Evidence that the negative relationship between seed mass and relative growth rate is not physiological but linked to species identity: a within-family analysis of Scots pine

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Summary Seed mass and relative growth rate (RGR) are important determinants of early seedling growth, and hence seedling establishment. Although a positive interspecific relationship between seed mass and seedling dry mass is well established, much less is known about the relationships among seed mass, seedling mass and RGR within species. We examined relationships among seed mass, seedling mass and RGR within and among maternal plant lines of Scots pine (*Pinus sylvestris* L.). To assess the effects of seed mass and maternal origin on RGR, individual seeds from two seed crops (years 2004 and 2005) of ten maternal plants growing under nursery conditions were weighed and then germinated. Seed mass was strongly determined by maternal plant, and seedling mass was largely determined by seed mass, with a positive correlation between these variables both across and within maternal plants. In contrast, RGR was weakly related to seed mass, with no consistent pattern in the sign of the relationship. It is well known that species differ in RGR and that RGR is related to seed mass across species. Lack of consistent evidence for this relationship within maternal lines, and for Scots pine overall, suggests that the relationship is not directly causal, but reflects consistent evolutionary covariation in these two physiologically independent traits.

Keywords: maternal effects, Pinus sylvestris, seedling growth.

Introduction

The relative performance of individual plants during the early stages of establishment has paramount consequences for seedling survival, growth and fitness (Silvertown and Lovett-Doust 1993). Two important determinants of initial seedling growth are seed mass and seedling relative growth rate (RGR). With few exceptions, seed mass is associated with seedling size and vigor, both across species (Long and Jones 1996, Milberg et al. 1998, Walters and Reich 2000) and within species (Reich et al. 1994, Castro 1999, Vaughton and Ramsey 2001, Halpern

2005), presumably reflecting the amount of reserves available for early seedling growth (Castro et al. 2006). Nevertheless, a negative relationship between seed mass and RGR has been widely reported, in particular across species (Reich et al. 1998, 2003, Wright and Westoby 1999, Grotkopp et al. 2002, Poorter and Rose 2005). A negative seed mass–RGR relationship may be a determinant of plant demography and community composition, because it could allow small-seeded species to compensate for their lower seed reserves and thereby overcome the initial advantage conferred to species with greater seed masses (Norgren 1996, Paz and Martínez-Ramos 2003). This explanation could apply also within species, so that individuals derived from small seeds could compensate for their small seed reserves by a high RGR (Zimmerman and Weis 1983).

The relationship between seed mass and RGR within species has rarely been analyzed, however. The few within-species reports available offer contrasting results, with either a negative correlation between seed mass and RGR (Meyer and Carlson 2001, Paz and Martínez-Ramos 2003), a lack of correlation (Wulff 1986, Choe et al. 1988, Reich et al. 1994, Tamet et al. 1996) or a positive correlation (Meerts and Garnier 1996), thus contradicting general trends in cross-species comparisons. Moreover, both across- and within-species comparisons are usually based on mean values of bulked seeds, thus masking the detection of traits at the individual seedling level (Castro et al. 2006).

We have analyzed the relationship between seed mass and RGR and their effects on early seedling growth in Scots pine (*Pinus sylvestris* L.). To reduce genetic differences that might affect the relationship between these parameters (Silvertown et al. 1997), we performed the analysis on a single species. Our experimental design—which involved studying seeds from ten maternal plants, with individual seeds as replicates—provided the opportunity to assess the effect of seed mass on individual seedling RGR by controlling for the effect exerted by maternal plants, which may be a source of variation (Castro et al. 2006).

Furthermore, we replicated the experiment with seed crops gathered in different years. We sought answers to three questions. What is the effect of seed mass on early seedling biomass and RGR? What is the effect of maternal origin on early seedling biomass and RGR? Do seedling growth and RGR vary among seed crops? To answer the first question, we determined the relative contribution of seed mass and RGR on seedling growth. Answers to the other questions were obtained by examining if seedling growth and RGR are invariant characters in the population or vary among maternal plants.

Materials and methods

Experimental set up

Seeds were collected from ten maternal trees in a natural population of Scots pine growing in the Sierra Nevada, Granada, SE Spain (37°10′30″ N, 3°27′10″ W, 1800 m a.s.l.; see Castro et al. 2005 for details). Seeds were collected at the time of cone maturation (January) in 2004 and 2005, extracted from the cones, and stored in paper bags under room conditions until the start of the experiment. Maternal trees were separated by at least 150 m and were open pollinated; thus seeds from each maternal tree are half-sibs (considered a family). Maternal trees were chosen from a pool of trees randomly marked several years previously, and were selected to include the range of among-tree variation in seed mass found in the population. There was no correlation between trunk diameter (an estimate of tree age) and mean seed mass per maternal tree for either year, indicating that there was no effect of tree age on seed mass.

For each year and maternal tree (hereafter referred to as treatments), we weighed (± 0.1 mg) 120 fully formed seeds that were individually identified. On May 16, 2005, the weighed seeds were germinated at room temperature and in ambient light on beds of filter paper moistened with distilled water. Germination of Scots pine seeds under laboratory conditions is rapid, being nearly completed in 1 week and peaking at 4–6 days (Castro et al. 2005). By using 120 seeds per maternal plant from each seed crop, we ensured that at least 44 seeds germinated on a single day. Germination (defined as visible radicle protrusion) was recorded daily for 10 days and ranged from 96.2 to 100% depending on maternal tree and year. Forty-four seeds that germinated on the same day (day 4 or 5, depending on the treatment) were transplanted to individual cylinders (2.5 cm diameter and about 5.5 cm in length) of Jiffy-7 sphagnum peat with a pH of about 5.3 (Jiffy Pots, Copenhagen, Denmark). Mean (± SE) nutrient concentration of the peat cylinders is 0.78 ± 0.03% for N and 0.14 ± 0.02% for P (n = 3). The peat cylinders, which were held in plastic trays (with drainage holes), were arranged in a completely randomized design and were watered once per day to ensure homogeneity in water availability. Once placed in the peat cylinders, the seedlings were allowed to establish for 4 days under room conditions and then placed outdoors in full sunlight at the Granada University campus. All live seedlings were harvested 19 or 20 days after transfer to the peat cylinders, the period of

likely maximum RGR in *Pinus* species (Grotkopp et al. 2002). Seedlings were gently washed free of residual peat and their dry mass was estimated after oven-drying for 48 h at 70 °C.

Of the 44 seedlings transplanted to the peat cylinders per treatment, the number of live seedlings at the end of the 19–20-day growth period ranged from 18 to 37, for a total of 620 seedlings harvested. The survival of seedlings was unrelated to seed mass in 19 of the 20 combinations (logistic regression, data not shown). Only in seedlings from seed crop year 2005 from maternal plant 27 was survival related to seed mass; mean seed mass of seedlings that died being slightly higher (7.72 ± 0.16 mg) than mean seed mass of seedlings that survived (7.21 ± 0.18 mg).

Data analysis

We calculated RGR as $(\ln W_2 - \ln W_1)/(t_2 - t_1)$, where W_2 is total dry mass of the seedling at the end of the experiment, W_1 is mass of the seed and $(t_2 - t_1)$ is 19 or 20 days, depending on the maternal plant × year combination. Differences in seed mass among maternal plants were tested by one-way analysis of variance (ANOVA). Relationships among seed mass, seedling mass and RGR were explored by two complementary approaches. First, differences in seedling mass and RGR among maternal plants were analyzed for each year by one-way analysis of covariance (ANCOVA), with maternal plant as the independent factor and seed mass as a covariate. Second, the relationships among seed mass, RGR and seedling biomass within each maternal plant were analyzed by linear regression. Among the 620 surviving seedlings at the end of the experiment, 12 had a lower mass than the seed from which they originated, and 11 showed an increase in mass from seed to seedling of less than 10% of seed mass, which resulted in negative or low values of RGR and suggests that seedlings were dying probably because of transplant shock. These 23 seedlings were eliminated from the analyses, resulting in 17 to 37 seedlings per treatment (Table 1). The masses of seeds from which these seedlings were derived followed a normal distribution in all cases (Shapiro-Wilk test). All values reported are mean values ±1 standard error (SE).

Results and discussion

Seed mass determination

Mean seed mass per maternal plant ranged from 7.2 to 14.0 mg, with little variation within a maternal plant (Table 1), and differed among maternal plants for both the 2004 crop ($F_{9,309} = 64.10$, $P < 0.0001$) and the 2005 crop ($F_{9,273} = 83.29$, $P < 0.0001$). Seed mass was stable across crop years within maternal plants (Table 1), as demonstrated by the significant positive linear correlation between 2004 and 2005 crops in mean seed mass per maternal plant ($r = 0.92$, $P = 0.0002$). These results indicate that seed mass is strongly determined by maternal plant (cf. Castro 1999, Debain et al. 2003), suggesting that maternal genotype is more important than embryo or parental genotype in determining seed mass (Perry 1976).

Table 1. Summary of biometric parameters for Scots pine (*Pinus sylvestris*) seeds used in the experiment (only those seeds from which were derived seedlings used for growth analyses were considered). Abbreviations: n = number of seeds per maternal plant and year combination; max/min = mass of the heaviest divided by mass of the lightest seed; and CV = coefficient of variation.

Mother plant	2004 Crop				2005 Crop			
	n	Seed mass (mg ± SE)	Max/min	CV (%)	n	Seed mass (mg ± SE)	Max/min	CV (%)
1	29	10.89 ± 0.22	1.69	11.1	34	10.94 ± 0.21	1.64	11.4
3	37	11.75 ± 0.21	1.49	11.0	33	12.03 ± 0.21	1.50	10.2
6	30	7.58 ± 0.14	1.49	10.1	26	7.70 ± 0.17	1.52	11.1
9	34	11.90 ± 0.25	1.71	12.0	29	14.02 ± 0.23	1.48	8.8
10	34	9.84 ± 0.20	1.79	12.1	31	9.66 ± 0.24	1.67	13.9
12	29	8.23 ± 0.21	1.63	13.8	26	8.82 ± 0.22	1.81	12.6
14	29	11.38 ± 0.20	1.37	9.5	26	12.64 ± 0.24	1.38	9.5
16	32	11.23 ± 0.24	1.64	12.2	34	10.29 ± 0.20	1.75	11.6
27	31	8.11 ± 0.13	1.45	9.1	17	7.23 ± 0.19	1.49	10.7
29	29	9.36 ± 0.16	1.38	9.1	27	9.66 ± 0.27	1.68	14.3

This implies that parameters correlated to seed mass have an underlying maternal effect.

Seedling growth

For both seed crops, seedling mass was largely determined by seed mass (Table 2), as has been reported previously for Scots pine families (Mikola 1985, Castro 1999, Wennström et al. 2002) and half-sib families of other coniferous species (Parker et al. 2004, St. Clair and Adams 1991). Within maternal lines

(by seed crop) there was a significant positive relationship between seed mass and seedling mass in 19 cases, and the relationship was marginally significant in the remaining case (Table 3). Seedling mass was also affected by maternal tree (Table 2), with a nearly twofold difference in seedling mass among families (Figure 1). Moreover, despite significant differences between years for some maternal trees, the pattern of seedling mass variation was almost constant between years across maternal trees, and differences in seedling mass were

Table 2. Summary of one-way analyses of covariance (ANCOVA) on seedling mass and relative growth rate 19–20 days after germination for seeds ripened in 2004 and 2005. The R^2 values refer to the fraction of the response variable explained by the whole model. Abbreviations: M = mother; and W = seed mass.

Source	df	SS	F	P
Seedling mass				
2004 Crop, $R^2 = 0.72$				
M	9	46.91	2.01	0.0382
W	1	205.70	0.40	< 0.0001
M × W	9	0.83	530.04	0.5849
Error	294			
2005 Crop, $R^2 = 0.80$				
M	9	59.02	1.90	0.0528
W	1	675.35	195.23	< 0.0001
M × W	9	45.54	1.46	0.1619
Error	263	909.76		
Relative growth rate				
2004 Crop, $R^2 = 0.14$				
M	9	591.84	2.29	0.0170
W	1	237.24	8.26	0.0043
M × W	9	365.08	1.41	0.1820
Error	294	8443.60		
2005 Crop, $R^2 = 0.05$				
M	9	430.67	1.31	0.2291
W	1	4.55	0.12	0.7239
M × W	9	552.61	1.69	0.0922
Error	263	9572.30		

Table 3. Summary of the slopes, r^2 values and P values for the linear regressions of seed mass as a function of (a) seedling mass and (b) relative growth rate for each Scots pine (*Pinus sylvestris*) maternal plant and seed crop year.

| Mother plant	2004 Crop			2005 Crop		
	Slope	r^2	P	Slope	r^2	P
(a) Seedling mass						
1	1.69	0.63	< 0.0001	1.26	0.36	0.0002
3	1.27	0.45	< 0.0001	1.41	0.52	< 0.0001
6	0.80	0.27	0.0035	1.92	0.70	< 0.0001
9	1.43	0.66	< 0.0001	0.88	0.21	0.0127
10	1.30	0.48	< 0.0001	1.69	0.56	< 0.0001
12	1.42	0.73	< 0.0001	2.11	0.72	< 0.0001
14	1.40	0.27	0.0038	1.46	0.33	0.0019
16	1.38	0.63	< 0.0001	1.92	0.69	< 0.0001
27	1.67	0.65	< 0.0001	1.20	0.33	0.0151
29	0.77	0.10	0.0939	1.39	0.52	< 0.0001
(b) Relative growth rate						
1	0.44	0.01	0.5469	−1.04	0.04	0.2575
3	−0.80	0.04	0.2510	−0.53	0.02	0.4648
6	−3.35	0.25	0.0049	1.57	0.08	0.1749
9	−0.48	0.03	0.3336	−1.64	0.14	0.0501
10	−1.09	0.06	0.1799	0.29	0.00	0.7637
12	−0.78	0.05	0.2581	2.72	0.20	0.0203
14	−0.13	0.00	0.9267	0.04	0.00	0.9691
16	0.10	0.00	0.8763	1.19	0.07	0.1322
27	0.43	0.01	0.6523	−0.71	0.01	0.7450
29	−3.08	0.12	0.0719	−0.65	0.02	0.5283
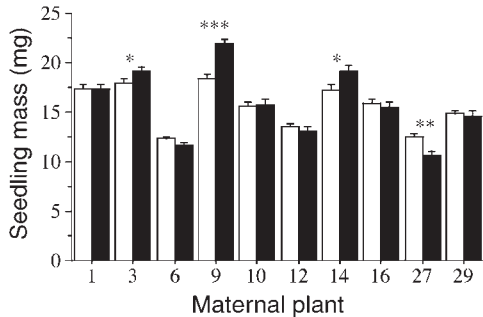
Figure 1. Mean values (± SE) of dry mass of Scots pine (*Pinus sylvestris*) seedlings 19–20 days after sowing for ten maternal plants in seed crop years 2004 (open bars) and 2005 (filled bars). Asterisks indicate significant differences between seed crops for each maternal plant (*, $P < 0.05$; **, $P < 0.001$; ***, $P < 0.0001$; absence of asterisks indicates a lack of significance; one-way ANOVAs).

larger among maternal lines than between years within maternal lines (Figure 1). A family effect on seedling growth has been also reported for other coniferous species (Surles et al. 1993, Kaya and Isik 1997, Mari et al. 2002). These data suggest that maternal origin is an important determinant of early seedling growth, at least in coniferous species.

Seedling relative growth rate

Seed mass had little effect on RGR. Although seed mass was significant in the full model for the 2004 crop, there was no effect for the 2005 crop (Table 2), and the significant effect of seed mass on RGR in the 2004 crop was much lower than the effect that seed mass exerted on seedling mass. In addition, when considered separately for each maternal tree, the seed mass–RGR relationship was significant or marginally significant in only one of ten cases for the 2004 seed crop (Table 3), and significant in only two of ten cases for the 2005 crop, with the slopes being either positive or negative (Table 3). This contrasts with the commonly reported negative correlation found between seed mass and RGR across species (Castro et al. 2006; and references cited in the Introduction section). Low variability in seed mass within a maternal tree cannot be invoked to explain this pattern, because the same within-tree variability resulted in a clear relationship between RGR and seedling growth (Table 3).

The effect of seed mass on RGR at the within-species level has been examined in relatively few studies, but most have shown a weak relationship or no relationship despite a positive correlation between seed and seedling masses. For instance, Vaughton and Ramsey (1998, 2001) found no relationship between seed mass and RGR for two *Banksia* species based on bulked seeds separated by size classes, and similar results were obtained for *Desmodium paniculatum* (L.) DC (Wulff 1986) and *Daucus carota* L. (Tamet et al. 1996). Lin and Sternberg (1995) found no correlation between propagule mass and RGR in *Rhizophora mangle* L. based on individually weighed seeds from a bulk collection from several plants as experimental units. The same trend was obtained after controlling for

family effect in *Pinus strobus* L. (Parker et al. 2004) and *Prosopis glandulosa* Torr. (Polley et al. 2006). In addition, the correlation between seed mass and RGR at the within-species level reported in some studies might be affected by the experimental procedure used. For example, Meyer and Carlson (2001) found a strong negative correlation between RGR and seed mass for *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & G.I. Baird. However, they compared populations (considered different subspecies) that differed sharply in achene mass, and pooled seeds from several maternal plants in each population; thus, a lack of correlation at the within-population level cannot be ruled out despite the negative correlation across populations (Castro et al. 2006). In contrast, Meerts and Garnier (1996) reported a positive correlation between seed mass and RGR for *Polygonum aviculare* L. But, again, the relationship emerged mostly because of an effect related to habitat type (linked to seed mass), whereas a within-habitat type comparison likely would not yield a positive correlation between seed mass and RGR, according to the data provided in their study (Figure 4a in Meerts and Garnier (1996)). In Scots pine, the combination of a lack of a relationship between seed mass and RGR across populations previously documented by Reich et al. (1994), together with our observation of an overall negligible effect across and within maternal trees, strongly suggests that seed mass has little or no effect on RGR in this species.

Maternal plant affected RGR of seedlings from seed gathered in 2004 but had no effect on RGR of seedlings from seed gathered in 2005 (Table 2). Relative growth rate thus varied less between years and among maternal trees than with seedling mass (Figure 2). Thus, whereas early seedling mass is likely a maternal-dependent trait mediated by seed mass, RGR appears to be a trait determined largely by species identity not by seed mass. As a result, seed mass is more important than RGR in determining early seedling growth in Scots pine (cf. Reich et al. 1994; and see van Rijn et al. 2000 for similar conclusions in *Hordeum* species).
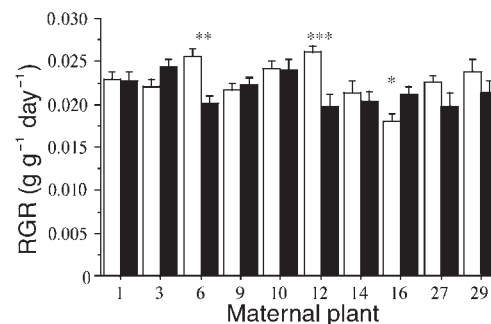

Figure 2. Mean values (± SE) for Scots pine (*Pinus sylvestris*) seedling relative growth rate (RGR) 19–20 days after sowing for the ten maternal plants in seed crop years 2004 (open bars) and 2005 (filled bars). Asterisks indicate significant differences between years for each maternal plant (*, $P < 0.05$; **, $P < 0.001$; ***, $P < 0.0001$; absence of asterisks indicates a lack of significance; one-way ANOVAs).

Relationships across species

Analysis of the seed mass–RGR relationship at the within-species level has generally been performed with bulked seeds and individual seeds from known maternal origin have not been considered as experimental units. The bulked-seed approach could confound the effect exerted by seed mass on RGR with the effect exerted by the genetic determination of the maternal plant (Castro 1999, Castro et al. 2006). For example, if we consider the mean values of seed mass and RGR per maternal tree, there is a negative correlation between these variables for the 2004 seed crop and no relationship for the 2005 seed crop (Figure 3). Moreover, even for the 2004 seeds, the relationship holds for only two out of ten cases when considered at the within maternal tree level (Table 3). Thus, we cannot conclude that seed mass determines seedling RGR in this species; rather, seed mass may be correlated with seedling RGR when mean maternal tree values are considered, but seed mass is unlikely to be the trait determining seedling RGR.

Seed mass was negatively correlated with seedling RGR across species (Castro et al. 2006). An unresolved question is whether this is due to a direct causal relationship (i.e., there is a physiological mechanism whereby plants grown from small seeds have a higher RGR than plants grown from large seeds), or whether RGR and seed size co-vary among species because of multiple trait selection pressures. Despite the scarcity of reports, a weak relationship or no relationship between seed mass and RGR, as we observed, has been documented for

other species (Villar et al. 1998, Castro 1999, Castro et al. 2006). Moreover, several studies have shown little or no variation in RGR among populations of the same species (Wilhelm and Nelson 1978, Cornelissen et al. 1996, Clevering 1999) and even at the genus level (Pohlman et al. 2005). Our results in combination with published data indicate that a small or negligible within-species effect of seed mass on seedling RGR is widespread, notwithstanding the negative correlation between seed mass and seedling RGR across species. Factors other than seed mass must thus account for most of the variation in RGR across species (Shipley and Peters 1990). This finding may have implications for trait correlations across species, because it implies that traits related to RGR could be embedded within other traits subject to natural selection.

Acknowledgments

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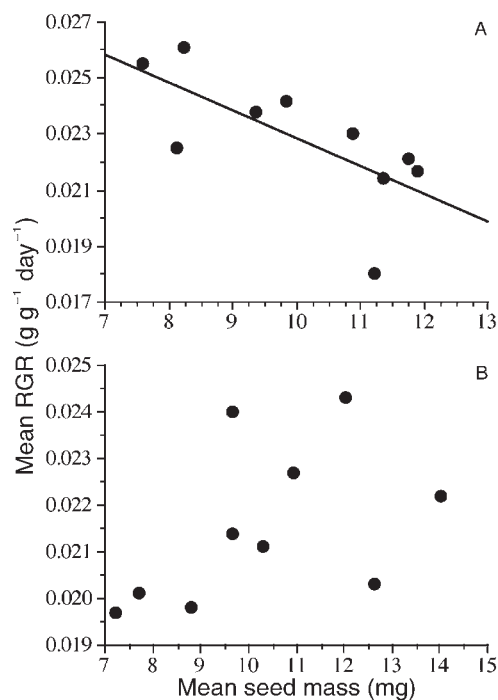

Figure 3. Relationship between mean seed mass and RGR per maternal plant after 19–20 days of growth for seeds from crop years (A) 2004 and (B) 2005. There was a significant, negative relationship for the 2004 crop ($y = 32.86 - 0.99x$; $r^2 = 0.50$, $P = 0.023$; linear regression), but no relationship for the 2005 crop ($P > 0.05$).

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