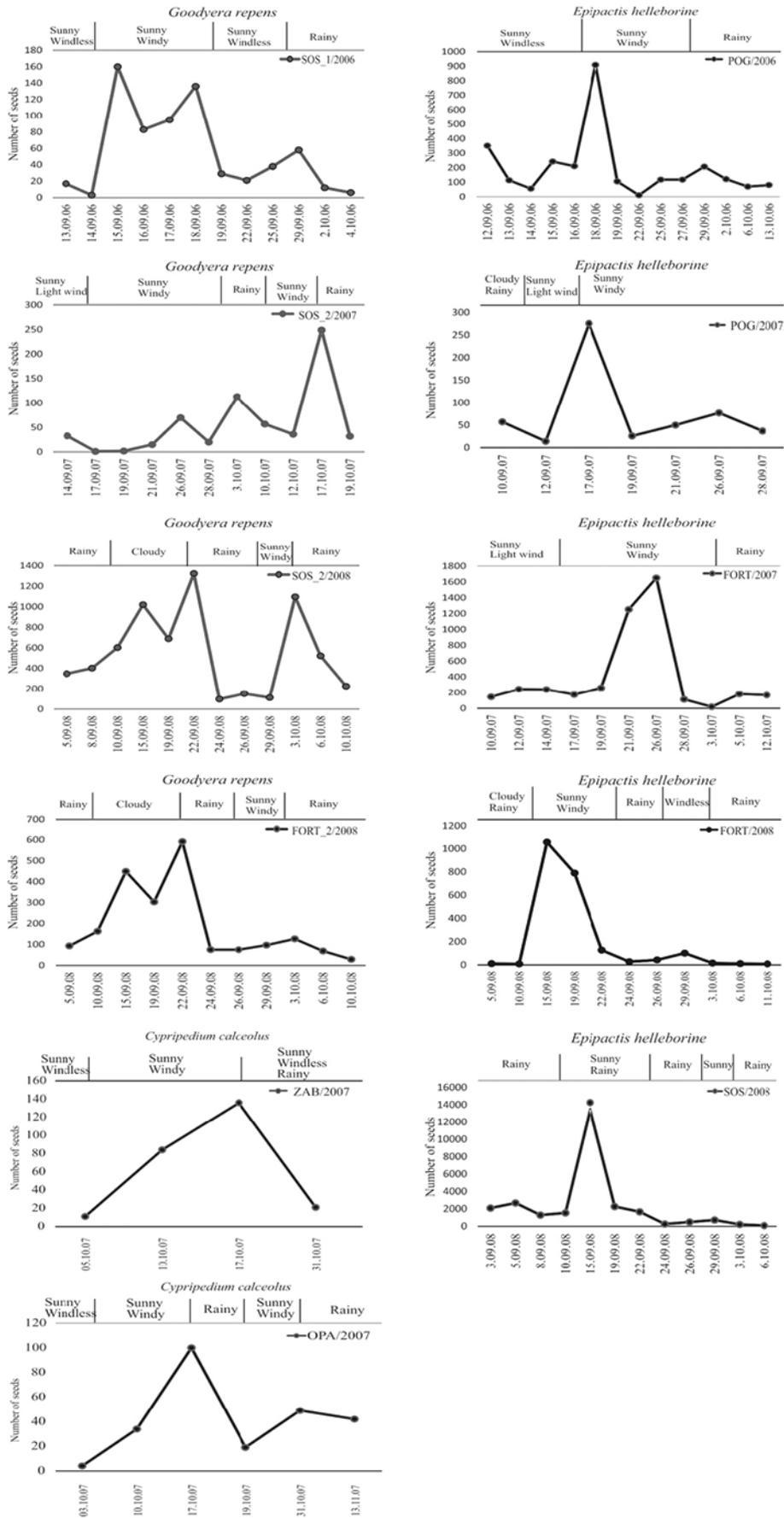
Fig. 2 Seed dispersal of six orchid species in Biebrza National Park during fruiting period according to weather conditions.

[47] found that 95% of *Spiranthes spiralis* seeds were trapped less than 1.35 m from infructescences, and 50% were noted within 5 cm of the nearest fruiting plants. In other plants with dust seeds, for example from the genus *Pyrola*, the vast majority of seeds are deposited close to the seed source [42]. Short-distance dispersal of orchid seeds is also suggested in studies presenting and interpreting results of population genetic variation [12,13,27,54]. The results of our experiments are largely consistent with the examples mentioned above. Most seeds of the six orchid species were found at shorter distances, near the vicinity of the fruiting plants. The seeds of the six studied species were recorded at maximum distances from 0.8 m to 15.4 m, depending on species, site, and year. This great differentiation of dispersal distances can have many causes. First of all, in anemochoric plants this process depends on wind characteristics such as intensity, direction, turbulence, and other factors which have been documented in seed dispersal experiments and models [6]. Murren and Ellison [16] found that modal dispersal distance depends on ambient wind velocity and turbulence. Some authors suggest that seed dispersal could be more restricted because wind speeds are significantly reduced near the ground in forest habitats, especially densely vegetated [41,55]. Harrod and Everett [53] and Harrod [56] found that seed dispersal in *C. fasciculatum* is relatively limited, because air circulation is inhibited in the understory of forested habitats. According to Willson and Traveset [57], horizontal seed distribution may be asymmetric with respect to the source (if, for example, the wind carries most seeds downwind). Variability of direction and strength of wind influences the dispersion pattern of wind-dispersed seeds in time and space [6]. This variability can explain our results, substantiating the differences between particular populations and in subsequent years in distances at which seeds were transported. We identified a relationship between the weather and the dispersal intensity. Most seeds of the studied species were dispersed during sunny and windy days, whereas both rainy and windless weather remarkably reduced seed dispersal.

Seed morphology often suggests a particular dispersal vector. The variable properties of seeds (shape, weight, proportion of air space) are among the causes of differentiated distances of seed dispersal in orchid species [38]. For example, Arditti and Ghani [38], Shimizu et al. [58], and Kiyoharaet et al. [59] found different seed velocities according to certain properties, such as weight or proportion of air space. Seeds with large air spaces drop more slowly, and therefore will have a lower settling velocity. Based on the study by Arditti and Ghani [38], we suggest that the large dispersion range of *E. helleborine* seeds could be caused by their flotation time in the air, which is the longest (9.1 s) of all the species studied. This is likely connected with the air space in the seeds of this species being above 90% [38]. However, one of the causes of the shortest dispersal of *Goodyera* seeds could be that they possess the lowest (compared with other orchids analyzed in our study) proportion of air space [38]. It appears that dispersal distances could also be connected with seed shape (relationship between seed length and width). Arditti and Ghani [38] and Eriksson and Kainulainen [60] reported that elongated seeds disperse farther. However, Eriksson and Kainulainen [60] stated that the low weight of orchid seeds enables them to disperse long distances regardless of shape. The wind on the forest floor is weak, and orchids that grow in this habitat have to adapt to the weak-wind environment to disperse their seeds; therefore, we can speculate that the seeds of orchids living on the forest floor may have evolved to be long, because increased length reduces the speed of the fall and increases the chance that the seed will be carried by wind [58,59].

The other factor influencing seed dispersal distance in orchids is the size of the fruiting plants [16,40,41]. Thomson et al. [5] analyzed the relationship between plant height and dispersal distance in 211 plant species, and found that seed dispersal distance is strongly dependent on plant height. Our results are largely consistent with these statements. We found statistically significant correlations between the height of fruiting shoots of orchid species and the maximum distance that seeds were trapped. A strong relationship was also noted between the height of plants and the number of seeds in their close vicinity. The nearest distances at which seeds were recorded were noted for *G. repens*, the species with the shortest shoots among the investigated orchids, while seeds of the tallest *E. helleborine* were recorded at the farthest distances. Willson and Traveset [57] suggested that wind dispersed plants were tall relative to other plants in the habitat. Many populations of investigated orchid species exist in poor, dry pine forests where orchids

were the tallest or one of the tallest plants of the species in the undergrowth. Lorts et al. [4] and Nathan et al. [61] reported that open environments are more favorable for long-distance dispersal than forests. It was confirmed in one *E. helleborine* population in an open area, where seeds were dispersed the farthest (maximum distance of seed dispersal was almost twice that of the other *E. helleborine* populations in the forests). Our results may also suggest, similarly to data of Heydel et al. [6], that vegetation type influences orchid seed dispersal. For example, in one *P. bifolia* population that is surrounded by different community types, the seeds dispersed the farthest (more than 9 m) were found in traps along the transect localized in short vegetation, whereas in tall vegetation (sedges, cane, and young birches), the farthest dispersion was 3.5–4.5 m. Topography appears to be another factor affecting dispersal. In *G. repens* populations that are located in homogenous, flat areas, the maximum distances of trapped seeds were similar in all transects in different directions. In other populations of this orchid located in topographically differentiated places, more seeds at farther distances were found in traps placed at the base of elevated areas rather than on top (data not shown). Venable et al. [62] noted that seeds of desert annuals dispersed further downslope than upslope. Similarly, Muñoz et al. [63] explained higher genetic differentiation between two populations of *Phragmipedium longifolium* in a lower elevation area vs. a higher elevation area by more difficult seed dispersion between different elevation levels. The number of trapped seeds and their dispersal distances could be connected with the direction that the fruiting shoots are oriented. We observed that more seeds of *G. repens* and *E. helleborine* were trapped in the direction that shoots were bending (Brzosko, personal observation, 2006–2008).

Although in the population scale we observed a pattern suggesting short-distance dispersal in six orchid species, we cannot exclude the longer transport of orchid seeds, for example by zoochory. Some authors have suggested the occurrence of long-distance transport of orchid seeds on the feathers or legs of birds [38,64]. Seutsugu et al. [55] also reported important avian seed dispersal in orchid *Cyrtosia septentrionalis*, which produces fleshy fruits rich in sugar. Viability of seeds sampled from birds' faces was comparable to viability of seeds taken directly from orchid's fruits. The long-distance transport of orchid seeds could be caused by secondary dispersal events from primary seed deposition – seeds can be simply transported further by wind. Primary dispersion patterns can be modified by rain (during downpours seeds may be transported via water jets). Moreover, seeds of orchid species growing in forests fall on tree leaves that accumulate on the ground, especially in fall, and during windy weather can be transported with them. Additionally, animals eat the leaves on which the seeds are deposited, and thus seeds could be farther dispersed. Probably, human vectors can influence the seed dispersal of the investigated orchids, especially of *G. repens*, which exists in forests that are often visited by people looking for mushrooms. The importance of secondary dispersal in increasing distances that seeds are transported is stressed by other authors [7,17,20,65,66].

Consequences of restricted seed dispersal in orchids

The migration success of flowering plants largely depends on effective seed dispersal, which determines many processes at different scales (from populations to landscapes) and has many consequences. Generally, the distribution of dispersed seeds is highly leptokurtic, with most seeds near the parents and progressively fewer farther away [67]. Such modes of seed dispersal explain the organization of plants into clusters [68,69]. Additionally, in populations of orchids, a decrease in seed germination with an increase in distance from the mother plants is connected with a higher probability of a fungal component near the maternal plants [13,31,50,70]. Furthermore, the genetically similar progeny (seeds) is dispersed mainly in the vicinity of the mother plants, enhancing reproductive isolation between particular plant groups [32,71–73]. In populations in which fruiting shoots form aggregations (e.g., in clonal species), spatial structure increases [54].

Information about short-distance seed dispersal in orchids can change how genetic data are interpreted. Results from seed dispersal studies are in most cases inconsistent with data reporting relatively low genetic differentiation between populations in

orchids (average: $F_{st} = 0.087$ [33]; $G_{st} = 0.187$ [26] and $F_{st} = 0.146$ [28]), which indicates a high gene flow between them. Dispersal limitation is an important driver of gene flow restriction as it causes isolation. How can these genetic data be explained? First, the current genetic status of populations/species derives from cumulative effects over many generations [34]. Most likely, genetic differentiation between populations mainly reflects historical gene flow when populations were more continuously dispersed, and the landscape was less fragmented [74]. Second, low genetic differentiation of orchid populations could be caused by the long-distance seed dispersal described above. Even occasional and accidental seed input from other populations is very important for enriching the gene pool of a given population, and can explain, at least partially, the low differentiation between orchid populations. Rare events of long-range dispersal play an important role in plant migration on a large spatiotemporal scale [1,3]. Even if seeds could be transported further, there is a low probability that they will encounter a fungal component required to develop new individuals. Restricted seed dispersal makes the colonization of suitable habitats often impossible, and this, along with other orchid traits (dependence on pollinators and mycorrhizal fungi) and ongoing human-induced environmental changes (habitat fragmentation and isolation), appears to be one of the main causes of orchids' rarity.

Supplementary material

The following supplementary material for this article is available at http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.3557/0:

Tab. S1 Statistical differences between densities of seeds dispersed at different distances.

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