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Quantification of plant dispersal ability within and beyond a calcareous grassland

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25 **Abstract**

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27 Question:

28 Many calcareous grasslands in Europe have declined in species richness in recent
29 decades. This loss of species may be partly due to habitat loss and fragmentation, leading to
30 increased distances and reduced connectivity by seed flow between calcareous grassland
31 patches as well as increased local extinction risk related to small population size, and partly
32 due to abandonment of traditional management practices that fostered dispersal within and
33 between patches. Here we quantify short- and intermediate distance dispersal ability of dry
34 calcareous grassland species and relate these to dispersal traits.

35 Location:

36 Schaffhauser Randen, Switzerland

37 Methods:

38 We studied wind dispersal of diaspores under natural conditions within and beyond
39 two replicate calcareous grassland patches. Funnel traps ($n = 230$) were set up at heights of
40 0.2m and 0.7m along ten transects traversing the calcareous grassland and extending 40m into
41 the surrounding landscape. We developed a new method for quantifying short - (0-1m) and
42 intermediate-distance (1-40m) dispersal ability, related these to species traits, and tested
43 whether they were able to explain dispersal rates into the adjacent landscape.

44 Results:

45 While grasses could be categorised as good dispersers over short or intermediate
46 distances, or both, forbs were generally poor dispersers over both distances. Only small
47 numbers of diaspores were found in the adjacent landscape, and these were predominantly
48 grasses. Diaspore traits such as terminal velocity or diaspore mass contributed little to
49 explaining dispersal ability, whereas release height was an important predictor especially for
50 intermediate-distance dispersal.

51 Conclusions:

52 Under natural field conditions, dispersal into the adjacent landscape depends on
53 release height rather than terminal velocity, and it is heavily biased towards grasses, so that
54 seed rain does not reflect the species composition of the calcareous grassland community.
55 Thus natural regeneration of species richness of degenerated calcareous grassland
56 communities even over short distances should not rely on wind dispersal alone.

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70 **Keywords**

71 Seed flow, meadow, grassland system, anemochory, seed traps

72 **Introduction**

73 Calcareous grasslands are amongst the most species-rich habitats in Central Europe
 74 (Wolking & Plank 1981). In the last few decades, however, agricultural intensification and
 75 abandonment of traditional land-use has led to a substantial decrease in the number and
 76 average size of these grasslands throughout Europe (Poschlod & WallisDeVries 2002). As a
 77 result, average distances between grassland fragments have increased considerably
 78 (WallisDeVries et al. 2002), which may impede pollen flow and seed flow between
 79 fragments. Diaspore dispersal among communities is important since it permits local
 80 colonization by new species, re-colonisation by species that were formerly present, and
 81 genetic enrichment of the existing population (Levin et al. 2003). Dispersal within a
 82 community may decrease extinction risk by increasing connectivity and reducing population
 83 vulnerability to disturbance. These processes are especially important in small communities,
 84 where populations suffer from increased extinction risk (Joshi et al. 2006), and may be
 85 essential for persistence (Jackel & Poschlod 1996; Willems & Bik 1998; Pywell et al. 2002;
 86 WallisDeVries, et al. 2002).

87 In addition to habitat loss and fragmentation, which have reduced the capacity of
 88 species to disperse between habitat patches (Soons et al. 2005), many traditional dispersal
 89 vectors that were provided by transhumance sheep herding or sowing of hayseed have
 90 disappeared (Jackel & Poschlod 1996; Poschlod et al. 1998; Poschlod & WallisDeVries
 91 2002). Current management practices might not promote diaspore dispersal in the same
 92 degree as traditional practices since the diaspores are not easily attached to the machinery that
 93 is used and transported long distances (Fenner & Thompson 2005). Hence dispersal within
 94 and between grassland patches increasingly relies on wind or potentially wild animals as
 95 dispersal vectors. Dry calcareous grasslands harbour a variety of plant species with distinct
 96 differences in their traits relevant for dispersal. Release height of diaspores varies from close to
 97 the ground (e.g. small forbs like *Linum catharticum*) up to high above the grassland canopy (e.g.
 98 tall grasses such as *Arrhenaterum elatius*), and diaspore morphology encompasses spherical

99 diaspores (e.g. *Salvia pratensis*), very small and light diaspores (e.g. *Cerastium fontanum*),
100 diaspores with Pappus (e.g. *Picris hieracioides*) or diaspores with long awns (e.g. *Helictotrichon*
101 *pubescens*). Both, the variety in release height and in diaspore morphology indicate differing
102 capacities for wind dispersal. Propagule pressure, i.e. the number of diaspores produced by a
103 species is, beside the dispersal traits mentioned above, also an important factor influencing the
104 number of diaspores captured, distances dispersed, and the probability of dispersal in general
105 (Eriksson 2000).

106 Wind tunnel experiments and mechanistic simulation studies suggest that wind
107 dispersal is strongly influenced by the terminal velocity of the diaspore and release height
108 (Hensen & Müller 1997; Jongejans & Schippers 1999; Tackenberg 2001; Bolli 2009), while
109 diaspore morphology or diaspore mass alone have little predictive power for dispersal
110 distance (Verkaar et al. 1983; Tackenberg 2003). Release height seems to be especially
111 important for dispersal in dense communities since it increases the chance of a diaspore to
112 encounter higher wind speeds and to escape from the canopy (c.f. Katul et al. 2005 for
113 grassland forbs; Sundberg 2010 for Turf moss; Zhang et al. 2011 for an invasive thistle). A
114 diaspore release experiment under field conditions indicated that dispersal kernels predicted
115 from terminal velocity and wind conditions may hold only for seeds released at vegetation
116 height, whereas for seeds released below vegetation height, the number of dispersed seeds
117 was much lower and unrelated to terminal velocity, and the distance and direction of dispersal
118 unpredictable (Bolli 2009; Diacon et al. submitted). Calcareous grassland forbs, which largely
119 determine the plant species diversity of the community, typically release their diaspores below
120 vegetation height (e.g. Verkaar, et al. 1983; Tackenberg 2001; Bolli 2009). Thus, common
121 dispersal models may be inadequate to explain dispersal processes within and beyond
122 grassland patches under natural field conditions, and -fail to explain spatial structure within
123 communities and landscape-scale biodiversity patterns.

Previous work suggests that similar grassland communities are likely to be dispersal-limited at small spatial scales (Verkaar, et al. 1983; Willems & Bik 1998; Coulson et al. 2001; Joshi, et al. 2006; Zeiter et al. 2006). Several studies have either measured the diaspore rain within plant communities (e.g. Jackel & Poschlod 1994; Willems & Bik 1998; Kalamees 1999; Pywell, et al. 2002) or used models to simulate potential long-distance dispersal (i.e. dispersal beyond a few 100 m (Nathan 2006); e.g. Tackenberg (2003), Soons et al. (2004)). However there have been few attempts to assess the wind dispersal ability of calcareous grassland species into the adjacent landscape under natural field conditions (but see Stadler et al. 2007) and at intermediate spatial scales between 1 m – 100 m. Nevertheless dispersal at such intermediate distances might play an important role for gene flow within communities, spread within a landscape or recolonisation of degraded grasslands (Levin, et al. 2003; Holderegger & Wagner 2006; Kiehl et al. 2010).

We developed a new method for quantifying short-and intermediate-distance dispersal ability of diaspores within a calcareous grassland community and into the adjacent landscape in order to assess the dispersal potential at the community level and the species level. We addressed the following specific questions: (1) Which species have good short- or intermediate-distance dispersal abilities? (2) Which dispersal-related traits explain the variation in short- and intermediate-distance dispersal ability under natural conditions? And finally (3), to what degree can short- and intermediate-distance dispersal ability explain dispersal into the adjacent landscape?

Methods

Study area

The study was conducted during the summers of 2006 and 2007 in calcareous grassland in the Schaffhauser Randen, Switzerland (51°15'18''N; 03°02'33''E; 765 m a.s.l.) from 10 June – 8 July 2006 and 7 June – 01 August 2007. The community is classified as

Mesobrometum Koch 1926 (Delarze & Gonseth 2008), with a total of 68 vascular plants species found within the two seasons, and is still used as hay meadow. The study area comprises two rectangular replicate calcareous grassland patches that lie perpendicular to each other, one facing south-west (approx. 5100 m²) and the other south-east (approx. 6000 m²), separated by a strip of woodland (Appendix S1). Both patches are gently sloping (10-20 %) and have a long border on the lower end with arable land (the south-eastern and south-western sides, respectively) and with woodland on the upper end (the north-western and north-eastern sides, respectively). During the study period, the calcareous grasslands, which were usually mown after July 1, remained unmown so as to maximise the supply of diaspores, and the vegetation was about 0.75m tall. However, the adjacent arable fields as well as the grass verges between the arable fields and forest edges were mown regularly to prevent undesired diaspores from these areas contaminating the experiment. Since there were no other calcareous grassland communities within 1km of the study area, it is safe to assume that all captured diaspores of calcareous grassland species originated from the study area.

Wind speed and direction during the study periods were recorded every ten minutes by a cup anemometer (A100R, Campbell) and a windvane (W200P, Campbell) connected to a digital logger installed in the centre of the southwest-facing calcareous grassland patch, at a distance of 20m from the forest edge and at a height of 1.2m. Wind speeds ranged from 0 to 12.5ms⁻¹ with a mean of $2.8 \pm 1.5\text{ms}^{-1}$ respectively $3.1 \pm 1.6\text{ms}^{-1}$ during the day (9.00 – 21.00; mean $\pm$ standard deviation) in the study period 2006, and from 0 to 9.1ms⁻¹ in the study period 2007 with a mean of $3.0 \pm 1.6\text{ms}^{-1}$ resp. $3.8 \pm 1.4\text{ms}^{-1}$ during the day. The most frequent wind direction was north-northwesterly in 2006, and northerly in 2007 (Bolli 2009). Total precipitation during the 2006 study period amounted to 47mm and mean temperature was $20.9^{\circ}\text{C} \pm 4.3^{\circ}\text{C}$; the corresponding values for 2007 were 108mm and $17.4^{\circ}\text{C} \pm 4.9^{\circ}\text{C}$ in 2007 (daily precipitation sum and hourly mean temperature data from the MeteoSwiss station, Schaffhausen, 8°37'12" E; 47°41'23" N).

Diaspore trapping

A total of 230 diaspore traps were installed along 10 transects, 5 transects per calcareous grassland patch, running from within the calcareous grassland patches into the adjacent arable fields (Appendix S1). Along each transect, two traps were placed at the border between the calcareous grassland patch and the arable field and at distances of 1, 2, 5, 10 and 15m into the calcareous grassland patch (120 traps in calcareous grassland patches), and at distances of 1, 2, 5, 10, 20 and 40m into the arable field (2006: 110 traps in arable fields, traps at 40 m in arable field adjacent to south-east calcareous grassland patch only. 2007: 60 traps in arable field adjacent to south-east calcareous grassland patch only. Two types of plastic funnel traps were used, as suggested by Kollman and Goetze (1998), Chabrierie and Alard (2005) and Jensen (1998): a low trap (capture area 254cm²) was placed at a height of 20cm to sample the diaspore rain within the vegetation, and a larger trap (1385cm²) was placed at vegetation height (70cm) to capture diaspores dispersed over longer distances. The pairs of traps were placed 1m apart at each sampling station along each transect. Traps were fixed above the ground with PVC pipes and diaspores were caught in a nylon filter bag attached to the base of the funnel traps that was protected from seed predators by the pipe (cf. Photo S1). Lateral holes ensured that water did not accumulate and allowed the diaspores to dry out. The traps were emptied every 3 - 5 weeks and the material collected was air-dried for five days. The diaspores were identified under a binocular microscope based on a seed identification key (Brouwer & Stählin 1975) and a reference collection made in the study area.

Vegetation assessment

We counted the number of mature inflorescences per species within a radius of 1m from each trap. Average diaspore production per inflorescence was estimated from ten

individuals per species, collected at more than 20m distance from the traps. We estimated local diaspore pressure for each trap as the product of the number of inflorescences counted within 1m radius around each trap, multiplied by the average diaspore production per inflorescence. Average diaspore pressure was pooled between all traps from both calcareous grassland patches.

Species-specific dispersal ability

We developed a new method to quantify the dispersal ability of species over short and intermediate distances, based on local propagule pressure and the numbers of diaspores caught. We argue that the number of diaspores originating from plants within 1m radius around a trap is expected to show a positive linear relationship with local propagule pressure within this radius, whereas the number of diaspores trapped originating from greater distances is not. For each species, therefore, we calculated a robust linear regression (see below) of the number of diaspores in each pair of traps -(both low and high traps) against the local propagule pressure (Fig. 1). The slope of this regression line represents a measure of short-distance dispersal ability (i.e. dispersal within 1m; SDA), while the intercept of the regression line (number of diaspores of a species caught in traps without mature inflorescences within 1m radius) represents a measure of intermediate-distance dispersal (> 1m; IDA). To facilitate comparison between species, the number of diaspores caught in each pair of traps for each species (response y) was divided by its average propagule pressure and square-root transformed to stabilize the variance of the residuals, and local propagule pressure for each species (predictor x) was normalised by dividing by its maximum observed local propagule pressure.

Data were pooled between high and low traps for a total of 120 traps. For robust estimation, only the ten species whose diaspores were caught in at least 20 % of traps (at least

24 traps; (Appendix S3) were included in this analysis (the remaining species were caught in ten or less traps). To minimize the potential effect of outliers, we performed Least Trimmed Squares (LTS) regression where the regression line was fitted by minimizing the sum of the 90 % smallest squared residuals.

Dispersal-related traits

We measured dispersal-related species traits using material collected in the study area (Appendix S2): Terminal velocity was determined in the lab for 10 diaspores per species by measuring the time of fall from 2.4 m height using a stopwatch. Release height was estimated by averaging field measurements of inflorescence height for each species (see vegetation assessment) over all 120 quadrats. Diaspores were classified into (1) diaspores with no adaptations for wind transport; (2) diaspores with potential wind adaptations, if small awns and bristles ($\leq 3\text{mm}$) were present or if the diaspore was wrapped in petals or glumes; and (3) diaspores with obvious wind adaptations, if long awns or bristles ($> 3\text{mm}$) or a pappus were present. Diaspore mass was determined by the average weight of 100 air-dried diaspores. There were no significant associations among these traits except for a positive relationship between release height and the presence of potential and obvious wind adaptations (Kruskal-Wallis rank sum test, $df = 2$, $p = 0.005$).

We related the estimated values of SDA and IDA to dispersal related traits. Because the response and some of the predictor variables were estimated themselves and thus associated with uncertainty, we accounted for species-specific uncertainty in both response y and predictor x where standard errors were available (Ripley and Thompson 1987; AMC 2002). This was achieved by weighted regression with weight $w_i = 1 / (\text{SE}(y_i)^2 + b^2 \text{SE}(x_i)^2)$, where b refers to the estimated regression coefficient, $\text{SE}(y_i)$ to the standard errors of quantitative species traits for species i (Appendix S3) and $\text{SE}(x_i)$ to the standard errors of the slope (SDA) or intercept estimates (IDA) from robust regression results (Table 2). Weights w_i

were optimized with regards to regression coefficient b by iteration using Functional Relationship Estimation with Maximum Likelihood (FREML) methods (Ripley and Thompson 1987; AMC 2002) as implemented in the Excel add-in AMC_FREML (AMC 2002). In two cases, a potential outlier was identified based on goodness-of-fit statistics and rescaled residuals as returned by AMC_FREML, and regression parameters were optimized without the outlier. The fitted models were tested in R version 2.14 (R Development Core Team 2004) using the function ‘coeftest’ of the R package ‘lmtest’ (Zeileis and Hothorn 2002). For predictors without uncertainty information (seed mass, wind dispersal adaptation; Appendix S3) we performed Weighted Least Squares (WLS) regression with weights $w_i = 1 / SE(y_i)$ to account for uncertainty in the response variable (SDA or IDA). As only one of the species in this analysis had no adaptations to wind dispersal, we merged categories 1 and 2 of this factor, resulting in a binary predictor variable distinguishing between those species with obvious adaptation (long awns or bristles ($>3\text{mm}$) or a pappus) and those without such obvious adaptation. It was not possible to perform multiple regression analysis while accounting for uncertainty, therefore we applied Bonferroni corrections by dividing the significance level α by k to account for the number k of tests performed on the same response variable.

To test whether dispersal into the adjacent landscape was related to the estimated values of SDA and/or IDA, we performed weighted Spearman rank correlation between the number of diaspores caught in traps outside of the meadow, divided by the average diaspore pressure for each species, and each of the two measures of dispersal ability, SDA and IDA, with weights inversely proportional to their species-specific variance estimates, i.e., $w_i = 1 / SE(y_i)$.

To test whether the main relationship identified in the above analysis is applicable to other species in the community, we tested the weighted Spearman rank correlation between number of diaspores caught in traps inside the meadow, divided by the average diaspore

pressure for each species, and release height, for all species whose diaspores had been caught in 1 – 10 traps. *Euphorbia cyparissias* was excluded from this analysis due to its inconsistent capture data between 2006 and 2007 (Appendix S3). All statistical analyses were conducted using R version 2.14 (R Development Core Team 2004).

Results

Community diaspore rain

Diaspore rain differed markedly between the study seasons 2006 and 2007. Overall, nearly 3 times as many diaspores were captured in the five-week period 07 June – 12 July 2007 as in the four-week period 10 June – 08 July 2006 (17,761 versus 6,014 diaspores, i.e., 184.3 versus 62.4 diaspores per m²). In the second part of the 2007 season (3 weeks between 12 July – 01 August) diaspore number was again lower (4,666 diaspores, i.e., 48.5 diaspores per m²). Since we observed no diaspore shedding before mid-June, we conclude that our study was conducted during the main period of diaspore dispersal. Out of a total of 72 species, we observed diaspore shedding in 40 species, of which 30 were recovered in the traps in 2006, and 28 in 2007. In 2007, ten species (all but one grasses) were found in 25 or more traps, whereas 18 species (all but one forbs) were found in 1 – 10 traps. Generally, more species were found in low than in high traps, but only slightly more diaspores (Appendix S3). The numbers of diaspores captured per species ranged from 1 to 7127. The data for the two types of traps were pooled for the analysis of species-specific dispersal ability.

Dispersal into the adjacent landscape

Only a small proportion of the diaspore rain was dispersed into the adjacent arable fields. The following results are based on the southeast calcareous grassland patch with two years of data and traps up to 40 m from the calcareous grassland (Table 1). Diaspores

captured in the adjacent arable field amounted to 5.9% in 2006 (183 of 3114 captured diaspores) and 6.5% in 2007 (570 of 8637 captured diaspores). The numbers of captured diaspores decreased abruptly with distance in a leptokurtic manner, and capture rates at distances of 20m and beyond were very small (2-3 diaspores). Very few forb diaspores were captured outside of the calcareous grasslands (e.g., 10 of 570 in 2007, Table 1).

Species-specific dispersal ability

Dispersal abilities were estimated for the ten species that were found in at least 20 % of traps (Table 2). Due to the low numbers of diaspores caught in 2006, this analysis was based on the data for 2007. Short-distance dispersal ability (SDA; quantified by the regression slope) and intermediate-distance dispersal ability (IDS; quantified by the regression intercept) were not significantly correlated ($r = 0.31$, $n=10$, $p=0.375$). Model fit varied between species, with very high LTS regression R^2 for *Arrhenatherum elatius* and *Festuca ovina*, and very low fit for *Salvia pratensis* and *Helictotrichon pubescens*. We observed a pronounced difference in capture rates of grasses and forbs. Only one forb (*Salvia pratensis*) had sufficient data for this analysis, whereas only one grass (*Anthoxanthum odoratum*) had to be excluded from this analysis. Dispersal ability SDA and IDA of 30 of the 40 species that were shedding diaspores during summer 2007 could not be estimated, either because their diaspores were not captured at all in 2007 (22 species) or in insufficient numbers, Appendix S3). With the exception of *Anthoxanthum odoratum*, these species were forbs.

Association of dispersal ability with dispersal-related traits

For the ten species included in the estimation of SDA and IDA (nine grasses and one forb), there were no significant correlations between release height, terminal velocity, diaspore mass, and diaspore adaptation to wind dispersal.

IDA was strongly and significantly related to release height, whereas a weaker association with terminal velocity was not significant after Bonferroni correction with $\alpha = 0.05 / 4. = 0.013$ (Table 3A, Fig. 2). Several traits showed a moderate association with SDA, with the strongest association for release height (Table 3B, Fig. 2). However, none of these associations was statistically significant after Bonferroni correction. Species whose diaspores possess obvious wind dispersal adaptations (long awns or bristles ($>3\text{mm}$), or pappus; $n = 5$) tended to have higher mean SDA values than those without such obvious adaptation ($n = 5$), whereas IDA was unrelated to adaptation for wind dispersal (Table 3B). Diaspore mass showed no significant relationship with either SDA or IDA (Table 3B).

Species-specific dispersal into the adjacent landscape

The number of diaspores captured in the adjacent arable fields, adjusted for species-specific average propagule pressure, was strongly and statistically significantly related to IDA, but not to SDA (Table 3C).

Applicability of relationship to other species in the community

The above results suggest that dispersal and especially intermediate distance dispersal ability IDA depends largely on release height. Such an association should also explain variation in the capture rates of other species in the community for which data were insufficient for estimating SDA and IDA with the LTS regression method. Indeed, analysis of the species that were caught in 1 – 10 traps in 2007 showed that the number of diaspores captured, scaled by the species-specific diaspore pressure, was significantly associated with release height (Table 3D).

Discussion

Dispersal ability of calcareous grassland species

Overall, our results show rather limited dispersal with important differences among species, the differences between grasses and forbs being particularly pronounced. Nine of the

ten species for which the amount of diaspore capture allowed for estimation of short- and intermediate distance dispersal ability parameters, were grasses – these species were captured in 20 – 120 traps. With one exception, the remaining species (with diaspores captured in 0 – 10 traps) were forbs. Thus wind dispersal ability may be generally lower in forbs than in grasses in a calcareous grassland system. This is likely to be an effect of lower release height of forbs compared to grasses (see below). However, it is surprising that none of the *Asteraceae* with pappi were not among the species that were trapped regularly (e.g. *Picris hieracioides*, *Leontodon hispidus*, *Hieracium pilosella* or *Tragopogon orientalis*). It has been shown that a pappus leads to low terminal velocity of the diaspore and that *Asteraceae* with pappi are theoretically amongst the most effective long-distance dispersers (Tackenberg 2001; Tackenberg et al. 2003).

Species traits related to dispersal ability

Variation in intermediate-distance dispersal ability IDA of the ten regularly trapped species was strongly related to release height, but only weakly to terminal velocity (not significant after Bonferroni correction). This confirms the results from a seed release experiment in the same study system, where seeds released at half the vegetation height (40cm) showed distinctly different dispersal rates and patterns than those released at vegetation height (80 cm), and seed morphology and thus terminal velocity only mattered for the latter ones (Bolli 2009; Diacon, et al. submitted).

There was no significant association between IDA and diaspore mass, suggesting that this parameter is not a useful predictor of dispersal distance (cf. Verkaar et al. (1983), Jongejans and Telenius (2001) and Tackenberg (2001)). Diaspore characteristics such as long awns, bristles or pappi were related to release height, but not to terminal velocity as might be expected. However, the adaptive significance of these structures, which are particularly well represented in grasses, need not necessarily relate to dispersal. For example, long awns or

bristles have also been interpreted as promoting the burial of the diaspore in the soil, thereby increasing establishment success (Elbaum et al. 2007).

Terminal velocity is often suggested as the most important determinant for dispersal at the diaspore level, and it is often considered to be a direct predictor of dispersal potential and dispersal distance (e.g. Andersen 1992; Jongejans & Telenius 2001; Tackenberg 2001; Soons & Heil 2002). However, our results suggest that this does not hold for the spatial scales considered here. A low terminal velocity offers a clear advantage for dispersal over large distances (100's of meters), since diaspores need to be uplifted by thermal turbulences and updrafts to reach higher wind streams (Soons & Heil 2002; Tackenberg, et al. 2003).

However, dispersal over intermediate distances (1 to 40 m) may be strongly linked to wind conditions close to the canopy, in which case the height of release relative to the surrounding vegetation appears to be much more important than terminal velocity of the diaspore. The vertical wind profile is shaped by the height and the denseness of the surrounding vegetation (Grace 1977). Species that release their diaspores above the canopy generally encounter higher wind speeds and therefore enhance the chance for their diaspores to be uplifted and carried further distances (Katul, et al. 2005; Zhang, et al. 2011). In dense vegetation as in the community studied, release height might therefore become more important for intermediate distance dispersal (1-40m) than terminal velocity of the diaspore. Clearly, the dispersal potential of species that release their diaspores below the vegetation height depends on vegetation density and the resulting wind profile (Verkaar, et al. 1983; Bullock & Moy 2004), and it may therefore differ between different grassland habitats (Marchetto et al. 2010). We conclude that under field conditions and in similar communities, release height is the most important factor for dispersal and should be taken into account when assessing diaspore dispersal of calcareous grassland species into the adjacent landscape.

Consequences for restoration

Dispersal at short and intermediate scales is likely to play an important role for the persistence of dry calcareous grassland communities as it ensures local colonization throughout the community, re-colonisation by species that were formerly present and genetic enrichment of the existing population within the community and with communities nearby (Levin, et al. 2003; Holderegger & Wagner 2006; Kiehl, et al. 2010) . However, this study suggests that the dispersal capacity over short and intermediate distances by wind (i.e. SDA and IDA) varies between species and is especially limited for forbs indicating that wind dispersal alone might not be the natural driving force for the spread of many dry grassland species at those scales.

It has been argued that successful restoration of calcareous grasslands requires diaspore rain from nearby intact communities (Pärtel et al. 1998; Willems & Bik 1998; Pywell, et al. 2002), since most of the characteristic species do not form a long-term persistent seed bank (Kalamees 1999). However, in our study we recovered only small numbers of diaspores, mainly of grasses, in traps placed 1 – 40 m outside of the two calcareous grassland patches (cf. Table 1), suggesting that restoration of plant species diversity of impoverished calcareous grasslands through wind dispersal from surrounding intact communities may be very slow and limited mostly to grass species, whereas forbs account for the largest part of habitat specialists of this endangered ecosystem type. Hence, measures such as transplanting sods (Pärtel, et al. 1998), sowing seeds (Kiehl, et al. 2010) or hay seeding (Poschlod, et al. 1998; Kiehl, et al. 2010) will usually be needed to ensure a successful result.

Conclusions

We investigated dispersal in a calcareous grassland community (*Mesobrometum*) under natural conditions including the effects of neighbouring plants, phenology and weather variations. Regarding the potential for wind dispersal of calcareous grassland communities, we reach three main conclusions. First, calcareous grassland species vary markedly in their

ability to disperse within 1m (short-distance dispersal) and beyond (intermediate-distance dispersal), with grasses being better dispersers than forbs. Second, release height relative to neighbouring vegetation is the most important factor determining intermediate-distance dispersal in calcareous grasslands, while terminal velocity of the diaspore is of limited importance. Third, very few diaspores travel more than a few metres into the adjacent landscape. This diaspore flow, which depends on intermediate-distance dispersal ability, is dominated by grasses and is not adequate for restoring species richness of isolated, impoverished calcareous grassland habitats.

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Tables

Table 1: Diaspore capture in the south-east calcareous grassland patch 2007. Number of captured diaspores in the calcareous grassland patch, capture rate per m², average estimated diaspore pressure per m² (based on the estimated number of mature diaspores 1m² around each trap), number of captured diaspores at different distances from the calcareous grassland patch, total number of captured diaspores in the adjacent landscape originating from the calcareous grassland patch, and captured diaspores relative to diaspore pressure.

Species	Captured diaspores within the SE grassland patch	Average diaspore pressure per m²	Captured diaspores in the adjacent landscape						Total	Captured diaspores relative to diaspore pressure
			1m	2m	5m	10m	20m	40m		
Grasses										
<i>Anthoxanthum odoratum</i> L.	1	6.43								
<i>Arrhenatherum elatius</i> L.	396	488.30	137	11	1			1	150	0.31
<i>Briza media</i> L.	562	790.76	1		3				4	0.01
<i>Bromus erectus</i> Huds.	3953	3895.06	59	9	6				74	0.02
<i>Dactylis glomerata</i> L.	814	1118.04	112	2			1		115	0.10
<i>Festuca ovina</i> L.	61	74.10								
<i>Festuca pratensis</i> Huds.	531	340.60	28				1		29	0.09
<i>Helictotrichon pubescens</i> Huds.	26	19.13								
<i>Poa pratensis</i> L.	52	180.61	2	1	1				4	0.02
<i>Trisetum flavescens</i> Beauv.	1437	1376.40	141	29	13	1			184	0.13
Forbs										
<i>Cerastium fontanum</i> Baumg.	6	32.65	2						2	0.06
<i>Hieracium pilosella</i> L.	5	15.55						1	1	0.06
<i>Knautia arvensis</i> Coult.	18	62.96								
<i>Leontodon hispidus</i> L.	0	1.17								
<i>Leucanthemum vulgare</i> Lam.	50	81.05								
<i>Linum catharticum</i> L.	2	35.97								
<i>Lotus corniculatus</i> L.	2	58.25								
<i>Medicago lupulina</i> L.	2	8.88								
<i>Myosotis arvensis</i> Hill.	17	17.95								
<i>Picris hieracioides</i> L.	18	78.40			1				1	0.01
<i>Plantago lanceolata</i> L.	16	253.44								
<i>Plantago media</i> L.	1	200.57								
<i>Ranunculus bulbosus</i> L.	33	32.41								
<i>Rhinanthus minor</i> L.	0	37.00								
<i>Salvia pratensis</i> L.	60	280.37	5						5	0.02
<i>Tragopogon orientalis</i> Celak.	2	4.22								
<i>Trifolium campestre</i> Schreb.	1	8.25	1						1	0.12

Table 2: Occurrence of the 10 species analysed and the short-distance dispersal and intermediate distance dispersal ability resulting from the Least Trimmed Squares (LTS) regression.

Species	Species Occurrence			LTS Robust Regression						
	n	Number of traps where the species was caught	Number of traps where the species occurred in the surrounding vegetation	Slope	SE	p-value	Intercept	SE	p-value	R ²
<i>Arrhenatherum elatius</i> L.	120	95	95	0.295	0.021	0.000	0.049	0.006	0.000	0.633
<i>Briza media</i> L.	120	88	84	0.084	0.024	0.001	0.037	0.004	0.000	0.100
<i>Bromus erectus</i> Huds.	120	120	120	0.099	0.018	0.000	0.084	0.009	0.000	0.209
<i>Dactylis glomerata</i> L.	120	115	112	0.178	0.034	0.000	0.077	0.007	0.000	0.203
<i>Festuca ovina</i> L.	120	26	27	0.219	0.016	0.000	0.003	0.002	0.132	0.657
<i>Festuca pratensis</i> Huds.	120	85	77	0.441	0.043	0.000	0.042	0.008	0.000	0.495
<i>Helictotrichon pubescens</i> Huds.	120	35	37	0.047	0.050	0.350	0.043	0.012	0.001	0.008
<i>Poa pratensis</i> L.	120	25	51	0.047	0.015	0.002	0.005	0.002	0.011	0.097
<i>Salvia pratensis</i> L.	120	30	113	0.004	0.011	0.686	0.009	0.004	0.015	0.002
<i>Trisetum flavescens</i> Beauv.	120	99	77	0.357	0.040	0.000	0.073	0.008	0.000	0.420

Table 3: Relationship between short (SDA; B) - and intermediate dispersal ability (IDA; A) and diaspore traits (species captured in more than 25 traps), diaspore number captured in the adjacent landscape, relative to diaspore pressure (C; species captured in at least 24 traps), and relationship between diaspore capture inside the meadow, relative to diaspore pressure, and release height of species that were captured in 1-10 traps. Significance level α was adjusted for the number k of tests performed on the same response variable. If regression parameters were fitted excluding one outlier (Fig. 2), p-values for the slope coefficient are reported with and without the outlier.

Response		Predictor	N	Estimate	SE	t-value	p-value	with outlier	k Tests	Bonferroni α	Rsquare	Method
A	IDA	Terminal velocity	9	-0.219	0.08	-2.76	0.028	0.059	4	0.013	0.52	FREML
		Release height	10	0.002	0.00	6.73	0.000		4	0.013	0.85	FREML
		Seed mass	10	0.018	0.01	1.42	0.194		4	0.013	0.20	WLS
		Wind adaptation	10	0.002	0.02	0.15	0.888		4	0.013	0.00	WLS
B	SDA	Terminal velocity	10	-1.623	0.56	-2.88	0.020	0.087	4	0.013	0.51	FREML
		Release height	9	0.013	0.00	3.27	0.014		4	0.013	0.80	FREML
		Seed mass	10	-0.007	0.06	-0.12	0.909		4	0.013	0.00	WLS
		Wind adaptation	10	0.153	0.06	2.46	0.039		4	0.013	0.43	WLS
C	Seeds.relative (outside meadow)	SDA	10	0.183	0.35	0.53	0.614		2	0.025	0.03	Weighted rank corr
		IDA	10	0.711	0.25	2.86	0.021		2	0.025	0.51	Weighted rank corr
D	Seeds.relative (inside meadow)	Release height	17	0.531	0.22	2.43	0.028		1	0.050	0.28	Weighted rank corr

Figure captions

Figure 1: Relationship between the number of trapped diaspores (divided by the average diaspore pressure) and local diaspore pressure (normalised by the maximum diaspore pressure around each trap) for the species *Bromus erectus*. The regression line was used to calculate species-specific dispersal ability (Slope = short-distance dispersal ability SDA ($\leq 1\text{m}$), intercept = intermediate-distance dispersal ability IDA ($< 1\text{m}$)).

Figure 2: Relationship between short (SDA; top) or intermediate distance dispersal ability (IDA; bottom) to terminal velocity [ms^{-1}] (left) and release height [cm] (right). Error bars: Standard error of the mean. Symbol area is proportional to weight $w_i = 1/(\text{var}(y) + b * \text{var}(x))$. Outliers are marked with a filled symbol. Dotted lines have p-values < 0.05 but are not significant after Bonferroni correction for four tests on each response variable. Arr.ela: *Arrhenatherum elatius*, Bro.ere: *Bromus erectus*, Bri.med: *Briza media*, Dac.glo: *Dactylis glomerata*, Fes.ov: *Festuca ovina*, Fes.pra: *Festuca pratensis*, Hel.pub: *Helictotrichon pubescens*, Poa.pra: *Poa pratensis*, Sal.pra: *Salvia pratensis*, Tri fla: *Trisetum flavescens*.

Figures

Figure 1

Figure 2

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721 Appendix for online publication only

722 Appendix S1: Aerial map of the study area

723 Appendix S2: Dispersal-related species traits assessed and estimated from field materials

724 Appendix S3: Total number of diaspores captured

725 | Photo S1: Pairs of diaspore traps

726

For Review Only

Appendix for online publication only

Appendix S1: The two rectangular replicate calcareous grassland patches separated by a strip of woodland. They have a long border on the lower end with arable land and woodland on the upper end. The transects are marked.

Appendix S2: Dispersal-related species traits assessed from field materials sampled in 2007 and estimated short-distance dispersal ability (SDA) and intermediate-distance dispersal ability (IDA): Terminal velocity [$\text{ms}^{-1} \pm$ standard deviation] (based on $n=10$ individuals per species), inflorescence height [$\text{cm} \pm$ standard deviation] (n : frequency of occurrence in vegetation assessments), and diaspore mass [mg] (mean mass of 100 individuals) were measured using diaspores and plant individuals from the study site. Diaspores were categorised into three groups according to adaptations for wind transport: 1 = diaspores with no adaptations; 2 = diaspores with potential wind adaptations (small awns and bristles ($< 3\text{mm}$), diaspores enveloped in petal or glume); 3 = diaspores with obvious wind adaptations (long awns or bristles ($> 3\text{mm}$), pappi).

Species	Terminal velocity [ms^{-1}]	Inflorescence height [cm]	Adaptations for wind transport	Diaspore mass [mg]
Grasses				
<i>Anthoxanthum odoratum</i> L.	0.9 ± 0.1	41.3 ± 12.7 ($n= 19$)	2	0.6
<i>Arrhenatherum elatius</i> L.	1.6 ± 0.3	96.7 ± 19.0 ($n= 84$)	3	1.8
<i>Briza media</i> L.	1.3 ± 0.3	50.9 ± 13.2 ($n= 70$)	2	0.5
<i>Bromus erectus</i> Huds.	2.0 ± 0.3	82.1 ± 10.4 ($n=119$)	3	2.3
<i>Dactylis glomerata</i> L.	1.6 ± 0.3	79.7 ± 13.5 ($n=103$)	2	0.6
<i>Festuca ovina</i> L.	1.7 ± 0.4	35.8 ± 7.9 ($n= 21$)	3	0.5
<i>Festuca pratensis</i> Huds.	1.7 ± 0.6	76.0 ± 16.0 ($n= 67$)	2	0.8
<i>Helictotrichon pubescens</i> Huds.	1.3 ± 0.3	68.1 ± 12.9 ($n= 20$)	3	3.2
<i>Poa pratensis</i> L.	1.2 ± 0.2	41.9 ± 16.7 ($n= 44$)	1	0.2
<i>Trisetum flavescens</i> Beauv.	1.0 ± 0.3	74.3 ± 12.7 ($n= 71$)	3	0.1
Forbs				
<i>Cerastium fontanum</i> Baumg.	1.8 ± 0.1	23.1 ± 7.0 ($n= 13$)	1	0.2
<i>Leucanthemum vulgare</i> Lam.	1.3 ± 0.4	33.6 ± 9.4 ($n= 29$)	2	0.5
<i>Linum catharticum</i> L.	1.4 ± 0.3	17.3 ± 4.7 ($n= 22$)	1	0.2
<i>Lotus corniculatus</i> L.	2.4 ± 0.2	21.8 ± 5.4 ($n= 60$)	1	1.3
<i>Myosotis arvensis</i> Hill.	1.7 ± 0.3	24.7 ± 5.2 ($n= 15$)	1	0.3
<i>Picris hieracioides</i> L.	0.8 ± 0.3	41.1 ± 10.9 ($n= 22$)	3	0.9
<i>Plantago lanceolata</i> L.	2.3 ± 0.3	27.6 ± 7.6 ($n= 94$)	1	1.7
<i>Ranunculus bulbosus</i> L.	2.2 ± 0.4	29.0 ± 7.3 ($n= 45$)	1	3.0
<i>Salvia pratensis</i> L.	2.2 ± 0.3	43.1 ± 11.0 ($n= 84$)	2	1.2

Appendix S3: Total number of diaspores and species captured in high and low traps in 2006 and 2007 (only within the community, 120 traps), the number of traps where the species occurred, SDA and IDA of the species (based on the data of 2007), standard error, p-value and R^2 of the Jackknife estimation.

	2006		2007			2007		
Species	High trap	Low trap	High trap	Low trap	n	Number of traps where the species occurred in the surrounding vegetation	Number of traps where the species was caught	
Grasses								
<i>Anthoxanthum odoratum</i> L.	9	15		11	120	20		8
<i>Arrhenatherum elatius</i> L.	403	223	614	324	120	83		95
<i>Briza media</i> L.	10	97	95	997	120	66		88
<i>Bromus erectus</i> Huds.	746	690	5122	4993	120	120		120
<i>Dactylis glomerata</i> L.	186	158	2007	1076	120	102		115
<i>Festuca ovina</i> L.			11	129	120	22		26
<i>Festuca pratensis</i> Huds.	345	431	883	460	120	65		85
<i>Helictotrichon pubescens</i> Huds.	320	309	30	40	120	32		35
<i>Poa pratensis</i> L.	15	90	17	56	120	43		25
<i>Trisetum flavescens</i> Beauv.	508	625	1274	1962	120	67		99
Forbs								
<i>Anthyllis vulneraria</i> L.		1						
<i>Cerastium fontanum</i> Baumg.	2	18	2	6	120	11		5
<i>Euphorbia cyparissias</i> L.	13	1		1				
<i>Hieracium pilosella</i> L.	1	5		5				
<i>Knautia arvensis</i> Coulter	1	3		18				
<i>Leontodon hispidus</i> L.				1				
<i>Leucanthemum vulgare</i> Lam.	3	20	1	49	120	29		4
<i>Linum catharticum</i> L.		6		4	120	22		4
<i>Lotus corniculatus</i> L.	1		7	4	120	69		7
<i>Medicago lupulina</i> L.		2		3				
<i>Myosotis arvensis</i> Hill.	6	43	1	17	120	16		7
<i>Onobrychis viciifolia</i> Scop.		162						
<i>Picris hieracioides</i> L.	4	12	2	18	120	22		10
<i>Plantago lanceolata</i> L.		25		16	120	103		4
<i>Plantago media</i> L.		2		1				
<i>Ranunculus bulbosus</i> L.		27		36	120	47		5
<i>Rhinanthus minor</i> L.	2	13		2				
<i>Salvia pratensis</i> L.	137	250	25	67	120	111		30
<i>Sanguisorba minor</i> Scop.		73						
<i>Tragopogon orientalis</i> L.	1		1	2				
<i>Trifolium campestre</i> Schreber				2				
Number of diaspores	2713	3301	10092	10300				
Species richness	21	27	17	29				

Photo S1: Pairs of diaspore traps (low and high) along a transect through the dry calcareous grassland patch into the adjacent field.

View Only

Species	Terminal velocity [ms ⁻¹]	Inflorescence height [cm]	Adaptations for wind transport	Diaspore mass [mg]
Grasses				
<i>Anthoxantum odoratum</i> L.	0.9 ±0.1	41.3 ±12.7 (n= 19)	2	0.6
<i>Arrhenatherum elatius</i> L.	1.6 ±0.3	96.7 ±19.0 (n= 84)	3	1.8
<i>Briza media</i> L.	1.3 ±0.3	50.9 ±13.2 (n= 70)	2	0.5
<i>Bromus erectus</i> Huds.	2.0 ±0.3	82.1 ±10.4 (n=119)	3	2.3
<i>Dactylis glomerata</i> L.	1.6 ±0.3	79.7 ±13.5 (n=103)	2	0.6
<i>Festuca ovina</i> L.	1.7 ±0.4	35.8 ± 7.9 (n= 21)	3	0.5
<i>Festuca pratensis</i> Huds.	1.7 ±0.6	76.0 ±16.0 (n= 67)	2	0.8
<i>Helictotrichon pubescens</i> Huds.	1.3 ±0.3	68.1 ±12.9 (n= 20)	3	3.2
<i>Poa pratensis</i> L.	1.2 ±0.2	41.9 ±16.7 (n= 44)	1	0.2
<i>Trisetum flavescens</i> Beauv.	1.0 ±0.3	74.3 ±12.7 (n= 71)	3	0.1
Forbs				
<i>Cerastium fontanum</i> Baumg.	1.8 ±0.1	23.1 ± 7.0 (n= 13)	1	0.2
<i>Leucanthemum vulgare</i> Lam.	1.3 ±0.4	33.6 ± 9.4 (n= 29)	2	0.5
<i>Linum catharticum</i> L.	1.4 ±0.3	17.3 ± 4.7 (n= 22)	1	0.2
<i>Lotus corniculatus</i> L.	2.4 ±0.2	21.8 ± 5.4 (n= 60)	1	1.3
<i>Myosotis arvensis</i> Hill.	1.7 ±0.3	24.7 ± 5.2 (n= 15)	1	0.3
<i>Picris hieracioides</i> L.	0.8 ±0.3	41.1 ±10.9 (n= 22)	3	0.9
<i>Plantago lanceolata</i> L.	2.3 ±0.3	27.6 ± 7.6 (n= 94)	1	1.7
<i>Ranunculus bulbosus</i> L.	2.2 ±0.4	29.0 ± 7.3 (n= 45)	1	3.0
<i>Salvia pratensis</i> L.	2.2 ±0.3	43.1 ±11.0 (n= 84)	2	1.2