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Frequency of plant species in remnants of calcareous grassland and their dispersal and persistence characteristics

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Abstract

Why should some species be so much more common than others? Here, we propose that traits affecting dispersal and persistence can be used to predict the frequency of occurrence of a species in grassland remnants in the Swiss Jura Mountains. We established the frequency of occurrence of 112 plant species in 96 remnants of calcareous grassland in NW Switzerland. We determined the following eight traits for each species: (1) dispersal category (unassisted, ant-, adhesion- or wind-dispersed), (2) terminal velocity of diaspores, (3) plant height, (4) mass per seed, (5) seed shape (variance of length, width and height), (6) onset of flowering, (7) duration of flowering, and (8) life form (clonal perennials, perennials without pronounced vegetative reproduction, short-lived species). Then we tested whether there is a correlation among these traits with the frequency of occurrence of a species in grassland remnants using stepwise multiple regression with the original data as well as with phylogenetically independent contrasts (PICs) calculated with a phylogeny based on recent molecular analysis. Species with an early onset of flowering ($p < 0.01$, $R^2 = 0.09$), a clonal life form ($p < 0.01$, $R^2 = 0.08$), a long duration of flowering ($p < 0.02$, $R^2 = 0.04$) and with heavy seeds ($p < 0.05$, $R^2 = 0.03$) occurred more frequently than others. In total the model explained 26% of the variance in species' frequency. Results were confirmed by the analysis with PICs except for the one concerning life form. Our results suggest that traits enhancing persistence are more important for the frequency of occurrence of a species in calcareous grassland than traits affecting dispersal. This might imply that in grassland remnants colonisations by far-distance dispersal are insignificant because of a lack of diaspore exchange among populations.

Warum sind bestimmte Arten so viel häufiger als andere? Wir gehen davon aus, dass Merkmale, welche Ausbreitung und Persistenz einer Pflanzenart beeinflussen, zur Vorhersage ihrer Häufigkeit in Restflächen der einstmals häufigeren Kalkmagerrasen im Schweizer Jura benutzt werden können. Wir bestimmten die Häufigkeit von 112 Pflanzenarten in 96 Kalkmagerrasen in der Nordwestschweiz. Folgende Merkmale wurden für jede Art festgestellt: (1) Ausbreitungstyp (keine Hilfsstrukturen, Ameisen-, Wind- od. Tierausbreitung), (2) Fallgeschwindigkeit der Diasporen, (3) Wuchshöhe der Pflanzen, (4) Gewicht eines Samens, (5) Samenform (Varianz von Länge, Breite und Höhe), (6) Blühbeginn, (7) Blühdauer, (8) Lebensform (klonal, langlebig aber nicht ausgeprägt klonal, kurzlebig). Mittels multipler, schrittweiser Regression wurde getestet, ob zwischen diesen Merkmalen und der Häufigkeit einer Art in Magerwiesen ein Zusammenhang besteht. Dazu wurden sowohl die Originaldaten, als auch phylogenetisch unabhängige Kontraste (PICs), beruhend auf

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einer Phylogenie mit neuesten molekularen Daten, benutzt. Arten mit einem frühen Blühbeginn ($p < 0.01$, $R^2 = 0.09$), ausgesprochen klonalem Wachstum ($p < 0.01$, $R^2 = 0.08$), einer langen Blühdauer ($p < 0.02$, $R^2 = 0.04$) und schweren Samen ($p < 0.05$, $R^2 = 0.03$) waren häufiger als andere. Insgesamt wurden 26% der Variation in der Häufigkeit der Arten durch das Modell erklärt. Die Resultate wurden, außer der die Wuchsform betreffenden, durch die Analyse mit PICs bestätigt. Unsere Resultate legen nahe, dass Merkmale, die die Persistenz begünstigen, für die Häufigkeit einer Art wichtiger sind als Eigenschaften, die ihre Ausbreitung begünstigen. Für die Restflächen ehemals ausgedehnter Halbtrockenrasen bedeutet dies, dass die Wahrscheinlichkeit, dass sich eine lokal verschwundene Art durch Fernausbreitung wiederansiedeln kann, klein ist, weil der Diasporenaustausch zwischen den Restflächen zu gering ist.

Key words: Biogeography – colonisations – diaspores – frequency of occurrence – Mesobromion – phylogenetically independent contrasts – seeds – terminal velocity

Introduction

Although the species in a given plant community might experience similar environmental conditions, some of them are rare and others are very abundant (Gaston 1994, Gaston & Kunin 1997). But what is it that makes the difference? At the regional scale, physiological constraints, historical events and evolutionary processes determine the regional species pool, while at the local scale dispersal ability and interspecific interactions are important processes (Morin 1999). Consequently, the species composition of communities has successfully been described as a function of colonisations and extinctions (MacArthur & Wilson 1967, Brown & Kodric-Brown 1977, Eriksson 1996), and traits affecting dispersal and persistence should be useful for predicting species' distribution and their frequency in particular habitats (Ehrlén & van Groenendael 1998). Important traits to obtain persistence are a long lifespan, a high reproductive capacity or long-lived seeds in the soil. Seed mass can positively influence seedling establishment, as heavier seeds provide larger nutrient reserves and thereby seedlings can produce larger seedlings and are competitively superior (Westoby et al. 1996). The formation of a seed bank depends on seed mass and shape. Small and more spherical seeds can survive longer in the soil than prolonged and flat seeds (Thompson et al. 1993, Bakker et al. 1996). Short-lived species without a seed bank usually produce many seeds to ensure the survival of their populations.

Once a species has disappeared in a habitat and no seeds are present in the seed bank a recolonisation is only possible by immigrating diaspores from neighbouring populations (Bakker et al. 1996). Diaspores are transported by wind, animals or water and dispersal can be enhanced by morphological adaptations to these vectors. For grassland species wind is considered to be one of the most important dispersal agents (van der Pijl 1982, Hodgson & Grime 1990, Bakker et al. 1996). The lower the terminal velocity (= velocity of falling bodies after a phase of acceleration) of seeds, the longer dispersal distances were observed (Sheldon & Burrows 1973, Burrows 1986, Matlack 1987). Small seeds enhance wind dispersal by a low terminal velocity (Burrows 1975, 1986, Harper 1977). In grazed communities transport of diaspores over long distances by grazing animals can be high (Fischer et al. 1996). Additionally, in historical and recent agricultural practice diverse anthropogenic mechanisms of seed dispersal have been identified (Bonn & Poschlod 1998).

This study focuses on characteristic Mesobromion species, many of which are rare or endangered in remnants of nutrient-poor calcareous grassland in the Swiss Jura Mountains. Such grasslands are among the more species rich habitats in Central Europe (Baur et al. 1996) and their flora includes many rare plant species (Zoller 1954, Ellenberg 1982, Zoller & Bischof 1980, Willems 1982). Due to changes in agricultural land use since World War II 75% of the former area of these extensively used grasslands in the Swiss Jura Mountains have been destroyed. This destruction was followed by a dramatic reduction of many of their characteristic species (Fischer & Stöcklin 1997). The ongoing destruction has been largely reduced or even stopped by conservation efforts in the last 20 years, but grassland remnants are now small in area and isolated, like islands in an intensively used landscape (Stöcklin et al. 2000). Today it is attempted by management practices to increase biodiversity in these habitats and to keep alive the remaining populations of endangered species. Noticeable improvements in environmental quality have been obtained (Wunderle 1999). Nevertheless, many populations of target species could not be increased and suitable habitats were not recolonized as expected. Considering the large input of financial and human resources better predictions of the success of restoration measures are desirable (van Groenendael et al. 2000). A good knowledge of the dispersal characteristics of seeds is essential to predict if after a restoration locally extinct species can recolonize remnants (Bakker et al. 1996). In the Swiss Jura Mountains the research focus was on temporal dispersal (Stöcklin & Fischer 1999) and only little is known about the importance of spatial dispersal.

As the increasing distances and barriers between the remnants of calcareous grassland impede or prevent the diaspore exchange between populations (Fischer et al. 1996), those that travel far are most important because they possess the highest capacity to reach other remnants. Several studies provided evidence that the number of available diaspores and their dispersal can limit the frequency of grassland species (Eriksson 1997, Eriksson 1998, Eriksson & Kiviniemi 1999, Jakobsson & Eriksson 2000, Zobel et al. 2000). Thus, if the exchange of diaspores is prevented, species with traits ensuring a high persistence should become more and more frequent.

The aim of this comparative study was to test whether the frequency of grassland species across sites is associated with traits affecting reproduction, persistence and dispersal. As the measurement of spatial dispersal in the field is difficult if not impossible (Jurado et al. 1991, Jackel & Poschlod 1994, Greene & Johnson 1995), morphological characteristics and the terminal velocity of the diaspores were used as predictors of the species' dispersal capacity. We also asked if other traits affecting reproduction and persistence are useful for predicting the success of grassland species. Conventional regression analysis as well as phylogenetically independent contrasts (Harvey & Pagel 1991, Harvey et al. 1995, Silvertown et al. 1997) were used to test the correlation of species' properties and their success in calcareous grasslands. The traits under investigation were dispersal category, terminal velocity of the diaspores, plant height, mass per seed, seed shape, onset of flowering, duration of flowering and life form. Among these, dispersal category, terminal velocity of the diaspores and plant height are connected with dispersal, and life form is connected with persistence. The other traits may influence both dispersal and persistence.

Population biology is primarily focused on patterns and processes involving individuals of a single species while the explanation of diversity patterns is the goal of community ecology. Of course, a strict separation of the biology of populations and communities is highly artificial. Our study question, whether plant traits affecting long-term population viability can be used to predict a species' frequency of occurrence in grassland communities, is at the borderline between the two disciplines. Our study thus illustrates the usefulness of population biological considerations for community ecology.

Materials and methods

Study area and frequency of occurrence of the species

The study area in the Swiss Jura Mountains covers a region of about 520 km^2 between 600 and 950 m of altitude and includes 96 remnants of nutrient-poor calcareous grasslands of the "Mesobromion"-type with areas between 0.1 to 19.6 ha. The sites are usually located on slopes unsuited for intensive farming or far from villages and are either extensively used or are now maintained by conservation efforts. Between 46 and 135 species are found at such sites, and species density per 100 m^2 varies from 27 to 70 (Ryf 1997, Wunderle 1999). The frequency of 112 species of these grasslands was determined as the percentage of the 96 study sites in which a species occurred. Species were a priori selected as to be species of the Mesobromion that are more or less confined to this community type. Orchidaceae and Orobanchaceae were not considered in the study because of their tiny seeds. The presence or absence of a species at a site was assessed by vegetation records complemented by walking on a wavy line over the whole area of a site. As a measure for the abundance of a species in the study area the mean cover of each species was calculated using cover values according to Braun-Blanquet (1964) estimated in a plot of 100 m^2 on each site (Ryf 1997, Wunderle 1999).

Seed and dispersal characteristics

A sample of seeds of each of the 112 species was used for measurement of the mass per seed and dispersal traits. Of each species at least 50 diaspores from three different sites in the study area were collected between June and October 2000. In each site seeds were taken from at least five individuals so that the sample included diaspores of at least 15 individuals per species. The diaspores were dried in an oven at 80 °C for 48 hours before being weighed. Seed mass, and if differing also the mass of diaspores (15 species) were weighed. A sample of 50 seeds per species was weighed and mean mass per seed was calculated. The tiny seeds of four species were weighed individually on a microbalance and mean mass per seed was calculated from 12 individual measurements. For Asteraceae (20 species) achenes were weighed. If seeds had a pappus, it was included in the seed mass.

The length, width and height of eight seeds per species were measured using a dissecting microscope and for each species a seed shape index was calculated after Bakker et al. (1996). The index is the variance of the length, width and height of a seed and indicates the degree of deviation from a sphere.

For 68 species values of terminal velocity were obtained from Tackenberg (2001). For one species data from Schulz et al. (1991) and for one species data from Askew et al. (1997) was used. For species with a mass per seed below 0.05 mg the terminal velocity was set to 0.1 m/s (Burrows 1975, 1986, Harper 1977, Bonn & Poschlod 1998). For the 36 remaining species the terminal velocity was measured experimentally according to Tackenberg (2001). Diaspores were dropped without accelerating them from 3.15 m in a room protected from any air currents and the falling time was measured with a stopwatch. In a preliminary test with five different species the falling time of the same diaspore was measured 30 times and the measuring error was found to be small and negligible. It has to be considered that with the above-mentioned method a systematical error is included as the final terminal velocity is only reached after a time of acceleration. This error was corrected using the method described in Tackenberg (2001).

As the dispersal vector of most species is unknown and field observations are difficult (Jurado et al. 1991) the diaspores were classified into four dispersal categories based on morphological features according to Leishman & Westoby (1994): (1) Unassisted (no morphological structures to assist dispersal), (2) ant dispersed (with elaiosomes or sweet secretes), (3) adhesion dispersed (with hooks, spines or barbs to assist attachment), (4) wind dispersed (with wings, hairs or a pappus to increase air resistance).

Plant height, life form, onset and duration of flowering

For each species the mean of the minimal and maximal plant height was calculated from literature data (Lauber & Wagner 1998), for 45 species the maximum values were modified after own field observations.

Life form categories indicate differences in longevity of individuals and variation in population fluctuations, and hence differences in population persistence. According to Fischer & Stöcklin (1997) species were classified into three life form categories: (1) clonal perennials with pronounced vegetative reproduction, (2) perennials including clonal species without pronounced vegetative reproduction, (3) short-lived species (annuals and biennials) with obligate reproduction by seeds.

Species were also scored for their onset and duration of flowering. After Mazer (1989) and Lauber & Wagner (1998) species were classified into (1) early flowering (onset of flowering from February until May), (2) middle flowering (June and July), and (3) late flowering (August until October). For each species the duration of flowering in months was taken from Lauber & Wagner (1998).

Statistical analysis

A stepwise multiple regression model with the frequency of occurrence as the dependent variable was used to test the effect of species' traits (Yadolah 1999). In the first step, the independent variables were tested separately and the variable with the lowest p-value remained as first variable in the model. In the second step, combinations with each of the remaining variables were tested and again the one with the lowest p-value remained in the model. Stepwise, further variables were introduced into the model by choosing at each step the combination of variables with the lowest p-values. After each step all the formerly introduced variables were tested again and removed if their p-value was above 0.20. Thereby a minimal set of variables explains maximal variability. Residuals were tested for normality. Frequencies were arcsine-transformed, seed mass and plant height were log-transformed to satisfy the requirements of the analysis. Since species traits usually are not completely independent of phylogeny we also used phylogenetically independent contrasts (PICs) (Purvis & Rambaut 1995). PICs were calculated by the statistical package WinCAIC (Purvis & Rambaut 1995, Hodkinson et al. 1998) using the "crunch" option. We assembled a phylogeny for the 112 species mainly based on recent molecular analysis. The phylogeny was resolved to 95% resulting in 108 PICs. The phylogeny along with the respective references is available from the second author. In analyses of PICs regressions were forced through the origin (Purvis & Rambaut 1995). A correlation matrix of all variables and linear regressions with original data and PICs were calculated to test for significant correlations among traits. All analyses were done with the programme JMP 3.2.2 (SAS Institute, Cary, North Carolina, USA).

Results

Frequency of occurrence and mean abundance of species

The ranked frequency of occurrence of 112 species in 96 remnants of unfertilized calcareous grassland in the Swiss Jura Mountains decreased continuously from 100% (occurence in all study sites) to 1%. The distribution of mean species abundance in a remnant showed a characteristic L-shaped pattern with few species being very abundant and most species being rare. Frequent species were also more abundant ($r = 0.83$, $p < 0.001$).

Seed and dispersal characteristics

The oven dried mass per seed of the 112 species ranged from 0.001 mg to about 22.6 mg (Table 1) with 52% of the species having seeds with a mass per seed below 1 mg. Although there were linear shaped seeds the majority was rather round with a low index of seed shape (Table 1). The terminal velocities covered a range of more than 4 m/s (Table 1).

Among the different dispersal categories the largest group were the unassisted seeds (63%). Among the species with morphological adaptations wind dispersed seeds were the most common (25%), while ant dispersal (9%) and adhesion dispersal (3%) were far less common.

Plant height, life form, onset and duration of flowering

As there were no shrubs and trees considered in this study the tallest plants reached a height of 140 cm and the smallest of 5 cm (Table 1). Among the different life forms perennials without pronounced vegetative reproduction were most common (74%) while short-lived (16%) and clonal species (10%) contained much smaller numbers. Most species had either an early (47%) or a middle onset of flowering (49%), and only few flowered late in the season (4%). The duration of flowering was about 3 months for most of the species, although there were extreme values of 1 and 10 months (Table 1).

Table 1. Minimum, maximum, medians and means (±SE) for mass per seed, index of seed shape, terminal velocity of the diaspores, plant height, and duration of flowering for 112 calcareous grassland species of NW–Switzerland.

Trait	Minimum	Maximum	Median	Mean ± SE
Oven dried mass per seed (mg)	0.001	22.56	0.94	1.95 ± 0.29
Index of seed shape	0.003	0.195	0.065	0.070 ± 0.04
Terminal velocity (m/s)	0.1	4.27	2.06	1.95 ± 0.09
Plant height (cm)	5.0	140	27.5	33.9 ± 2.1
Duration of flowering (months)	1	10	3	3.5 ± 0.1

Correlations among traits

Several correlations among combinations of traits in a correlation matrix using either the original data or phylogenetically independent contrasts were significant (Table 2). Heavier seeds fall faster (linear regression with original data: $R^2 = 0.23$, $p < 0.001$, with PICs: $R^2 = 0.23$, $p < 0.001$). However, if only wind dispersed seeds were considered, there was no correlation of mass per seed with terminal velocity. Seeds without adaptation to wind dispersal fall faster when they are round than when they are linear (linear regression with original data: $R^2 = -0.18$, $p < 0.001$, with PICs: $R^2 = -0.18$, $p < 0.001$). There was also a positive correlation of plant height with mass per seed (linear regression with original data: $R^2 = 0.11$, $p < 0.001$, with PICs: $R^2 = -0.10$, $p < 0.001$) and with the onset of flowering (linear regression with original data: $R^2 = 0.09$, $p < 0.01$, with PICs: $R^2 = 0.05$, $p < 0.05$). Early flowering species are smaller.

Influence of traits on a species' frequency of occurrence

The final model after stepwise multiple regression with the frequency of occurrence as dependent variable contained five of the eight investigated species' traits, which explained 26% of the variation (Table 3). Species with an early onset of flowering (Fig. 1a), a clonal life form (Fig. 1b), a long duration of flowering

Table 2. Correlation matrix showing correlations between the eight investigated traits of 112 calcareous grassland species in NW-Switzerland calculated with original data (plain) and PICs (*italic*).

	Duration of flowering	Onset of flowering	Life form	Log plant height (cm)	Seed shape	Dispersal type	Log mass of 1 seed (mg)	Terminal velocity (m/s)
Duration of flowering (months)		–0.11	0.02	–0.07	–0.04	–0.17	–0.05	–0.01
Onset of flowering	***–0.38***		0.03	**0.19**	0.02	–0.07	–0.18	–0.17
Life form	*0.08*	*–0.10*		–0.13	0.12	–0.12	**–0.20**	**–0.23**
log plant height	*–0.16*	***0.28***	*0.01*		**0.25**	0.13	**0.32**	0.03
Seed shape	*–0.11*	*0.08*	*0.07*	*0.04*		0.16	–0.14	**–0.55**
Dispersal type	*–0.02*	*0.08*	*0.08*	*0.08*	*–0.01*		**0.26**	–0.15
Log mass of 1 seed	*–0.08*	*–0.03*	*–0.08*	*0.06*	*–0.11*	*0.14*		**0.50**
Terminal velocity (m/s)	*–0.09*	***–0.16***	***–0.26***	*–0.09*	***–0.28***	***–0.32***	***–0.43***	

Bold letters indicate significance with $p < 0.05$.

(Fig. 1c) and large seeds (Fig. 1d) showed a significantly higher frequency of occurrence in grassland remnants. The strongest influence had the onset of flowering which accounted for 9% of the variation. The analysis with abundance as dependent variable gave a similar result (data not shown).

When the influence of species' traits on their frequency of occurrence in calcareous grassland was tested using phylogenetically independent contrasts the model contained four traits explaining 24% of the variation (Table 4). The mass per seed, the onset of flowering, and the duration of flowering still showed a significant effect on the frequency of occurrence of a species, but not life form.

Discussion

Traits affecting the frequency of occurrence of a species in calcareous grassland were more related to persistence than to dispersal. Species with an early onset and a long duration of flowering, with larger seeds and with a clonal life form were significantly more frequent. The frequency of occurrence of a species did not depend on traits like terminal velocity, dispersal category and plant height or seed shape. Small seeds that were expected to disperse more easily over long distances also did not enhance the frequency of occurrence of a species. Frequent species in general were also more abundant.

Distribution of and relationship among seed properties

The range and distribution of seed mass observed in species of calcareous grassland are similar to those of the semi-arid and arid floras of West-New South Wales and Central Australia (Leishman et al. 1995), the flora of the Indiana Dunes (Mazer 1989), of California (Baker 1972) and Sheffield (Grime et al. 1988). Only the very large seeds are missing in our data, probably because in our study only herbaceous species were included with a maximal height of 1.4 m, while woody species with frequently very large seeds are not present in calcareous grasslands.

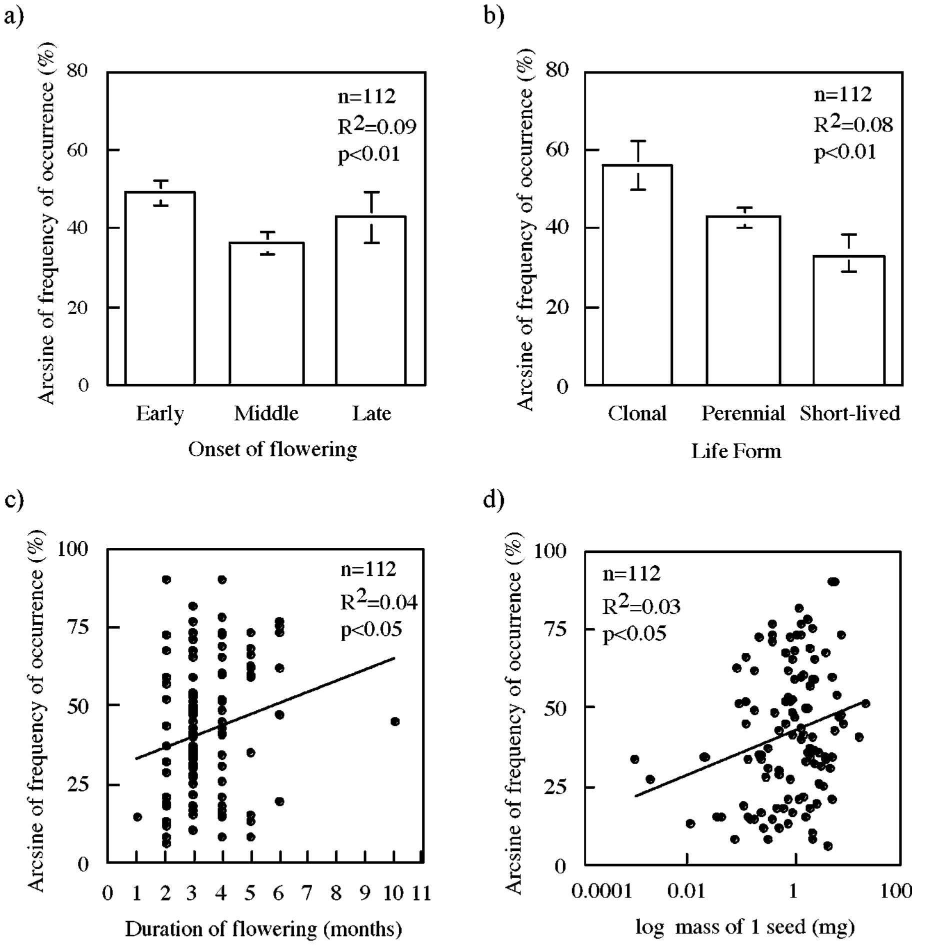

Fig. 1. The influence of four significant traits on the frequency of occurrence of 112 calcareous grassland species of NW-Switzerland. Indicated R^2- and p-values refer to the stepwise multiple regression model with the original data (Table 3). a) Mean ± SE of three classes of onset of flowering, b) Mean ± SE of three classes of life form, c) Regression with the duration of flowering, d) Regression with the mass per seed.

Table 3. Stepwise regression of frequency of occurrence for 112 calcareous grassland species of NW–Switzerland with five out of eight traits remaining in the model (see methods for details).

Trait	df	F	p	R^2
Onset of flowering	2	6.18	**0.003**	0.09
Life form	2	5.48	**0.006**	0.08
Duration of flowering (months)	1	5.86	**0.017**	0.04
Log oven dried mass per seed (mg)	1	4.05	**0.047**	0.03
Terminal velocity (m/s)	1	2.55	0.113	0.02
Model	7	5.11	**< 0.001**	0.26
Total	111			

Bold letters indicate significant p–values.

Table 4. Stepwise regression of frequency of occurrence for 112 calcareous grassland species of NW–Switzerland using phylogenetically independent contrasts (n = 108) with four out of eight traits remaining in the model (see methods for details).

Trait	df	F	p	R^2
Duration of flowering (months)	1	12.04	**0.008**	0.09
Onset of flowering	1	7.61	**0.0069**	0.06
Log oven dried mass per seed (mg)	1	5.27	**0.0237**	0.04
Terminal velocity (m/s)	1	1.73	0.1915	0.01
Model	4	8.19	**< 0.0001**	0.24
Total	108			

Bold letters indicate significant p-values.

Seeds and diaspores of almost two thirds of the species in the present study have no morphological adaptations to a particular dispersal category. Among the other species those with adaptations to wind dispersal were most common. Such a distribution is probably characteristic for open habitats. However, case studies from Australia, New Zealand and North America (Willson et al. 1990) showed that even among similar habitat types the proportion of dispersal categories can vary considerably. Ant- and adhesion-dispersed seeds are, with only few exceptions, rare as they were in our study (9% and 3%, respectively). The proportion of species with wind-dispersed seeds varies from 10 to 30% in other studies and was 25% in our survey. Species with unassisted seeds and diaspores are characteristic for the semi-arid and arid floras of West-New South Wales and Central Australia (Leishman et al. 1995) and were also the largest group in the semi-dry grassland of the Swiss Jura Mountains. However, as soon as a high number of woody species are included in a flora the proportion of various dispersal categories may be different. Oakwood et al. (1993) as an example found a very large proportion of ant-dispersed seeds in woody plants.

As might be expected heavier diaspores had a larger terminal velocity than smaller seeds. However, this correlation does not hold for seeds with adaptations for wind dispersal. The terminal velocity of diaspores with structures to increase air resistance does not depend on their mass or size. The effectiveness of such adaptations seems to surpass the influence of seed mass on terminal velocity. This coincides with the results from Sheldon & Burrows (1973) who observed that the fine structure of the pappus considerably enhances the dispersal capacity of diaspores. The relationship of terminal velocity and seed weight observed for seeds without adaptations for wind dispersal may cause a trade-off between their dispersability and the success of seedlings. Smaller seeds can be dispersed more easily, but they contain fewer nutrients for the early development of their embryos (Harper 1977). This indicates that dispersability is negatively related to persistence, a trade-off which is also affected by the shape of seeds. The wind dispersal potential of more spherical seeds is lower than that of more linear seeds because they fall faster. But round seeds are considered to be more long-lived in the soil (Thompson et al. 1993) and a high persistence in an already occupied site is in contradiction to a high dispersability.

Traits that enhanced the frequency of occurrence of a species

Short-cut biological interpretations why most plant communities consist of a few very abundant and of a lot more rare species consider only simple systems with some single key resource or key ecological factor dominating community structure. May (1975) pointed out that in species-rich communities diversity pattern will be caused by many, more or less independent factors and MacArthur (1960) noted that factors affecting population dynamics are expected to have small multiplicative effects. In our analysis four traits significantly enhanced a species' frequency of occurrence. (1) The onset of flowering explained most of the variation in frequency of occurrence with species flowering early being more frequent than others. Obviously, in mown or grazed grassland an early reproduction may ensure a sufficient seed production. Poschlod & Jackel (1993) observed a high proportion of early flowering species in calcareous grassland in southern Germany, and Bonn & Poschlod (1998) considered this to be an adaptation to the timing of mowing. Also, in calcareous grassland with frequent summer droughts climatic conditions early in the season are better for seed ripening. There might also be an effect of seed eating birds. The main breeding time during which birds fly frequently between feeding places and nest to feed their partners and later on the nestlings coincides more with the phenology of early flowering than middle and late flowering species (Glutz von Blotzheim 1966). Thereby these species might be more effectively dispersed than others. (2) Longer flowering species occurred more frequently, probably because a long duration of flowering enhances the possibility that at least part of the population can reproduce successfully. This is especially important for short-lived species without a persistent seed bank because their survival depends on the yearly reproduction. (3) Species with larger seeds occurred more frequently, indicating the importance of regeneration from seeds. Larger seeds with more nutrients are an advantage for seedling establishment because of longer roots and higher competitiveness (Stebbins 1971, Primack 1987, Tilman 1988, Leishman et al. 1995, Westoby et al. 1996). (4) Finally, species with pronounced clonal reproduction occurred more frequently, but this trait had an effect only when not controlled phylogenetically. This implies that there was a phylogenetic bias in the data indicating that the importance of a clonal life form for the frequency of occurrence of a species, though ecologically relevant in calcareous grassland, should not be interpreted as caused by independent evolution but may result from common descent. There are of course many reasons why a clonal life form should have a positive effect on the frequency of occurrence of a species. Clonal plants are inherently persistent, long-lived, frequently very competitive and therefore usually very abundant (van Groenendael & de Kroon 1990). It has been shown, however, that certain categories of clonal plants are particularly frequent among rare plants (Klimeš & Klimešová 2000).

Dispersal characteristics did not enhance the frequency of occurrence of a species

The two traits most obviously related to dispersal, the dispersal category and the terminal velocity, had no effect on the frequency of occurrence of a species. In addition to dispersal category, terminal velocity is expected to influence dispersal because slowly falling diaspores can be dispersed by wind more easily which is said to be the most important dispersal vector in grasslands (Ridley 1930, van der Pijl 1982). The lack of such effects in this study could result from the fact that the spatial separation of the highly fragmented remnants of calcareous grassland is too large for colonisation events to occur frequently. However, it could also be that far-distance dispersal is strongly dependent on rare events not directly related to dispersal characteristics. For instance, the presence of species on open cast mining sites or coal spoil piles in Germany after long-distance dispersal seems not to depend on their dispersal characteristics (M. Brändle and T. Pitsch, pers. communication). Fischer et al. (1996) observed that dispersal by grazing sheep was also frequent among unassisted seeds. Plant height was another trait usually connected with dispersal but having no effect on the frequency of occurrence of a species in our analysis. However, plant height was correlated with seed weight as well as with the onset of flowering, two traits which significantly affected the frequency of occurrence of a species. Tall species with large seeds were frequent, but early flowering species of low height with small seeds were frequent too. This complex relationship among seed weight, onset of flowering and plant height may explain why there was no effect of plant height on the frequency of occurrence of a species.

Seed shape was the only trait connected with persistence that did not at all show an influence on the frequency of occurrence of a species. Species with round seeds should be expected to occur more frequently as their seeds can survive longer in the soil and ensure the survival of populations of short-lived species. This result coincides with the finding of Fischer & Stöcklin (1997) that in calcareous grasslands in the Swiss Jura Mountains only few species build up a persistent seed bank.

Conclusions

Our results clearly indicate that in calcareous grassland traits enhancing persistence are more important for the frequency of occurrence of a species than traits affecting dispersal. Unfertilized calcareous grasslands in the Swiss Jura Mountains are now isolated habitats and their frequently endangered plant species face the challenge to compensate local extinctions by moving between suitable sites. We actually largely ignore how important natural processes or agricultural practices are for such events. This study, however, suggests that colonisations by far-distance dispersal events are insignificant because of a lack of diaspore exchange between populations, possibly resulting from the recent fragmentation and increasing isolation of the remaining Mesobromion grassland. In the long run, this will not only affect the presence of species in a given site but also genetic processes within and gene flow among populations causing difficulties for endangered species to survive or to adapt to changing conditions (Young et al. 1996). Unfortunately, we still know very few about a plant species' capacity to move and even less how far this capacity has been impaired by recent changes in the way we manage our landscapes. Our results indicate that the inevitable loss of local populations in remnants of calcareous grassland might not be replaced by natural recolonisations given their actual fragmentation and isolation.

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