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Habitat dependence of seed-size value to recruitment

Recruitment advantage of large seeds is greater in shaded habitats

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Abstract

Large seeds are assumed to have higher probability of successful recruitment than small seeds. This is because larger seeds give rise to larger seedlings and larger seedlings better withstand environmental hazards like deep shade and drought. Biotic and abiotic limitations to seedling growth and survival, and conversely availability of safe sites for recruitment, vary along environmental gradients and between habitat types. Thus, the value to plant species of possessing large seeds may differ between plant communities. We analyzed the relationship between seed mass and per-seed recruitment success (seedlings established per quantity seed produced) along an environmental gradient from open grassland to closed-canopy forest using data collected by Uuno Perttula in southern Finland in 1941. We found that larger seeds have greater recruitment success relative to smaller seeds in all investigated communities. However, the recruitment success of large seeds relative to small seeds strongly increased from grassland and open forest to closed-canopy forest. Of the measured environmental variables, canopy closure most strongly explained this increase. This indicates a strong direct effect of deep shade on seedling survival in natural plant communities. Additional explanatory power was associated with soil moisture. Litter cover, moss cover, and soil pH did not contribute to explaining the variation in relative recruitment success of larger seeds. Thus, the advantage of large seeds in recruitment success is pronounced in deeply shaded forest, but may be insignificant in open vegetation.

Keywords: colonization/competition, colonization/establishment, seed size/seed number, seedling recruitment, litter, soil moisture

Nomenclature: Tutin *et al.* (1964-1980)

Introduction

In most plant communities, all suitable space is usually filled, and the reproductive capacity of the sum of all species in the community greatly exceeds what is necessary to successively populate empty space as it appears. Thus, only a small fraction of the seeds produced result in eventual recruitment of new individuals. At the same time, seed mass of species inhabiting a plant community usually varies one or more orders of magnitude (Salisbury, 1942; Leishman et al., 2000). These observations together open the question whether seed mass matters to recruitment success of species.

Over the last decade, a body of theory has accumulated that attempt to explain the within-community variation in seed mass as the result of an evolutionary game, known as the seed size/seed number trade-off (SSNT) model (Geritz, 1995; Rees & Westoby, 1997; Geritz, van der Meijden & Metz, 1999). The idea is that large-seeded and small-seeded species may coexist due to a trade-off between their abilities to reach and compete for vacant microsites. The theory has generated numerous studies of the relationship between seed mass and abundance in plant communities (reviewed by Murray *et al.*, 2002). The theory is based on two assumptions: (1) With reference to the negative relationship between seed mass and number of seeds per plant per year per unit reproductive effort (Harper, Lovell & Moore, 1970; Shipley & Dion, 1992; Moles *et al.*, 2004), it is assumed that greater seed output enables mother plants to distribute their off-spring to more vacant microsites (Eriksson & Jakobsson, 1999; Bullock *et al.*, 2002). This assumption has received scanty interest and empirical evidence is equivocal (Leishman, 2001; Jakobsson, Eriksson & Bruun, 2006). (2) There is a positive relationship between seed mass and seedling competitive ability (Geritz, 1995; Rees & Westoby, 1997). While there is little empirical evidence for the importance of seedling-seedling competition (Moles & Westoby, 2004a), many experimental studies have shown that larger-seeded species better survive environmental stress, e.g. drought, deep shade, deep litter or defoliation, including competitive suppression by established plants (reviewed by Westoby *et al.*, 2002). Thus, the positive linear relationship between seed mass and per-seed recruitment success predicted by SSNT model appears to be well-supported empirically (Gross, 1984; Burke & Grime, 1996; Jakobsson & Eriksson, 2000; Kidson & Westoby, 2000; Turnbull, Manley & Rees, 2005; but see counterexamples in Moles & Westoby, 2004b). It remains, however, untested to what degree the magnitude and importance of the positive relationship between seed mass and recruitment success is dependent on plant community context and local environment. It has been suggested that seed mass is of less importance to recruitment in open and disturbed vegetation (Salisbury, 1942; Gross, 1984; Westoby, Leishman & Lord, 1996; Jakobsson & Eriksson, 2000), but the question has never been investigated thoroughly.

If one assumes that all seedlings face the same hazards and are affected by these hazards in similar ways across community types, one should expect identical slopes of the seed-mass : recruitment-success relationship for all communities. If, on the other hand, the relative recruitment success of large seeds changes along a gradient in environmental stress, such as shade, we would expect different slopes of the seed-mass : recruitment-success relationship. In the specific case of shade, we expect the steepest slope in the most deeply shaded environment.

Here we investigate whether the importance of seed mass for recruitment success changes along a gradient from open to shaded plant communities (dry grassland to closed forest). We hypothesize that the relative recruitment success of larger seeds relative to smaller seeds increases in forested communities. This could be expected to result from deeper shade and a thicker layer of leaf litter on the ground (Suding &

Goldberg, 1999; Fröborg, 2001; Dzwonko & Gawroński, 2002). Conversely, small-scale disturbances in grassland may provide competition-free space for recruitment (Bullock *et al.*, 1995; Eriksson *et al.*, 2006), rendering seed mass less important to recruitment success. We define the recruitment success as the number of seedlings divided by the number of seeds of that species in the seed rain within the same area.

We tested the hypothesis using data collected by Uuno Perttula in southern Finland in 1934 (Perttula, 1941). An important reason why quantitative assessments of the relationship between seed mass and recruitment success under field conditions are lacking, is that it requires knowledge of the seed rain and tedious counting of seedlings. Perttula's data are unique in offering both these variables over a range of plant communities.

Material and methods

Study area

The study of Perttula (1941) is a representative of a Finnish-Russian tradition for empirical studies of regeneration of herbaceous plant communities by surveying seedling emergence and survival (Bogdanovskaya-Guihéneuf, 1926; Linkola, 1932; Söyrinki, 1938; Rabotnov, 1950) long before the concept of regeneration niche (Grubb, 1977). The study was undertaken in southern Finland, some 110 km to the West of Helsinki and a few kilometres from the Baltic Sea, at the forest reserve Solböle (60° N, 23° E). The landscape is undulating, with granite outcrops and depressions with lakes and deposits from ice or sea. At the time of investigation, the vegetation cover consisted of a mosaic of forest, open meadows and rock outcrops with shallow soils. Forests consisted mostly of mixed stands dominated to variable degree by *Picea abies*, *Betula* spp., *Populus tremula*, *Quercus robur*, and *Acer* *platanoides*. Less abundant was heath-forest, which was characterized by a field layer dominated by ericaceous dwarf-shrubs and with overstories dominated by *Picea abies*, *Pinus sylvestris*, and *Betula* spp. in mesic sites and by *Pinus sylvestris* in dry sites. Embedded in the forest matrix were mesic and dry meadows and rock outcrops. Mesic meadows were wooded meadows with a sparse canopy layer formed by *Pinus sylvestris* and deciduous trees like *Populus tremula* and an understory of *Juniperus communis*, *Corylus avellana* and other shrubs. Dry meadows had scattered *Juniperus communis*, while rock outcrops had no woody plant cover at all. Rock outcrop vegetation was characterized by almost no soil, but also dry meadow and *Calluna*-type dry heath-forest occurred on shallow soil over bedrock, whereas other communities were found on deeper soils. Perttula (1941) distinguished 12 types of herbaceous plant community of forest field-layer, meadow and rock outcrop (Table 1).

A number of environmental variables were measured or estimated in each habitat type. Soil pH was measured on dried soil samples and soil moisture estimated subjectively on a 10-grade ordinal scale. Only minimum and maximum values were given in the original published source, so median values were calculated in addition. The following descriptors of vegetation structure were assessed: percentage cover of litter/thatch and moss layers and, where present, their depth; percentage cover of the field layer (ranges given in Table 1); light penetration (in percent of light above the tree canopy, Eder-Hecht-Graukeil photometer); and the canopy closure as an estimated percentage.

Data collection

In each plant community type, approximately ten 50 m^2 plots of variable shape were placed, totalling 100 plots over all 12 community types. In each plot, four 1 m ×1 m subplots were placed for estimates of seed production and seedling recruitment. In each subplot, the number of sterile and fertile ramets was counted for each species on at least 5 occasions during the summer and autumn. The average number of fully developed undamaged seeds per fertile ramet was estimated from ramets collected in the plots, but not in close vicinity to the subplots, in order not to change the seed rain in these. The number of fertile ramets multiplied by the average number of seeds per ramet gave the seed productivity per unit area (seed yield in the terminology of Rabotnov 1950). In each subplot, seedlings were counted twice, in May/June and in August. For species with larger and more conspicuous seedlings, all seedlings were counted. For smaller species, seedlings were counted in destructive microplots (0.35 m × 0.35 m), two per subplot on each occasion. The average density for the whole subplot was calculated. By assuming that all seeds produced by one species within a subplot were dispersed inside that subplot only, one may calculate the average recruitment success for each species in each community type (Perttula, 1941, Tab. 10). Forty out of 468 observations consisted of seedlings only, but no seeds in the extrapolated seed rain estimate. These were not included in the analyses. Unfortunately, only the range, not the mean and spread, in seed production and seedlings per m^2 for each species in each community type are given by Perttula (1941), and the original plot-wise data have been lost. Thus, the otherwise appropriate use of binomial regression, requiring both successes and failures, was not possible and, consequently, all calculations have been done in the traditional way – on arcsine transformed percentages.

Data on seed mass (mg, air-dried weight) were retrieved from various sources, chosen by geographical proximity, which in practice means that most records (75%) were from Scandinavia, and the rest mainly from Central Europe and the British Isles. Seed mass data and their sources are listed in Appendix 1. For one species, *Calamagrostis purpurea*, which rarely sets seed, no data were available. Consequently, it was omitted from the analysis.

Data analysis

Differences between community types in average seed mass and average seed number per ramet per year between plant communities (both log transformed) were investigated by one-way analysis of variance. The overall relationship between seed mass and seed number per ramet per year (both log transformed) and its interaction with plant community was investigated using analysis of covariance (with the factor community added first; as implemented in R version 2.5.1.). The assumptions of normal distributed errors and homoscedasticity were justified for the log transformed data.

Recruitment success was calculated, for each species in each community separately, as the proportion of seedlings to total yield of fully developed, undamaged seeds (average over ten plots). Standardised Major Axis (SMA) regression was used to estimate the slope for each community type of the seed-mass : recruitment-success relationship. This model II regression is more appropriate than the usual model I regression for estimating the slope of a relationship when the independent variate is not controlled by an experimenter and has an associated measurement error and when the purpose is to identify the best line of fit, not to make predictions (Warton et al., 2006). We used the R package SMATR ver. 2.1 (by Daniel Falster, David Warton and Ian Wright) to estimate slopes and test for between-community differences. Recruitment success was arcsine transformed (Sokal & Rohlf, 1995) and seed mass was log10 transformed prior to analysis. The SMA procedure was as follows: an SMA slope common to both groups in a pair of community types was estimated using a likelihood ratio method following Warton & Weber (2002). The significance of this estimate was determined by testing for significant heterogeneity among slope estimates by permutation (Manly, 1997). After fixing the position of individual points along the estimated common slope, residuals were permuted among groups 999 times, with the common slope and test statistic recalculated after each iteration.

In order to investigate if differences in relative recruitment success of large seeds between community were attributable to differences in environment (Table 1), the SMA slopes (of the recruitment success to seed mass relationship) for communities were regressed on environmental variables using linear regression and statistical significance was tested by a permutation test using 999 permutations of residuals of the full regression model (Legendre & Legendre, 1998, pp. 606-612; Anderson & Legendre, 1999) as implemented in the programme Regressn (Legendre, 2002). Reported p-values are for two-tailed tests.

Results

Average seed mass (log10 transformed) varied among communities (Table 2), but differences were not statistically significant (one-way ANOVA; $F_{11, 422} = 1.61$, $p = 0.09$). The difference between communities in average seed number per ramet was statistically significant (one-way ANOVA; $N = 414$, $F_{11, 422} = 2.07$, $p = 0.02$), but had no systematic relationship with differences in light, moisture or other environmental factors. The fundamental assumption of the SSNT model – a negative relationship between log seed mass and log seed number - was supported by the data (Fig. 1) and the slope or intercept of the regression model did not differ significantly between communities (Table 3). However, most of the variation in seed number per ramet per year was not explicable in terms of seed mass (ANCOVA; $r^2 = 0.19$).

All communities had positive Standardised Major Axis (SMA) slopes of the seed-mass : recruitment-success relationship (Table 2). The SMA regression procedure showed significantly different slopes of the recruitment success to seed mass relationship between communities. Two rather distinct groups of communities appeared (Fig. 2). Communities 1 to 5 had relatively shallow slopes, meaning relatively small difference in recruitment success related to seed mass. In contrast, communities 6 to 12 had relatively steep slopes, suggesting a relatively large gain in recruitment success with increased seed mass (Table 2). SMA slopes for the two groups were significantly different (0.14 and 0.25, respectively; $p << 0.01$).

Four environmental variables had significant relationships with the variation in seed-mass related recruitment success among communities, namely two related to shade (canopy cover and light penetration percentage) and two related to water regime (minimum and average moisture). Canopy cover had the strongest explanatory power ($r^2 = 0.610$, $p = 0.004$; Fig. 3). Minimum moisture ($r^2 = 0.544$, $p = 0.010$) and light penetration ($r^2 = 0.537$, $p = 0.005$) were somewhat weaker, and average moisture the weakest ($r^2 = 0.369$, $p = 0.037$). Multiple regression analysis entering canopy cover first gave no significant two-factor models, meaning that shade-related and moisture-related variables explained the same part of the variation in SMA slope between plant communities. Thus, the communities in which species with heavier seeds had the largest relative recruitment success (steep SMA slope) were field layer vegetation under deep shade with a relatively moist microclimate. Conversely, the communities in which heavier-seeded species had a comparatively small recruitment advantage (shallow SMA slope) were open forests, grasslands (meadow) and rock outcrop.

Discussion

A positive relationship between seed mass and recruitment success has been documented for a wide range of communities (Gross, 1984; Burke & Grime, 1996; Jakobsson & Eriksson, 2000; Kidson & Westoby, 2000; Turnbull, Manley & Rees, 2005; this study). Our analysis provided evidence that the strength of this relationship depends on the degree of shading a plant community experiences. We found a significantly higher relative recruitment success of large seeds in field-layer communities under closed forest canopies than in other community types. Thus, larger-seeded species appeared to have a much greater recruitment advantage relative to smaller-seeded species in closed forest than in open forest and grassland. This overall pattern was clear despite much variation in recruitment success unrelated to seed mass variation (scatter in Fig. 2). This residual variation is attributable to species-specific characteristics, e.g. germination behaviour. A number of species appeared to deviate more systematically from the predicted relationship. These were all relatively large-seeded plant species with very low recruitment success, which was explicable by their association with specialized seed predators dwelling inside the seed (and thus seeds being scored as fully developed and undamaged by the investigator; *Lathyrus*, 4 spp.; *Vicia*, 3 spp.; Convallariaceae, 4 spp.; *Actaea spicata*) and species with idiosyncratic germination requirements (*Geranium bohemicum* and *Rubus saxatilis*). For these species, seed productivity and effective seed rain density may have been overestimated.

Contrary to our expectation, no differences in relative recruitment success of large seeds were seen between open forest and meadow, or between meadow and rock outcrop vegetation. This may suggest that seed-mass related recruitment success changes abruptly at a certain – high – threshold in light extinction, rather than gradually along the clinal variation in shade at the forest-floor level. This field-based result is nevertheless in accordance with experimental findings of Leishman & Westoby (1994), who found no seed-mass related difference in seedling survival when varying shading from 50 – 95%, only at 99% shade.

The difference between plant communities in seed-mass related recruitment success was not confounded by systematic variation in seed mass, since differences in average seed mass were insignificant. This observation is slightly at odds with the frequently found pattern that shade tolerant species tend to have large seeds (Salisbury, 1942; Grubb, 1998; Thompson & Hodkinson, 1998), but perhaps reflects the rather forested character of all communities, even the meadow and rock outcrop communities investigated, which were situated as isolates in a forest matrix.

The cause for the observed difference among communities in relative recruitment success of large seeds appeared to be variation in shade. Light penetration percentage and canopy cover correlated strongly, and soil moisture weakly, with this difference, whereas litter cover and litter depth appeared to have no effect. This indicates a major direct effect of deep shade, probably acting on seedling survival. This is in accordance with evidence from greenhouse experiments on herbaceous (Leishman & Westoby, 1994) and woody species (Walters & Reich, 2000). However, both of these studies found the seed-mass related shade : seedling-survival relationship to be mainly driven by seed weights above 10-100 mg. In the present – field-based – study, the positive relationship (Fig. 2) was driven by all seed size classes, except the largest, probably due to a disproportionately strong seed-predation pressure on the largest seeds. In addition to the effect of shade on seedling survival, light conditions might work already on the level of seed germination because smaller-seeded species appear to have a light requirement for germination more often than larger-seeded species (Grime *et al.*, 1981; Milberg, Andersson & Thompson, 2000) and because seed matured under canopy-filtered light may have an induced light requirement for germination (Pons, 2000).

Deep litter has previously been shown to hamper recruitment of herbaceous forest floor species, particularly species with seed mass below 10 mg (Fröborg, 2001; Dzwonko & Gawroński, 2002). In the present study, accumulation of a deep litter layer was found in several of the studied communities (e.g. 100% cover and 4.5 cm depth on average in 'Mixed forest of *Melica-Lathyrus* type'). However, litter appeared to be less important than deep shade in influencing recruitment differences among species with different-sized seeds.

The direct effect of shade suggests that environmental adversity, not competition among seedlings, is a selective force acting on seedling size (and hence seed mass). Had recruitment taken place in gaps below the canopy level, and the relative recruitment success of large seeds been expressed through a competitive superiority of larger seedlings, one would have expected stronger correlation with features of the forest floor environment, such as field layer cover, moss cover or litter cover. This result is in line with the literature review by Moles and Westoby (2004a), finding that seedlings more often die from environmental hazards (herbivory, pathogens, drought) than from direct seedling-seedling competition. In slight contrast to this survey, Silvertown & Bullock (2003) found that seedling mortality in grassland gaps was somewhat density dependent. Seedling competition probably matters only when seedlings stand close to each other, and seedlings arising from larger seeds probably have an advantage.

Recruitment success of ericaceous dwarf-shrubs was very low. It is well-known that, despite insurmountable annual fruit production, seedlings are rarely observed in the field (Vander Kloet & Hill, 1994; Eriksson & Fröborg, 1996). However, although dominant in some of the investigated communities, only three species of ericaceous dwarf-shrubs were found. Omission of four dwarf-shrub dominated communities on podzolic soils (see Table 1) did not change the overall results.

A number of assumptions were made in the course of this study. The first assumption was that all seeds produced within a 1 m^2 subplot were dispersed inside that subplot only, or at least that seeds outflux was balanced by influx from the surroundings. Of course, seeds may be dispersed further away from the mother plant than 1 m, and direct assessment of the seed rain by trapping would have been preferable. However, for the quantitative composition of the seed rain it was a reasonable assumption, as most seeds fall in the close vicinity of their mother plant (Verkaar, Schenkeveld & van de Klashorst, 1983; Jongejans & Telenius, 2001; Jakobsson, Eriksson & Bruun, 2006). Pre-dispersal seed predation, but not post-dispersal, was taken into account. Larger seed are thought to be more prone to seed predation by both rodents and insects (Thompson, 1987; Reader, 1997; but see Moles, Warton & Westoby, 2003), and empirical studies have found support for this idea in both grassland (Hulme, 1994) and forest (Fröborg, 2001). Thus, if larger seeds were disproportionately consumed by seed predators, one would expect them to have a lower recruitment advantage, making the present estimate of a relative recruitment advantage of larger seeds a conservative one.

Perttula (1941) counted seedlings, but did not follow their survival to reproductive maturity, let alone to the next year. This means that there is a big leap from recruitment success to plant fitness. However, the seed dispersal and seedling germination and establishment phases are usually considered most critical in the plant life cycle. In most cases, only a negligible fraction of the seeds produced get as far as to become established seedlings. Moreover, the reserves provided by the mother plant are spent during this short but critical phase. For the purpose of a study of the seed-mass effect on recruitment, the seedling establishment phase is appropriate to consider, while survival during the juvenile phase is much less dependent on seed mass (Moles & Westoby, 2004b).

In conclusion, the importance of seed mass for recruitment success changed along the gradient from dry grassland to closed forest. This change, however, was not gradual, but abruptly shifting between forest with dense canopy cover and open forest, with little difference between open forest, grassland and rock outcrop communities. This knowledge is important in attempts of turning SSNT theory into mechanistic models of colonization and competition (e.g. Eriksson & Jakobsson, 1998), comparison of model results from different formations or geographic areas (e.g. Bruun, 2001) and in reviews and meta-analyses (e.g. Murray *et al.*, 2002; Murray *et al.*, 2005).

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Table 1. The 12 plant community types investigated and features of their environment. Original data from Perttula (1941).

No	Type	Podzol	Soil pH	Soil moisture	Litter cover (%)	Litter depth (cm)	Moss cover (%)	Moss depth (cm)	Field layer cover (%)	Light (%)	Canopy cover (%)
1	Dry heath-forest of *Calluna* type	1	3.9	2	100	1	10	4.5	15-50	45	20
2	Dry heath-forest of *Vaccinium vitis-idaea* type	1	3.9	2	0	2	65	4	20-60	28	43
3	Rock outcrop	0	4.8	2.5	0	0	15	2	5-80	100	0
4	Mesic meadow	0	5.1	4	100	2	25	2.5	65-100	75	10
5	Dry meadow	0	4.9	3	100	4	100	4	45-100	100	0
6	Mixed forest of *Hepatica*-*Oxalis*-type	0	5.6	4.5	82.5	2.5	20	2.5	45-100	16	50
7	Mesic heath-forest of *Oxalis*-*Vaccinium myrtillus*-type	1	4.4	4	100	2	80	4	10-70	15	65
8	Alder forest of fern-type	0	5.3	7	17.5	0	20	0	26-75	9	100
9	Mesic heath-forest of *Vaccinium myrtillus*-type	1	4.2	3	0	0	100	7	10-75	20	53
10	Mixed forest of *Melica*-*Lathyrus* type	0	6.0	3	100	4.5	0	0	30-98	30	100
11	Alder forest of *Silene dioica* type	0	5.3	4.5	0	0	20	0	45-100	37	58
12	Mixed forest of *Oxalis*-*Maianthemum*-type	0	5.2	4.5	100	1.5	45	5	30-80	3	90

Table 2. The 12 plant community types investigated and the number of species encountered as seedlings, the median no. seedlings per m^2 (both from Perttula, 1941), mean seed mass (un-weighted average) and standard deviation (SD) around the mean, Standardised Major Axis (SMA) slope with lower and upper 95% confidence interval (CI).

No.	Community type	Median no. species m^{-2}	Mean seed mass (mg) ± SD	SMA slope (lower CI - upper CI)
1	Dry heath-forest of *Calluna* type	4	2.14 ±3.55	0.13 (0.11 - 0.16)
2	Dry heath-forest of *Vaccinium vitis-idaea* type	6	1.50 ±2.92	0.17 (0.08 - 0.36)
3	Rock outcrop	20	2.67 ±8.23	0.13 (0.08 - 0.20)
4	Mesic meadow	55	4.04 ±6.75	0.14 (0.11 - 0.19)
5	Dry meadow	45	2.54 ±6.41	0.16 (0.11 - 0.21)
6	Mixed forest of *Hepatica-Oxalis*-type	75	3.39 ±5.95	0.22 (0.18 - 0.28)
7	Mesic heath-forest of *Oxalis-Vaccinium myrtillus*-type	34	2.32 ±3.95	0.26 (0.19 - 0.36)
8	Alder forest of fern-type	48	3.62 ±14.15	0.28 (0.21 - 0.37)
9	Mesic heath-forest of *Vaccinium myrtillus*-type	17	3.00 ±5.00	0.27 (0.17 - 0.44)
10	Mixed forest of *Melica-Lathyrus* type	72	4.25 ±7.36	0.23 (0.18 - 0.29)
11	Alder forest of *Silene dioica* type	39	1.61 ±1.54	0.33 (0.25 - 0.45)
12	Mixed forest of *Oxalis-Maianthemum*-type	13	3.79 ±4.65	0.37 (0.20 - 0.67)

Table 3. Analysis of covariance of the seed mass : seed number relationship over 12 plant community types ranging from closed-canopy forest to grassland and rock outcrop. For each model term, the degrees of freedom (d.f.), sum-of-squares (Sum Sq), F-value and *p*-value are given.

	d.f.	Sum Sq	F	*p*
Plant community	1	9.5	2.96	0.09
Log seed mass	1	323.1	100.15	< 0.001
Community * log seed mass	1	0.1	0.04	0.84
Residuals	430	1387.0		

Fig. 1. Relationship between log seed mass and log seed number per ramet (n = 414). An ordinary linear regression model was highly significant ($p << 0.001$), but had low predictive power ($r^2 = 0.225$). Species may be represented by more than one point if they occurred in more than one plant community, but all points for a particular species have the same x coordinate.

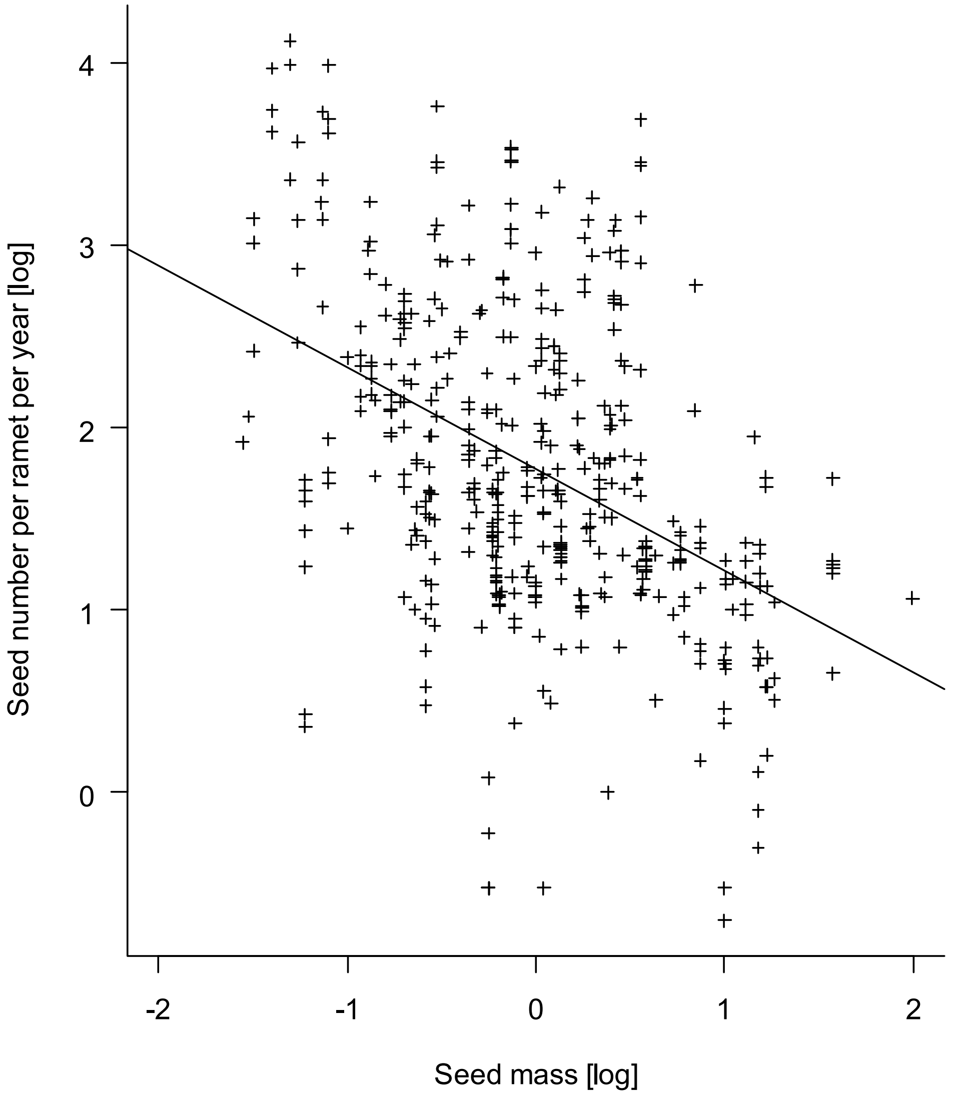


Fig. 2. Recruitment success in relation to seed mass in 12 plant communities ranging from closed-canopy forest to grassland and rock outcrop, with Standardised Major Axis (SMA) regression lines. Two groups of community types are shown separately, deeply shaded forest field-layer communities (type 6-12, filled circles, full line, adjusted $r^2 = 0.065$) and open forest field layer, grassland and rock outcrop communities (type 1-5, empty circles, broken line, adjusted $r^2 = 0.033$). The slope of regression lines indicates the strength of the relative recruitment success of heavy seeds.

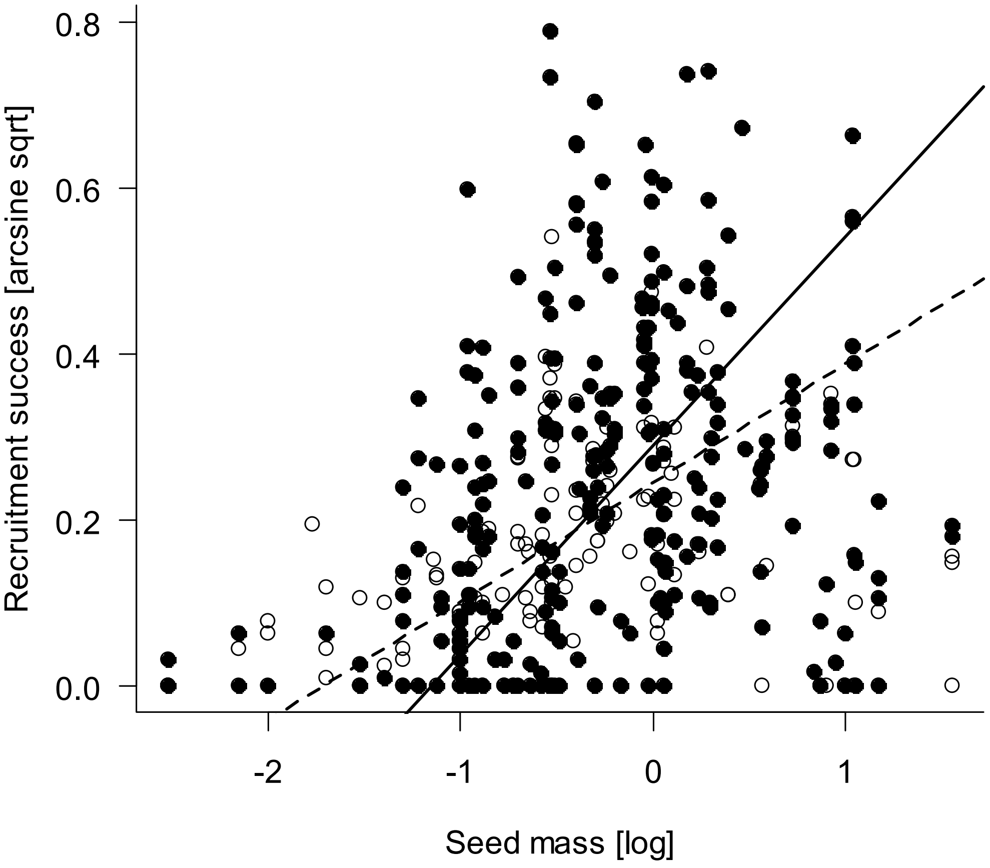
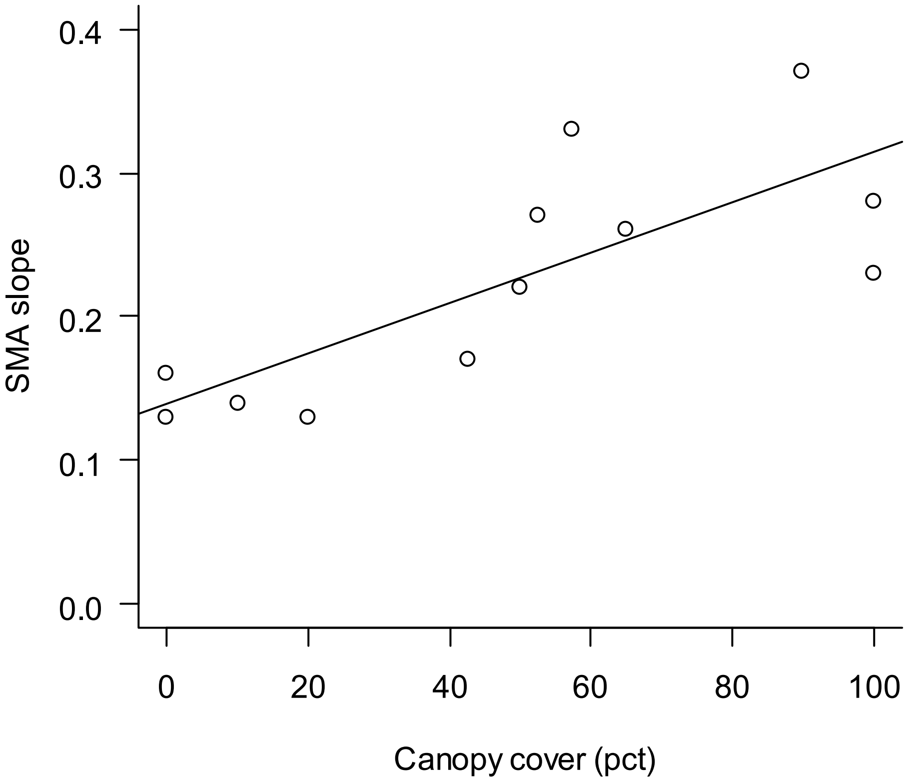


Fig. 3. Relative recruitment success of heavy seeds (Standardised Major Axis regression slope of recruitment success vs. seed mass) in relation to canopy cover (%) in 12 plant community types ranging from grassland to heavily shaded forest field-layer communities.



Appendix 1. List of species with seed mass data and their sources.

Species	Seed mass (mg)	Source
Achillea millefolium	0.133	Eriksson & Jakobsson (1998)
Actaea spicata	6.91	Fröborg (2001)
Aegopodium podagraria	2.59	Jakobsson & Eriksson (2002)
Agrostis capillaris	0.06	Grime et al. (1981)
Alchemilla sp.	0.487	Eriksson & Jakobsson (1998)
Anemone nemorosa	3.82	Fröborg (2001)
Anemone ranunculoides	1.1	BiolFlor Datenbank; http://www.ufz.de/biolflor
Angelica sylvestris	3.597	This study
Anthoxanthum odoratum	0.615	This study
Anthriscus sylvestris	2.832	Eriksson & Jakobsson (1998)
Arabidopsis thaliana	0.028	Eriksson & Jakobsson (1998)
Avenula pubescens	1.308	Eriksson & Eriksson (1997)
Briza media	0.23	Grime et al. (1981)
Bromus hordeaceus	2.90	Akinola, Thompson & Hillier (1998)
Calamagrostis arundinacea	0.55	Jakobsson & Eriksson (2002)
Calamagrostis epigejos	0.06	Csontos, Tamás & Balogh (2003)
Calamagrostis purpurea	na	
Calluna vulgaris	0.032	Eriksson & Jakobsson (1998)
Caltha palustris	0.99	Grime et al. (1981)
Campanula persicifolia	0.074	This study
Campanula rotundifolia	0.08	Welling & Laine (2002)
Cardamine bulbifera	98.6	Jakobsson & Eriksson (2002)
Carex digitata	0.64	Jakobsson & Eriksson (2002)
Carex pallescens	1.363	This study
Carum carvi	2.457	This study
Centaurea jacea	1.064	Eriksson & Jakobsson (1998)
Cerastium fontanum ssp. triviale	0.118	Eriksson & Jakobsson (1998)
Chelidonium majus	0.76	Fröborg (2001)

Circaea alpina	0.512	Mazer (1989)
Cirsium helenoides	2.01	Akinola, Thompson & Hillier (1998)
Cirsium palustre	2	Grime et al. (1981)
Cirsium vulgare	2.64	Grime et al. (1981)
Convallaria majalis	18.38	Fröborg (2001)
Corydalis solida	1.7	Müller-Schneider (1986)
Crepis tectorum	0.318	Andersson (1990)
Dactylorhiza maculata	0.003	Salisbury (1942)
Deschampsia cespitosa	0.202	This study
Deschampsia flexuosa	0.63	Welling & Laine (2002)
Dianthus deltoides	0.141	Eriksson & Jakobsson (1998)
Elymus caninus	3.44	Graae, Hansen & Sunde (2004)
Epilobium angustifolium	0.05	Grime et al. (1981)
Epilobium montanum	0.13	Grime et al. (1981)
Euphrasia sp.	0.226	This study
Fallopia dumetorum	4.30	Müller-Schneider (1986)
Festuca ovina	0.468	This study
Festuca rubra	1.04	Welling & Laine (2002)
Filipendula ulmaria	0.3	Jakobsson & Eriksson (2002)
Filipendula vulgaris	0.518	Eriksson & Jakobsson (1998)
Fragaria vesca	0.3	Jakobsson & Eriksson (2002)
Galium boreale	0.746	This study
Galium palustre	0.91	Grime et al. (1981)
Galium uliginosum	0.292	This study
Galium verum	0.659	Eriksson & Jakobsson (1998)
Geranium bohemicum	7	Almquist (1899)
Geranium robertianum	2.02	Jakobsson & Eriksson (2002)
Geranium sylvaticum	5.329	This study
Geum rivale	1.34	Eriksson & Jakobsson (1998)
Glyceria fluitans	1.2	Grime et al. (1981)
Hepatica nobilis	2.18	Jakobsson & Eriksson (2002)

Hieracium sect. Vulgata	0.44	Jakobsson & Eriksson (2003)
Hieracium umbellatum	0.44	Jakobsson & Eriksson (2003)
Hierochloë australis	1.2	BiolFlor Datenbank
Hypericum maculatum	0.04	Jakobsson & Eriksson (2002)
Hypochaeris maculata	1.112	Eriksson & Jakobsson (1998)
Impatiens noli-tangere	4.5	Graae, Hansen & Sunde (2004)
Knautia arvensis	2.469	Eriksson & Jakobsson (1998)
Lathyrus montanus	15	Eriksson & Jakobsson (1998)
Lathyrus pratensis	10.119	Eriksson & Jakobsson (1998)
Lathyrus sylvestris	37.44	Kornaś (1972)
Lathyrus vernus	15.3	Fröborg (2001)
Leucanthemum vulgare	0.44	Eriksson & Eriksson (1997)
Linnaea borealis	2.403	This study
Listera ovata	0.003	Salisbury (1942)
Luzula multiflora	0.418	Salisbury (1942)
Luzula pilosa	0.59	Jakobsson & Eriksson (2002)
Lychnis viscaria	0.055	Eriksson & Jakobsson (1998)
Lysimachia vulgaris	0.29	Kornaś (1972)
Maianthemum bifolium	9.97	Fröborg (2001)
Melampyrum pratense	7.453	This study
Melampyrum sylvaticum	13	Jakobsson & Eriksson (2002)
Melica nutans	1.752	This study
Milium effusum	1.25	Jakobsson & Eriksson (2002)
Moehringia trinervia	0.22	Grime et al. (1981)
Mycelis muralis	0.31	Jakobsson & Eriksson (2003)
Myosotis stricta	0.1	BiolFlor Datenbank
Oxalis acetosella	0.99	Eriksson & Eriksson (1997)
Paris quadrifolia	5.84	Fröborg (2001)
Pimpinella saxifraga	1.073	Eriksson & Jakobsson (1998)
Plantago lanceolata	1.918	Eriksson & Jakobsson (1998)
Poa angustifolia	0.19	Grime et al. (1981)

Poa nemoralis	0.17	Jakobsson & Eriksson (2002)
Polygonatum odoratum	37.3	Salisbury (1942)
Potentilla argentea	0.073	Eriksson & Jakobsson (1998)
Potentilla crantzii	0.440	This study
Potentilla erecta	0.770	This study
Prunella vulgaris	0.612	Eriksson & Jakobsson (1998)
Pulmonaria officinalis	6.11	Jakobsson & Eriksson (2002)
Ranunculus acris	1.1	Welling & Laine (2002)
Ranunculus auricomus	0.28	Jakobsson & Eriksson (2002)
Ranunculus ficaria	1.35	Salisbury (1942)
Ranunculus polyanthemos	2.5	BiolFlor Datenbank
Ranunculus repens	2.96	Jakobsson & Eriksson (2002)
Rhinanthus angustifolius	2.21	Jensen (2004)
Rhinanthus minor	1.873	Eriksson & Jakobsson (1998)
Rubus idaeus	1.8	Jakobsson & Eriksson (2002)
Rubus saxatilis	10.930	This study
Rumex acetosa	1.286	This study
Rumex acetosella	0.4	Grime et al. (1981)
Rumex crispus	1.33	Grime et al. (1981)
Rumex longifolius	1.88	Milberg, Andersson & Thompson (2000)
Scrophularia nodosa	0.08	Grime et al. (1981)
Sedum acre	0.03	Grime et al. (1981)
Sedum telephium	0.05	Jakobsson & Eriksson (2002)
Silene dioica	0.67	Jakobsson & Eriksson (2002)
Silene nutans	0.35	Eriksson & Eriksson (1997)
Solidago virgaurea	0.740	This study
Stachys sylvatica	1.67	Fröborg (2001)
Stellaria graminea	0.273	Eriksson & Jakobsson (1998)
Stellaria holostea	3.70	Salisbury (1942)
Stellaria longifolia	0.1	BiolFlor Datenbank
Stellaria nemorum	0.34	Fröborg (2001)

Trientalis europaea	0.559	This study
Trifolium medium	2.77	Jakobsson & Eriksson (2002)
Trifolium pratense	2.334	This study
Trifolium repens	0.228	Eriksson & Jakobsson (1998)
Urtica dioica	0.16	Jakobsson & Eriksson (2002)
Vaccinium myrtillus	0.201	This study
Vaccinium vitis-idaea	0.236	This study
Valeriana officinalis ssp. officinalis	0.95	Grime et al. (1981)
Valeriana sambucifolia	1.077	This study
Veronica chamaedrys	0.26	Fröborg (2001)
Veronica officinalis	0.135	Eriksson & Jakobsson (1998)
Vicia cracca	14.29	Grime et al. (1981)
Vicia hirsuta	2.19	Grime et al. (1981)
Vicia sepium	16.7	Fröborg (2001)
Vicia sylvatica	16.52	Fröborg (2001)
Vicia tetrasperma	3.6	Müller-Schneider (1986)
Viola canina	0.905	Eriksson & Jakobsson (1998)
Viola canina ssp. montana	0.905	Eriksson & Jakobsson (1998)
Viola mirabilis	1.65	Jakobsson & Eriksson (2002)
Viola palustris	0.63	Grime et al. (1981)
Viola riviniana	1.354	This study
Viola tricolor	0.503	Eriksson & Jakobsson (1998)