

Seed mass versus seedling performance in Scots pine: a maternally dependent trait

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SUMMARY

It is generally accepted that larger seeds give rise to seedlings with better performance. On the other hand, the size that a seed reaches is genetically determined by at least two different traits; the genetic variability of the developing embryo and the genetic variability of the maternal plant. Thus, the relative contributions of these two traits affect seedling performance by influencing seed size. In this paper, I investigate the effect of seed size on seedling performance in the Scots pine (*Pinus sylvestris*). From eight maternal plants, 50 seeds were planted in each of two soil types (800 seeds in total), and seedling performance was monitored for 1 yr. Seed mass proved to be highly constant within maternal plants. Soil type influenced emergence and survival; however, the effect of soil type differed depending on maternal origin. Seed mass was positively correlated with seedling emergence, although this relationship was not found for seedling survival or date of emergence. The initial growth of the shoot was also positively correlated with seed mass. However, after one growing season, seed mass had no effect on seedling performance, which depended exclusively on maternal origin. Nevertheless, the mean mass of seeds produced by plants was positively correlated with mean values of growth parameters. Thus, first-year seedling performance seems to be a maternal trait indirectly associated with seed size.

Key words: maternal effects, *Pinus sylvestris* (Scots pine), seed mass, seedling performance.

INTRODUCTION

The effects of intraspecific seed mass variation on seedling germination and performance reported in the literature are variable. In general, it is accepted that, relative to large seeds, small seeds usually have reduced emergence (Zimmerman & Weis, 1983; Weller, 1985; Winn, 1988; Tripathi & Khan, 1990; Hendrix & Trapp, 1992; Rice *et al.*, 1993; Prinzie & Chmielewski, 1994), higher mortality (Schaal, 1980; Tripathi & Khan, 1990; Bonfil, 1998) and lower seedling growth (Wulff, 1986a; Hendrix *et al.*, 1991; Dawson & Ehleringer, 1991; Baker *et al.*, 1994; Moegenburg, 1996; Weiner *et al.*, 1997; Vaughton & Ramsey, 1998; Bonfil 1998). However, other studies show no relationship between seed size and seedling performance in some species, as described by Cipollini & Stiles (1991), Rice *et al.* (1993) and Vaughton & Ramsey (1998) for seed germination; Hendrix & Trapp (1992) for seedling survival; Dolan (1984) and Marshall (1986) for seedling growth.

These contradictory results might be due in part to the species studied and also to the experimental conditions used. For example, the effect of seed size might change markedly if experiments are performed in a glasshouse or under field conditions (Stanton,

1984; Marshall, 1986). Similarly, in natural populations the consequences of variation in seed size depend on the environmental conditions undergone by the progeny (such as competitive environment or water stress), with performance differences between large and small seeds generally being greatest under adverse conditions and lower or even null in more favourable environments (Dolan, 1984; Gross, 1984; Wulff 1986a,b; Gross & Smith, 1991).

Some additional conflicting results might arise from the fact that many experiments have been performed with mixed groups of genotypes, confusing sources of genetic variation attributable to different traits that might determine seed size. Seed mass can be determined genetically by different traits related to the embryo, the pollinating plant and the seed-bearing plant (Roach & Wulff, 1987; Nakamura & Stanton, 1989), although these can be summarized in two different traits (Antonovics & Schmitt, 1986; Mazer, 1987; Silvertown & Lovett-Doust, 1993). First, the genotype of a developing embryo can influence the size that the seed attains. Second, maternal plants can control the amount of resources invested per seed. Provided that higher reserves (and hence higher mass) is of advantage to developing seedlings, a size–number conflict be-

tween the maternal plant and the offspring can develop (Casper, 1990; Silvertown & Lovett-Doust, 1993): whereas for an individual offspring it might be advantageous to germinate from a seed as large as possible, the maternal genotype might favour the partitioning of resources between a higher number of smaller seeds. Thus, the relative contribution of maternal or embryonic components in determining the size of the seeds of a particular species can influence the performance of seedlings.

As a consequence, if experiments pool seeds, the results could be influenced by the particular set of seeds used. For example, let us consider a given population having (1) minor differences in seed mass within the maternal plants, attributable to a lack of genetic embryonic effect; and (2) clear differences in seed mass between maternal plants, attributable to genetic maternal effects. Let us also assume that larger seeds give rise to larger seedlings. If from this population we collect seeds mostly from maternal plants that produce similar-sized seeds, we might conclude that seed mass is not related to seedling performance. However, if we collect seeds mostly from plants that differ substantially in the size of seeds produced, we might positively correlate seed mass and plant performance, a relationship that in reality was due to maternal plants. Similarly, if we perceive a positive relationship, we might not know whether to attribute it to a maternal effect on seed mass or an effect exerted by the embryo on seed size. Thus, a knowledge of maternal origin is crucial to an accurate interpretation of the results.

Here I investigate the effect of seed mass on seedling emergence and performance in autochthonous populations of Scots pine in southern Spain. As seedling performance can depend on environmental conditions, I conducted experiments in two types of soil found in the distribution area of the species. In addition, the maternal origin of the seeds was considered in relation to seedling performance.

MATERIALS AND METHODS

Species and study area

Seeds used in this study came from a natural, autochthonous population of Scots pine (*Pinus sylvestris* L.) from the Sierra Nevada (locality of Trevenque, 37° 10' 30" N, 3° 27' 10" W), a mountain range in southeast Spain formed by a central siliceous core surrounded in part by a calcareous belt (Molero *et al.*, 1992). In the locality of Trevenque, Scots pine reaches its southernmost distribution area (Boratynski, 1991) and is considered to be the variety *nevadensis* Christ of the species. At this site, Scots pines grow almost exclusively on calcareous soil at an altitude of 1600–2000 m above sea level, forming the treeline. However, Scots pine reforestation in the siliceous core at the same altitude is common, and

Table 1. Analysis of the soils used in the experiments

	Siliceous soil	Calcareous soil
Clay (%)	12.6	22.7
Loam (%)	33.2	41.4
Sand (%)	53.8	35.4
Apparent density (g cm ⁻³)	1.8	1.9
Assimilable phosphorus (ppm)	6	6
Assimilable potassium (ppm)	4	8
Total nitrogen (%)	0.14	0.18
Oxidizable organic material	2.3	3.1
pH (1:2.5)	7.3	8.0
Cation-exchange capacity (cmol (+) kg ⁻¹)	11.7	12.4

The samples were taken after thoroughly mixing each type of soil, and were analysed in the Laboratorio Agroalimentario de la Junta de Andalucía, Atarfe (Granada province).

such saplings have normal growth (J. Castro, unpublished).

In this area, Scots pine pollination occurs in late May, and seed maturation lasts for 21 months, until December of the second year. An extreme drought persisted in the region from 1993 to 1995, ending on November 1995; thus, seeds collected in January 1996 were formed during conditions of extreme water shortage (528 mm from cone pollination to seed maturation; climatic data from a meteorological station from La Cortijuela Botanical Garden, located in the study area). By contrast, precipitation was unusually high during 1996 and 1997; seeds collected in January 1998 had therefore formed under conditions of water abundance (2093 mm from cone pollination to seed maturation).

Experimental design

In January 1996, cones were collected from eight arbitrarily chosen trees, all having a healthy, normal aspect, and 100 randomly chosen filled seeds were weighed from each tree. These seeds were used in the sowing experiment that year (see later). In 1998, cones were again collected from the same trees and 30 randomly chosen filled seeds were weighed to determine whether the pattern of seed-mass variation remained constant between years.

Sowing experiments began on 26 March 1996. One hundred seeds were sown individually, outdoors, on a private farm in Granada (660 m above sea level), using 40-cell seedling trays of 200 cm³ (12 cm in height) that were placed in two separate but adjacent small concrete ponds located under full exposure to the sun. Two types of soil were used, a calcareous soil collected from the natural area of distribution of the species and a siliceous soil from a nearby area of Sierra Nevada reforested with Scots pines. The two soil types differed mainly in their texture (Table 1), the calcareous soil having a higher

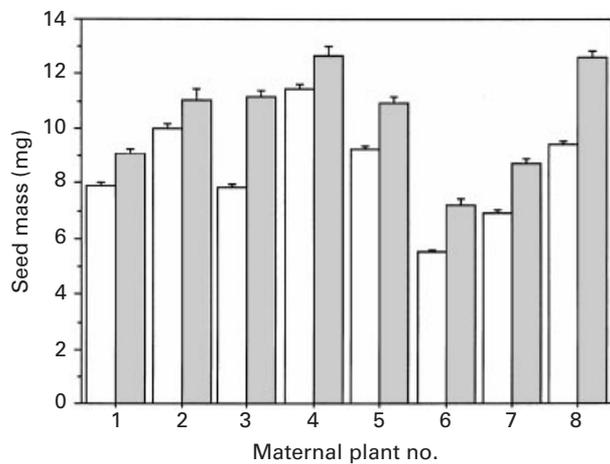


Fig. 1. Masses (mean \pm SE) of seeds collected from the maternal plants used in the study. For each year (open bars, 1996; grey bars, 1998), there were between-tree differences in seed mass ($F = 231.01$, $df = 7$, 793; $P < 0.0001$, $n = 100$ for 1996; $F = 47.41$, $df = 7$, 232; $P < 0.0001$, $n = 30$ for 1997). By contrast, seed mass was consistently higher in 1998 for all maternal plants (one-way ANOVAs, treatment (year) $df = 1$, error df from 127 to 130, F values from 7.05 to 205.63, $P < 0.01$ in all cases).

proportion of clay, which seemed to be responsible for the higher compaction of this soil during the experiment (J. Castro, unpublished). From each mother-tree 50 seeds were distributed at random within each soil type and were sown at a depth of 1 cm. Watering was done daily at sundown during the germination period (and every 2–3 d after that) by flooding the trays with 2–3 cm of water until soil saturation. Soil moisture at saturation was $23.6 \pm 0.4\%$ and $24.1 \pm 0.4\%$ for calcareous and siliceous soils, respectively (gravimetric measurement), with no statistical differences between them (one-way ANOVA, $F = 0.757$, $df = 1$, 18; $P > 0.05$, angular transformation of data). The mean maximum and minimum daily temperatures during the first 8 wk of the experiment were 22.0 ± 0.6 and 11.4 ± 0.4 , respectively (mean \pm SE, $n = 38$ d).

Simultaneously, at the beginning of the sowing experiment, the viability of seeds was checked in a growth chamber. For this, seeds were placed in glass Petri dishes 9 cm in diameter containing paper-disk filters resting on a single layer of 5 mm glass beads, all materials having previously been sterilized. At the beginning of the experiments, 15 ml of sterilized distilled water was added to each dish, and moisture was replenished as needed. Each Petri dish contained 30 seeds, with seven replicates per plant (except for one case with four dishes, owing to a lack of seeds). Germination, identified as visible radicle protrusion, was recorded daily for 2 wk.

Seedling emergence outdoors was monitored daily. On 9 June (75 d after sowing), I measured the hypocotyl and stem length of surviving seedlings, and those from siliceous soil (112 in total) were transplanted to 1200 cm³ pots with a mix of original

soil and river sand (2:1). Seedlings from the calcareous soil were not transplanted owing to the low survival rate. Pots, randomly distributed in a completely open environment on agricultural land, were buried to soil level and irrigated when necessary. In January 1997, after one growing season, seedlings were uprooted and leader shoot length (from root collar), leaf area per plant (using a Li-Cor 3000 portable area meter; Li-Cor Inc., Lincoln, NE, USA), aboveground (stem+leaves) dry mass and root dry mass (80°C, 48 h) were recorded. Only four seedlings died during this period.

Data analysis

Analyses of seed mass within and among trees were performed with ANOVAs. The percentage of germination in the growth chamber was analysed with the Kruskal–Wallis test. For each maternal plant, differences in germination and in survival rates were analysed for the two soil types with the χ^2 test. The effect of seed size on emergence and survival was analysed for each maternal plant in each type of soil by using a logistic regression (all seeds used in the analysis of emergence; only seeds that emerged were used in the analysis of survival). Because seed size differed considerably between trees (see the Results section), logistic regressions for individual plants might have failed to detect trends that otherwise might appear on pooling all the seeds. An additional logistic regression using all mother plants pooled was therefore performed for each type of soil in which the independent variable was the residuals from an ANOVA of maternal plant and seed mass (all seeds were used in the analysis of emergence, whereas only seeds that emerged were used in the analysis of survival). This procedure was followed to ensure the independence of seeds with a common origin, performing the logistic regression with the part of variability explained by the seed mass. The relation between seed mass and date of emergence was similarly analysed for all maternal plants pooled by a regression in which the independent variable was the residuals from a previous analysis of variance between the maternal plant and seed mass (using only seeds that emerged), and was also performed independently for each type of soil.

Hypocotyl and shoot growth 75 d after sowing were analysed with analyses of covariance (ANCOVAs), with seed mass as a covariate. However, as seedling survival in the calcareous soil was low for some maternal plants, two additional steps were followed. First, I performed a two-way ANCOVA to test simultaneously the effect of maternal plant and soil type with four trees having adequate sample sizes. Second, to increase the number of maternal plants, I performed a one-way ANCOVA with all maternal plants but only for siliceous soil. The analysis of growth parameters

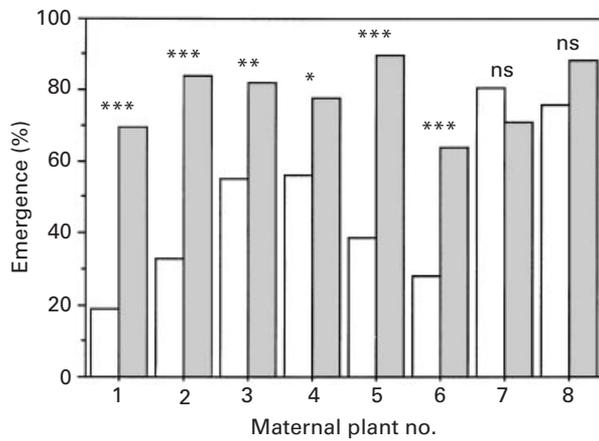


Fig. 2. Percentage of seedling emergence in calcareous (open bars) and siliceous soils (grey bars). Differences within maternal plants were analysed with the χ^2 test (χ^2 from 1.35 to 28.41, df = 1). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

after one growing season for seedlings transplanted to siliceous soil was performed by using a one-way ANCOVA. In addition, the correlation between mean size of seeds produced by maternal plants and mean values of growth parameters was analysed by using the Spearman rank correlation coefficient.

In parametric analyses, the maternal plant was considered to be a random factor and soil type a fixed factor; data were transformed (angular transformation for percentages, logarithmic transformation in the other variables) to reach normality and homoscedasticity (Zar, 1996). Analyses, performed with the computer software JMP 3.1.5 (SAS Institute, 1995), were initially run with full models; however, when interactions proved non-significant, they were pooled with the error df to improve the model (Zar, 1996). Type III sum of squares were used owing to the unbalanced nature of the data (Shaw & Mitchell-Olds, 1993). Throughout the paper, values are means \pm SE.

RESULTS

Seed mass and growth-chamber germination

Mean seed mass differed between trees, ranging from 5.50 ± 0.08 to 11.46 ± 0.14 mg in 1996 and from 7.22 ± 0.20 to 12.64 ± 0.37 mg in 1998; seed mass was heavier in 1998 for all maternal plants, with no mean rank change between maternal plants (Fig. 1). However, seed mass was quite constant within each maternal plant, with a coefficient of variation that ranged from 12% to 17% in 1996 and from 11% to 21% in 1998; extreme values never exceeded a twofold difference. Viability of seeds was very high; germination in the growth chamber ranged from $92.8 \pm 1.1\%$ to $99.0 \pm 0.6\%$. Although there were between-tree differences in germination percentages (Kruskal–Wallis test, $H = 23.80$, df = 7, $P = 0.0012$), this minor difference is likely to have inconsequential effects on seed emergence outdoors, and is therefore not considered further.

Seedling emergence and mortality

Seeds emerged between 13 and 26 d after sowing. A greater proportion of seeds (78.32%) emerged in the siliceous soil than in the calcareous soil (48.86% ; $\chi^2 = 75.25$, df = 1, $P < 0.0001$), although this trend was not consistent for all genotypes (Fig. 2). Thus, seed emergence was higher in the siliceous soil for trees 1–6, but there were no statistical differences for trees 7 and 8. Logistic regressions for each plant showed that seed mass was positively related to seedling emergence only for three trees in the calcareous soil and one in the siliceous soil; the positive relationship persisted when all maternal plants were pooled (Table 2), although in any case the proportion of variance explained by seed mass was very low (r^2 from 0.02 to 0.12; see Table 2). The mean germination rate was similar for both types of

Table 2. Results of the logistic regressions performed to analyse the relation between seed mass and emergence in each type of soil

Plant	Calcareous soil				Siliceous soil			
	SE	χ^2	P	r^2	SE	χ^2	P	t^2
1	488.27	3.40	0.0652		253.15	0.78	0.3757	
2	188.94	4.18	0.0409	0.06	321.68	5.19	0.0227	0.12
3	327.22	6.13	0.0133	0.09	352.49	0.06	0.8105	
4	252.31	5.13	0.0235	0.07	240.00	0.59	0.4422	
5	260.41	0.23	0.6335		401.30	2.24	0.1348	
6	369.58	1.36	0.2432		418.39	0.46	0.4954	
7	310.65	0.13	0.7135		334.33	2.61	0.1065	
8	259.83	1.32	0.2502		326.36	2.68	0.1015	
All pooled	1.62	11.50	0.0007	0.02	1.90	7.10	0.0077	0.02



Analyses for all maternal plants pooled were performed by using residuals of seed mass as the independent variable. The coefficient of determination, r^2 , is shown only for significant analyses. Each test has 1 df. Sample sizes for individual plants range from 48 to 50.

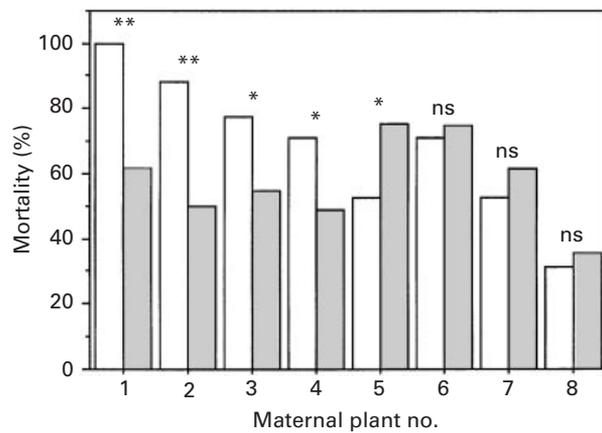


Fig. 3. Percentage of seedling mortality at 75 d after being sown in calcareous (open bars) and siliceous soils (grey bars). Differences within maternal plants were analysed with the χ^2 test (χ^2 from 0.06 to 7.44, $df = 1$). *, $P < 0.1$; **, $P < 0.05$.

soil (16.57 ± 0.12 d for siliceous soil, 17.14 ± 0.16 d for calcareous soil); no relationship was found between seed mass and date of emergence for either

calcareous soil ($F = 0.0490$, $df = 1$, 188; $P > 0.05$) or siliceous ($F = 0.7157$, $df = 1$, 308; $P > 0.05$).

Overall, seedling mortality at 75 d was similar between soil types (61.14% in calcareous vs 57.23 in siliceous, $\chi^2 = 0.75$, $df = 1$, $P = 0.3845$). However, there were significant differences within maternal plants for trees 1 and 2 ($P < 0.05$) and trees 3, 4 and 5 ($P < 0.1$; see Fig. 3); in those cases, seedling mortality was generally higher in calcareous soil, although this trend was reversed in maternal plant 5 (Fig. 3). In general, seed size was not related to seedling survival except for one tree in siliceous soil (maternal plant 5: $\chi^2 = 4.65$, $df = 1$, $P = 0.0311$, $r^2 = 0.09$; logistic regression); this relationship did not appear when all seeds were pooled (results not shown).

Early growth (75 d after sowing)

The two-way ANCOVAs showed that hypocotyl and stem length were affected by all of the parameters considered, namely maternal plant, soil type and seed mass (Table 3). However, hypocotyl length was

Table 3. Summary of the two-way ANCOVAs on hypocotyl and stem length at 75 d after sowing

	Source	df	Type III SS	F	P
Hypocotyl length ($R^2 = 0.09$)	Plant	3	0.11	3.23	0.0244
	Soil	1	0.10	8.72	0.0037
	Mass	1	0.07	6.03	0.0154
	Error	129	1.41		
Stem length ($R^2 = 0.09$)	Plant	3	0.10	3.39	0.0200
	Soil	1	0.04	3.73	0.0555
	Mass	1	0.08	7.99	0.0054
	Error	129	1.27		

R^2 is the variability of the response variable explained by the whole model; SS, sum of squares. Only four maternal plants were used (4, 5, 7 and 8). The sample size ranged from 8 to 29 seedlings per maternal plant. Non-significant interaction terms have been pooled in the Error SS.

Table 4. Summary of the one-way ANCOVAs on hypocotyl and stem length at 75 d after sowing for plants growing in siliceous soil (all maternal plants used)

	Source	df	Type III SS	F	P
Hypocotyl length ($R^2 = 0.10$)	Plant	7	0.16	2.07	0.0514
	Mass	1	0.03	3.18	0.0768
	Error	126	1.35		
Stem length ($R^2 = 0.29$)	Plant	7	0.14	1.68	0.1431
	Mass	1	0.15	16.17	0.0001
	Plant \times mass	7	0.15	2.25	0.0349
	Error	116	1.09		

R^2 is the variability of the response variable explained by the whole model; SS, sum of squares. The samples size ranged from 8 to 29 seedlings per maternal plant. Non-significant interaction terms have been pooled in the Error SS.

Table 5. Summary of the one-way ANCOVAs on growth parameters after one growing season for plants grown in siliceous soil (all maternal plants used)

	Source	df	Type III SS	F	P
Stem length ($R^2 = 0.28$)	Plant	7	0.15	3.6802	0.0014
	Mass	1	0.01	1.0233	0.3142
	Error	99	0.58		
Leaf area ($R^2 = 0.24$)	Plant	7	0.64	3.09	0.0055
	Mass	1	0.03	0.99	0.3224
	Error	97	2.85		
Aboveground mass ($R^2 = 0.24$)	Plant	7	0.33	2.27	0.0348
	Mass	1	0.03	1.42	0.2355
	Error	97	2.02		
Root mass ($R^2 = 0.18$)	Plant	7	0.29	2.41	0.0254
	Mass	1	0.01	0.41	0.5213
	Error	99	1.69		

R^2 is the variability of the response variable explained by the whole model; SS, sum of squares. The sample size ranged from 8 to 23 seedlings per maternal plant. Non-significant interaction terms have been pooled in the Error SS.

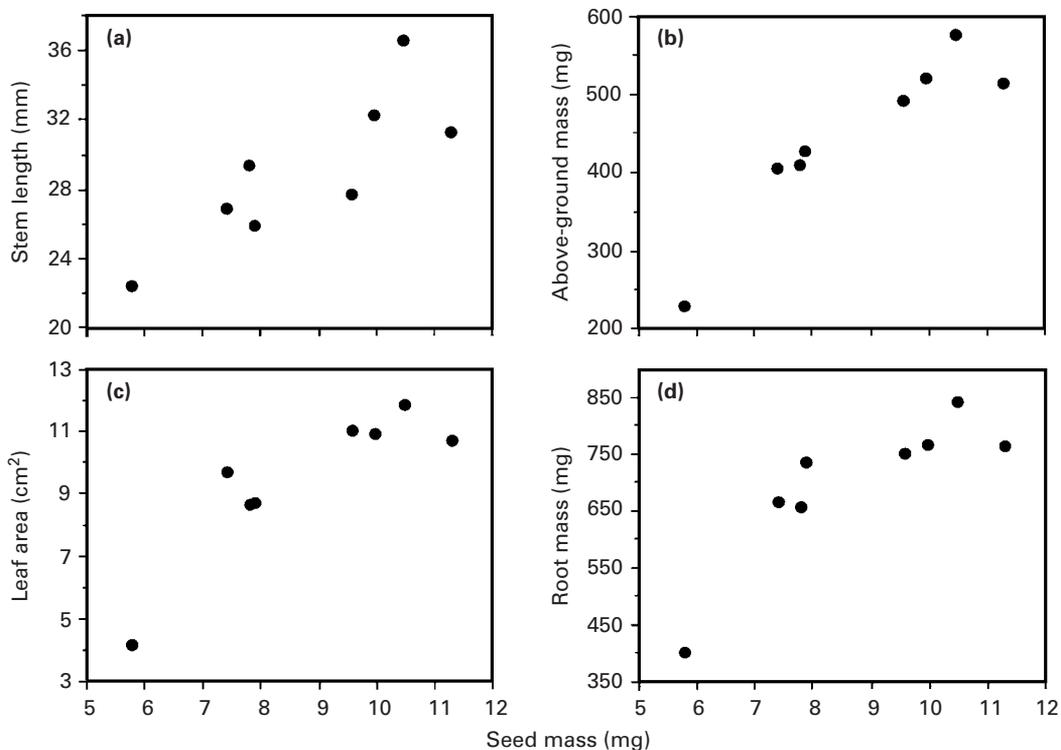


Fig. 4. Relationship between mean seed mass per maternal plant and mean values of growth parameters of seedlings after one growing season. (a) Stem length ($r_s = 0.81$; $P = 0.0322$); (b) above-ground mass ($r_s = 0.93$; $P = 0.0140$); (c) leaf area ($r_s = 0.76$; $P = 0.0438$); (d) root mass ($r_s = 0.90$; $P = 0.0167$).

influenced mainly by soil type (Table 3; 9.28 ± 0.31 mm in calcareous soil, 10.42 ± 0.30 mm in siliceous soil); in addition, neither maternal plant nor seed mass had a significant effect when considering only seedlings from the siliceous soil (Table 4). On the contrary, stem length (12.32 ± 0.01 mm) was affected mainly by seed mass, as determined either by the two-way or the one-way ANCOVA (Tables 3, 4).

Growth at the end of the first growing season

Factors affecting seedling performance changed with time. Thus, after one growing season, seed size had no significant effect for either growth parameter measured, which were influenced exclusively by the identity of the maternal plant (Table 5). By contrast, mean values of seed mass per maternal plant were

positively correlated with mean growth values for all of the parameters measured (Fig. 4).

DISCUSSION

Seed emergence

Seed emergence in *Pinus sylvestris nevadensis* proved to be related to seed mass, as revealed both by the analysis considering all maternal plants pooled as well as by the analysis considering plants individually (Table 2). This latter analysis revealed that the relationship holds only for some maternal plants and was more common in the calcareous soil (three of eight plants) than in the siliceous soil (only in one plant, see Table 2). This must have been due to the nature of the soils. As stated previously, the calcareous soil had a higher clay content, which might have translated to the higher compaction observed during the course of the experiment, as well as other possible related effects, such as more anoxic conditions. This situation might have discouraged seedling emergence and therefore might be regarded as a more stressful environment for emerging seedlings. In fact, under higher environmental stress, larger seed size might favour germination or development even when any relationship is absent under less extreme conditions (Dolan, 1984; Gross, 1984; Wulff, 1986a,b; Gross & Smith, 1991; Housard & Escarré, 1991). In any case, the proportion of the variance in seed emergence explained by seed mass was very low (Table 2, $r^2 < 0.15$ in all cases), indicating that emergence was considerably dependent on other factors, presumably genetic variability. This could be especially relevant for plant species that do not form a permanent seed bank (which is true of Scots pine), as genetic variability cannot accumulate with consecutive crops (McCue & Holtsford, 1998).

Seedling emergence was not only influenced by seed size and soil type but was also a maternally dependent trait. Thus, the seeds of some maternal plants emerged preferentially on siliceous soil, whereas seed emergence from other plants showed no differences between soils (Fig. 2). Furthermore, patterns of seedling mortality between soil types were even more affected by maternal origin, with maternal plants 6–8 showing no differences between soils, plants 1 to 4 registering higher seedling mortality in calcareous soil, and plant 5, by contrast, registering higher mortality in siliceous soil (Fig. 3). The fact that patterns of phenotypic response in seed emergence or survival varied between families depending on environmental conditions (i.e. soil type) suggests the possibility of heritable genetic variation for seedling emergence or survival. This might be an important adaptive response for seedlings in heterogeneous environments, allowing seeds to explore a wider range of conditions.

Seedling growth

Hypocotyl length was influenced mainly by soil type (Tables 3, 4) and was shorter in calcareous soil, probably owing to higher soil compaction. This implies that a higher proportion of seed reserves is devoted to overcome physical resistance to the detriment of hypocotyl elongation. In addition, as in most studies (e.g. Weller, 1985; Wulff, 1986b; Tripathi & Khan, 1990; Moegenburg, 1996; Bonfil, 1998; see also the references cited in the Introduction section), a positive relation was found between seed mass and early growth, measured in this case as stem length (Tables 3, 4). However, the effect of seed mass on growth parameters changed with time, and after one growing season the ANCOVAs showed that seedling performance was influenced only by maternal origin (Table 5), whereas within-tree variation in seed mass had no effect.

Several features suggest that seed mass in Scots pine is strongly influenced by the genetic constitution of the maternal parent. First, there was low within-tree variation in seed mass that persisted in different years; if this were a trait more affected by the embryo genotype, we could expect more variation in seed size within maternal plants, as parent donors should be highly diverse. Second, the pattern of variation within maternal plants was constant between years; that is, all maternal plants increased their mean seed mass in a similar way in 1998 (Fig. 1). This increase coincided with a period of higher rainfall and is a common phenotypic effect under circumstances of higher nutrient levels or water availability (Marshall *et al.*, 1986; Roach & Wulff, 1987; Aarsen & Burton, 1990; Wulff & Bazzaz, 1992). In fact, experiments have generally failed to detect consistent effects of embryo genotype on seed size, suggesting that the embryo genotype is relatively unimportant in comparison with the genotype of the maternal parent in determining the seed size (Antonovics & Schmitt, 1986; Mazer, 1987; Nakamura & Stanton, 1989; Mojonmier, 1998). In any case, whatever the genetic control or other unknown phenotypic effect, seed mass is clearly dependent on maternal origin. By contrast, mean seed size per maternal plant was positively correlated with the mean values of growth parameters (Fig. 4), whereas within tree variation in seed size had no effect (Table 5). Thus, seedling performance in Scots pine after one growing season is dependent on maternal origin, although its effect is concomitantly associated with seed size.

These results contrast, at least initially, with those reported by Reich *et al.* (1994), who found a positive relationship between seed mass and seedling biomass in the Scots pine over several years. These authors, however, pooled the seeds in four size classes, because they were not investigating maternal effects. Nevertheless, by separating the seeds into four size

categories, Reich *et al.* were in reality probably dividing the seeds according to the maternal tree, which is related to seedling performance via seed size, as indicated by the present results. The effect on seedling performance that these authors attribute to seed size would therefore most probably be due to the maternal origin, and both their results and those reported in the present study could have the same basis.

In conclusion, seed size has little effect during early development in Scots pine (seedling emergence and early growth) but, after one growing season, seedling performance depends exclusively on maternal plants, although the effect is related to seed size. The result that larger seeds give rise to larger seedlings could be also obtained with the use of pooled seeds. This is in fact the case and all growth parameters measured after one growing season are related to seed mass when seeds from all maternal plants are pooled (R^2 from 0.11 to 0.18, $df = 1, 106$; F values from 13.70 to 24.26, $P \leq 0.0003$ in all cases). However, knowledge of the source of variation is crucial to a correct interpretation of the results, and reports such as the present paper suggest that the evolution of seed size might be driven by selection on maternal plants.

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