Effects of acorn size on seedling survival and growth in *Quercus rubra* following simulated spring freeze

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Abstract: Seed size is an important phenotypic trait commonly associated with the fitness of young seedlings exposed to environmental stress. Spring frosts can cause leaf necrosis and seedling mortality in young oak seedlings, and seedling mortality following spring freeze events is a factor limiting the northern range limits of *Quercus gambelii* (Nutt.). We examined the relationship between acorn size and seedling survival following spring freeze by exposing 1-month-old *Quercus rubra* (L.) seedlings from two sites in Massachusetts to −3°C for 8 h. Mortality of 1-month-old frost-exposed seedlings (20−25%) was 10 times higher than control mortality, with survival directly related to acorn size. Seedling size at the end of the first growing season was negatively affected by frost exposure and positively associated with acorn size. Overwintering mortality (<5%) was negatively associated with seedling size. The production of large acorns should confer a selective advantage in habitats susceptible to spring frosts through a positive effect on seedling establishment success under stress.

Key words: red oak, acorn size, frost, seedling survival.

Résumé : La dimension de la graine est un caractère phénotypique généralement associé avec l'adaptation des plantules exposées au stress environnemental. Les gels printaniers peuvent causer des nécroses foliaires et la mortalité des plantules de chêne, et cette mortalité des plantules après un gel printanier constitue un facteur limite à la distribution du *Quercus gambelii* (Nutt.), vers le nord. Les auteurs ont examiné la relation qui existe entre la dimension du gland et la survie des plants, suite au gel printanier, en exposant des *Quercus rubra* L. provenant de deux régions du Massachusetts et âgés d'un mois, à −3°C pendant 8 h. La mortalité des plants d'un mois exposés au gel (20−25%) est 10 fois plus élevée que celle des témoins, la survie étant indirectement reliée à la dimension des glands. La dimension des plants à la fin de la première saison de croissance est négativement affectée par l'exposition au gel et positivement corrélée avec la dimension des glands. La mortalité hivernale (<5%) est négativement associée avec la dimension des plants. La production de gros glands devrait conférer un avantage sélectif dans les habitats susceptibles au gels printaniers via un effet positif sur l'établissement des plants soumis à un stress.

Mots clés : chêne rouge, dimension des glands, gel, survie des plantules.
[Traduit par la rédaction]

Introduction

Seed size commonly affects progeny fitness under a variety of stressful conditions (e.g., Salisbury 1942; Baker 1972; Rockwood 1985; Gross 1984; Stanton 1985; Strauss and Ledig 1985; Wulff 1986*a*, 1986*b*; Manasse 1990; Stromberg and Patten 1990; Tripathi and Khan 1990; Armstrong and Westoby 1993). Theoretical resource allocation models predict that total maternal plant fitness will be maximized at an intermediate seed size because of nonlinear seed number versus seed size trade-offs (Smith and Fretwell 1974; Lloyd 1987) but also predict that optimum offspring size favored by natural selection will increase as conditions for juvenile survival become more stringent (Brockelman 1975; Kolding and Frenchel 1981; McGinley et al. 1987; Perrin 1988). Spring frost is one form of environmental stress to which plants in temperate regions may be exposed. Toward the northern range limits of the deciduous white oak *Quercus gambelii* (Nutt.), the likelihood of seedling exposure to spring frost increases, and seedling mortality following spring freezing is one of the primary factors limiting the northern distribution of this species (Neilson and Wullstein 1983).

Red oak, *Quercus rubra* (L.) (subg. *Erythrobalanus*), occurs throughout most of eastern North America, with a range lying between 31°N and 48°N (Little 1971). Although *Quercus* species that produce larger acorns tend to reach higher latitudes than species with small acorns (Aizen and Patterson 1990), *Q. rubra*, like most eastern North American oaks, shows a within-species decline in acorn size with increasing latitude (Aizen and Woodcock 1992). These contrasting patterns pose the question of whether there is, in fact, any fitness advantage, in terms of offspring success, in the production of large acorns.

In this study we investigated the relationship between red

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oak acorn size, seedling size, growth rate, and survivorship when seedlings are exposed to a spring freeze. Specifically, our experiments were designed to answer the following questions. (*i*) Is there a relationship between acorn size and date of seedling emergence (and hence risk of frost exposure)? (*ii*) Does acorn size have a direct or indirect (i.e., mediated by seedling size) effect on survivorship of 1-month-old seedlings following frost exposure? (*iii*) Is there a relationship between acorn size and seedling size over the first growing season? (*iv*) Is there a direct or indirect effect of acorn size on survivorship of overwintering seedlings?

Methods

Acorn collection

Ungerminated, sound *Q. rubra* acorns were collected in early March 1991 in central Massachusetts (42°20′N), towards the northern part of the species' range. To determine whether results were replicable across two separate acorn sources, acorns were collected from sites 2 km apart. Both collection sites were located at an elevation of approximately 300 m in a mixed-hardwood forest on excessively drained, deep, sandy loam soils. Acorns were collected from approximately 500-m^2 areas, one under the canopy of a dominant tree (Gulf Rd. sample, n = 326) and the other in a gap near several codominant trees (Cadwell sample, n = 188). Acorns from the two sites differed in external morphology and were individually labelled so that differences between acorns from the two sources, if any, could be assessed.

Acorn germination and planting

The experimental treatments were carried out at the University of Massachusetts, Amherst, Mass., 14 km from the collection sites and 250 m lower in elevation. Fresh seed and acorn weights of a random sample of the acorns collected were closely correlated (r = 0.970, n = 30), so acorn and seed size were considered equivalent. Acorns were weighed to the nearest 0.001 g, labeled, covered with moist paper towels, and placed on trays on an outdoor balcony where acorns and seedlings were exposed to ambient temperatures while protected from herbivory. Minimum air temperature was recorded daily. As they germinated, the acorns were sown 2 cm deep in 13 cm deep 450-mL styrofoam containers with perforated bottoms in a 1:1 mixture of a seed starting mix (Terralite, Grace Horticultural Products, Cambridge, Mass.) and peat moss (Fafard, Canada). After emergence the seedlings were fertilized every 2 weeks with 80 mL of a 1.2 g/L solution of plant food (20:20:20, Peter's Fertilizer Products, W.R. Grace & Co, Pa.). Seedlings from double embryos (about 10% of seedlings) were discarded.

Frost treatment and seedling survival estimation

The experimental frost regime was designed to simulate a normal late frost for Amherst, Mass. Mean last frost date for the period 1930 to 1984 is May 2 at Amherst; the latest recorded frost occurred on May 31 (Bradley et al. 1987). Between April 30 and May 20 the probability of the temperature dropping to 0°C in Amherst decreases approximately linearly from 60 to 10%. The probability that a recently emerged red oak seedling will be exposed to ≤0°C in Amherst on or after May 16, the date selected for the frost treatment, is about 20% (estimated from data published by Bradley et al. 1987).

On May 16, one month after the first seedling emerged, half the seedlings were randomly selected for frost treatment. Seedlings were brought into the lab at 2230, sprayed to avoid dehydration during freezing, cooled to −3°C±1°C, and held for 8 h at this temperature. Crowding the styrofoam containers into flats afforded the soil in the pots some protection from freezing and only the surface layer of soil froze. After thawing at 2°C, seedlings were returned to the balcony and intermixed with untreated control seedlings. Survival of control and frost-treated seedlings was recorded 1 month later.

On July 16, the seedlings were transplanted to an open level area 300 m from the Gulf Rd. collection site in a 16 × 18 grid 20 cm apart, and watered and weeded as needed. Survivorship was checked 2 months later (September 17), just prior to leaf senescence, and in the following spring after the seedlings had broken dormancy.

Seedling size and growth

Two estimates of seedling size, shoot length (from the root collar to the most distant live bud), and length of the largest leaf were measured on May 16 (prior to the first frost treatment), June 18, July 16, and September 17. To determine the relationship between these parameters and total seedling dry weight, 37 seedlings (including control and treated seedlings) were measured, harvested, and the dry weight of roots, stems, and leaves determined at intervals during the first growing season.

Data analysis

The relative frequency of dead seedlings between frost-treated and control seedlings for each acorn collection site was compared using a 2 × 2 Fisher's exact test (SAS Institute Inc. 1988). Differences in median values of acorn size, days to germination, and days to emergence between acorns from the two collection sites were compared using Mann−Whitney's test (SAS Institute Inc. 1988).

Initial acorn weight, and shoot and maximum leaf length (measured just prior to frost treatment) were compared for live and dead classes, using ANOVA, for both control and frost-exposed seedlings. The two seedling size estimates were analyzed separately as they were only partially correlated (r = 0.700) and might reflect different size aspects of oak seedlings. Seedling size at the end of the growing season (September 17) was compared between control and frost- treated seedlings. The effects of initial acorn size and emergence date were included as covariates in a multiway ANCOVA. Collection site, which was considered to be a fixed effect because the samples differed in their genetic background and probably the amount of genetic variation represented, was included as an independent factor in the analyses described above. Separate tests were also run for the two samples to inspect whether trends were consistent across sites.

Changes in seedling size over time (May 16, June 18, July 16, September 17) for each sample and treatment category were compared using a repeated-measure ANOVA in which individuals were considered as a random factor and sampling dates as a fixed factor (Sokal and Rohlf 1981).

Analyses were performed on untransformed data, which better approached assumptions of normality and homoscedasticity than transformed data. In the few instances where these assumptions were not met, results from ANOVAs are reported, as they were robust and never differed qualitatively from those of comparable Kruskal−Wallis and Friedman tests (Sokal and Rohlf 1981). All the ANOVA and ANCOVA models were analyzed by the SAS procedure GLM. Because the data sets were unbalanced, hypothesis tests used type III sums of squares (SAS Institute Inc. 1988).

To summarize the direct and indirect (i.e., mediated by seedling size) effects of acorn size on seedling survival after (*i*) early frost exposure and (*ii*) following the first winter, simple path diagrams were constructed (Sokal and Rohlf 1981). Path diagrams can include categorical variables, such as survival, as well as continuous variables. Path coefficients, which may vary between −1 and +1 and indicate the strength and sign of a given path, were calculated following Mitchell (1992). Acorn size was used as a predictor variable of seedling size, and acorn and seedling size as predictor variables of survivorship. Survivorship was coded 1 and 0 for live

Table 1. Germination and emergence characteristics of *Q. rubra* acorns collected for this study.

	Gulf Rd. (N = 326)	Cadwell (N = 188)	P
Acorn size (g)	4.12 (1.46–6.23)	5.68 (1.19–8.03)	<0.0001
Germination (%)	91.1	95.7	0.052
Days to germination*	6 (0–41)	14 (0–37)	<0.0001
Emergence (%)	82.8	88.3	0.10
Days to emergence*	43 (34–72)	45 (40–64)	<0.0001

Note: Values for the continuous variables are medians (range). Differences between percentages were evaluated through Fisher's exact test, and differences between medians through Mann–Whitney's test.
*March 12, date of first observed germination, was considered day 0.

Table 2. Results of linear regressions of germination time, emergence time, and seedling size measures (dependent variables) on acorn size in grams (independent variable).

	Gulf Rd.					Cadwell				
Dependent variable	n	Intercept	Slope	r^2	P	n	Intercept	Slope	r^2	P
Days to germination*	288	16.69	−2.44	0.069	<0.001	174	14.39	−0.09	0.001	0.82
Days to emergence*	270	47.35	−0.92	0.025	<0.01	166	49.15	−0.56	0.037	<0.05
Shoot length (cm)										
May 16	227	1.30	1.60	0.067	<0.0001	144	2.43	1.17	0.137	<0.0001
Sept. 17	162	7.74	1.67	0.041	<0.01	110	12.64	0.79	0.027	0.08
Max. leaf length (cm)										
May 16	227	−0.265	1.13	0.156	<0.0001	144	−0.29	0.86	0.109	<0.0001
Sept. 17	162	5.32	1.03	0.067	<0.001	110	8.22	0.60	0.060	<0.05

*March 12, date of the first observed germination, was considered day 0.

and dead seedlings, respectively. Path diagrams were constructed for acorns from each collection site, separately and combined, for shoot and leaf length on May 16 (for early spring frost survival) and on September 17 (for overwinter survival) as estimates of seedling size.

Results

Germination and seedling emergence

The germination rate exceeded 90% in both samples (Table 1). Acorn size did not significantly affect emergence success ($F_{1,473}$ = 0.313, P = 0.54). Acorn size was negatively associated with days to emergence in both samples (Table 2; r = −0.159 for the Gulf sample, r = −0.197 for the Cadwell sample). Using the regression coefficients of these relationships (Table 2), we found average differences in days to emergence of 4.4 and 3.9 days for the range of acorn sizes of the Gulf Rd. and Cadwell samples, respectively (Table 1).

Relationships between size parameters

Shoot length and largest leaf length were both strongly correlated with total seedling dry weight excluding the attached acorn (r = 0.810, P < 0.0001, and r = 0.900, P < 0.0001 respectively; N = 37). Leaf and stem measures were thus good indications of total seedling dry weight.

At 1 month of age (May 16), shoot length was positively correlated with acorn size (Table 2; r = 0.259 for the Gulf Rd. sample, r = 0.370 for the Cadwell sample) and maximum leaf length (Table 2; r = 0.395 for the Gulf Rd. sample, r = 0.330 for the Cadwell sample). By the end of the first growing season (Sept. 17), relationships between seedling size parameters and acorn size were qualitatively similar but the relationships were weaker (Table 2).

Frost-related mortality

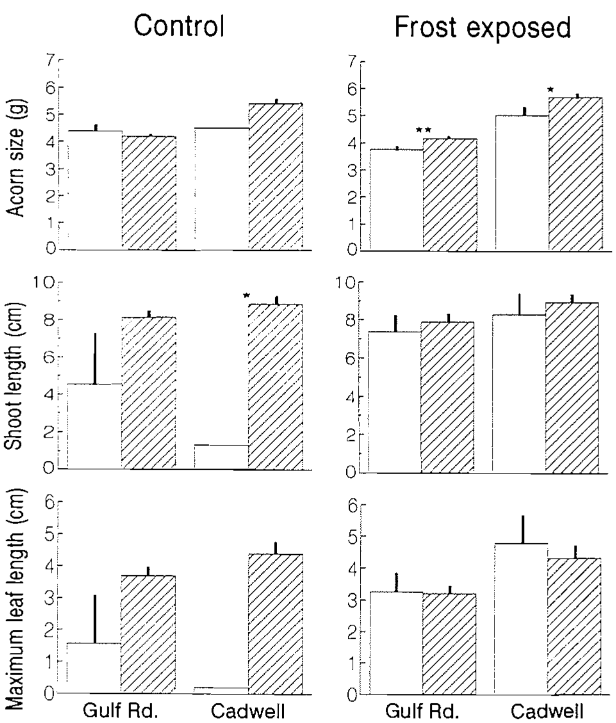
Control (no frost treatment) seedling mortality was not related to natural frost events since temperatures did not fall below 0°C on the balcony after seedling emergence. All the seedlings subjected to artificial frost on May 16 suffered at least some shoot necrosis and almost total leaf necrosis as a consequence of frost injury. By June 16, when mortality was recorded, significantly more frost-exposed seedlings had died compared with the controls (Gulf Rd.: 3 dead out of a total of 112 seedlings (2.7%) vs. 28 out of 112 (25%), P < 0.0001; Cadwell: 1 out of 70 (1.5%) vs. 14 out of 70 (20%), P < 0.0005). For both samples, mean acorn size of dead frost-exposed seedlings was consistently smaller than mean acorn size of the surviving group (Fig. 1). Differences in mean acorn size were significant (Fig. 1; Table 3), but differences in the two seedling size measures between dead and surviving frost-treated seedlings were not significant (Fig. 1; Table 3). On the other hand, seedling size, but not acorn size, was significantly correlated with seedling survival among the control seedlings (Fig. 1; Table 3). Acorn size of dead control seedlings did not differ from acorn size of live control seedlings, but dead seedlings were significantly smaller as estimated by both size measurements (Fig. 1; Table 3). There were no significant differences in seedling mortality between samples for either the frost-

Table 3. Summary of F statistics and significance levels for ANOVAs testing for the differences in mean initial acorn size, seedling shoot length, and maximum leaf length between dead and live seedlings (status) and between collection sites (sample) for control (no frost exposure) and frost-exposed seedlings.

	Control seedlings				Frost-exposed seedlings			
	df	Acorn size	Shoot length	Leaf length	df	Acorn size	Shoot length	Leaf length
Status	1	0.43	6.28*	3.55(*)	1	13.19***	0.67	0.23
Sample	1	1.47	0.38	0.06	1	88.32****	1.84	6.28*
Status × sample	1	1.01	0.87	0.43	1	0.63	0.01	0.14
Error (SS)	178	(160.30)	(2732.3)	(1573.1)	178	(114.43)	(2686.9)	(1479.9)

Note: Seedling size variables were measured just prior to frost treatment (May 16). Mortality was recorded 1 month after treatment (June 16). (*), $0.05 < P < 0.10$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$.

Fig. 1. Mean acorn size, shoot and maximum leaf length (+1 SE) of dead and surviving frost-exposed and control seedlings on May 16 (approximately 1 month old). Seedling size variables were measured on May 16, just prior to frost treatment. Mortality was recorded 1 month after treatment (June 16). Differences between categories were analyzed by ANOVA for each sample separately (*, $P < 0.05$, **, $P < 0.01$). See Table 3 for overall significance levels. □, dead; ▨, live.



exposed or control categories ($P > 0.20$) despite significant differences in mean acorn size (Table 1).

Seedling size and growth

In control seedlings, expansion and growth of aerial parts leveled off approximately 2 months after seedling emergence (Fig. 2). Surviving frost-exposed seedlings resprouted, but 1 month after frost exposure had only regrown to their pretreatment shoot size (Fig. 2). In these seedlings, shoot growth leveled off about 1 month later than the controls (Fig. 2).

Acorn size had an overall significant and positive effect on final seedling size at the end of the first growing season ($F_{1,266} = 11.28$, $P < 0.01$ and $F_{1,266} = 24.81$, $P < 0.0001$ for shoot and leaf length, respectively), and early spring frost exposure also had a significant but negative effect (Fig. 2; $F_{1,266} = 69.09$, $P < 0.0001$, and $F_{1,266} = 40.71$, $P < 0.0001$ for shoot and leaf length, respectively). There was no evidence that the slope of the final seedling versus acorn size relationship differed between frost-exposed and control seedlings ($F_{1,265} = 2.40$, $P = 0.12$, and $F_{1,265} = 2.00$, $P = 0.16$ for shoot and leaf length, respectively). There was no significant correlation for either sample or size measure between relative growth rate (RGR), calculated as the difference between log-transformed seedling size measurements made on May 16 and June 18, and acorn size for control seedlings ($P > 0.10$).

Overwintering mortality

Overwintering mortality was 7 dead out of a total of 162 seedlings (control was 4 out of 95; frost was 3 out of 67) and 3 dead out of a total of 110 (control was 1 out of 64; frost was 2 out of 46) for the Gulf Rd. and Cadwell samples, respectively, and did not differ significantly between the treatment categories ($P = 0.12$ and $P = 0.78$). After pooling across categories, we found that overwinter survival was related to both initial acorn size (Fig. 3; $F_{1,268} = 10.08$, $P < 0.01$), and to final seedling size measures (Fig. 3; $F_{1,268} = 6.05$, $P < 0.01$, and $F_{1,268} = 19.23$, $P < 0.0001$ for shoot and leaf length, respectively). Significance levels of differences in seedling size between survival classes remained the same when acorn size was included as a covariate ($F_{1,267} = 3.75$, $P = 0.05$ for shoot length, $F_{1,267} = 13.79$, $P < 0.0005$ for maximum leaf length).

Path analysis

Qualitatively similar path diagrams were obtained for samples from the two collection sites considered separately (results not shown) and combined. Similar results were obtained whether shoot length (results not shown) or leaf length was used as an estimate of seedling size. Figure 4 shows results for seedlings from both collection sites combined, using leaf length as the seedling size estimate. Results of path analysis are in accordance with ANOVA results, with a direct, significant, positive effect of acorn size on seedling survival after exposure to a simulated early spring frost (Fig. 4*a*). Survival following frost exposure was not directly related to

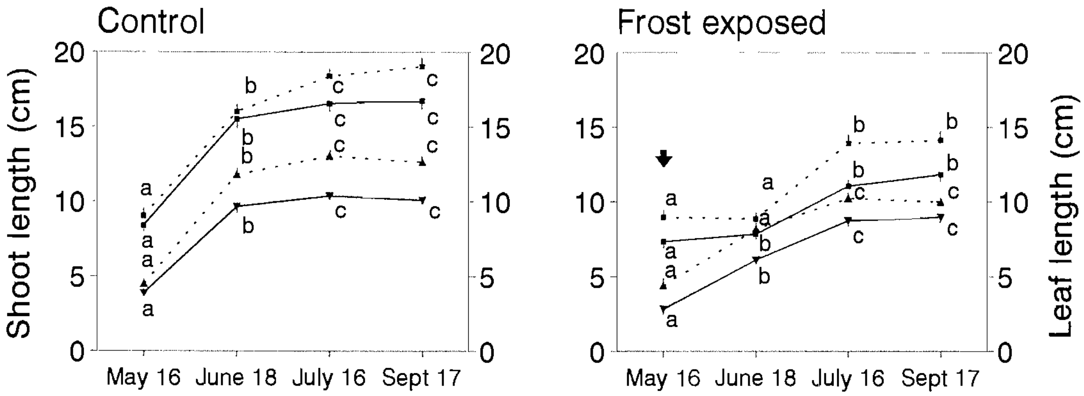


Fig. 2. Seedling growth curves for control and frost treatments for seedlings that survived through the complete growing season. Values are means (±1 SE). For each curve, means were compared through a repeated-measure ANOVA. Means that share the same letter did not differ significantly (Ryan's Q test, $P > 0.05$). Solid lines, Gulf Rd. sample; broken lines, Cadwell sample; ■, shoot length; ▲, leaf length. Control: N = 95 for Gulf Rd. and N = 64 for Cadwell. Frost exposed: N = 67 for Gulf Rd. and N = 46 for Cadwell.

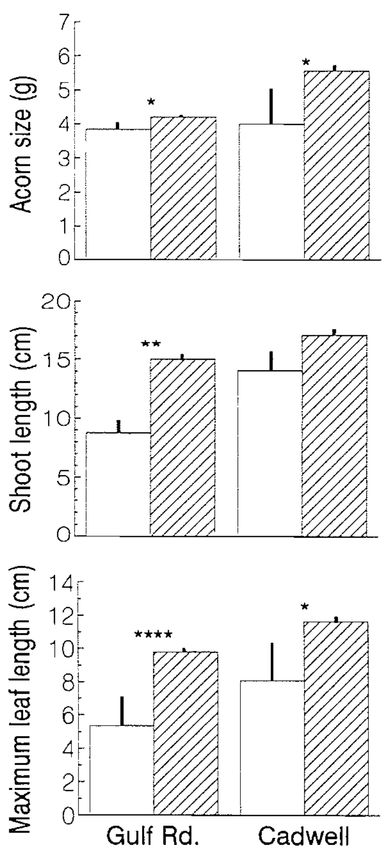
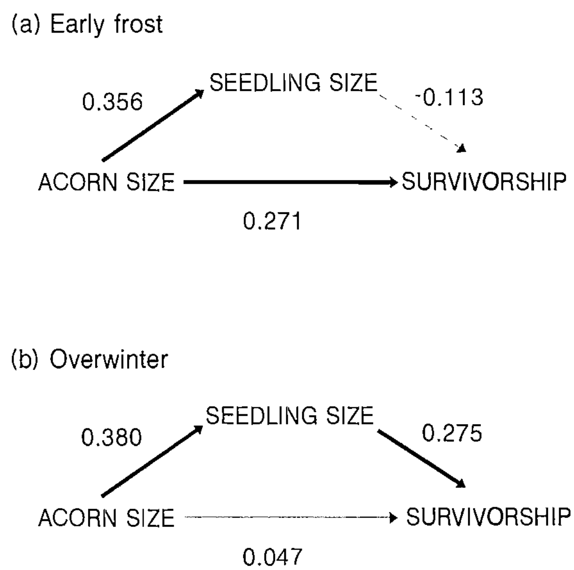


Fig. 3. Mean acorn size, shoot, and maximum leaf length (+1 SE) of dead and surviving overwintering seedlings. Seedling size variables were measured at the end of the first growing season (September 17) and overwintering mortality was recorded the following spring. Differences between categories were analyzed by ANOVA for each sample separately (*, $P < 0.05$; **, $P < 0.01$; ****, $P < 0.0001$). □, dead; ▨, live.

Fig. 4. Path diagram measuring the direct and indirect (mediated by seedling size) effects of acorn size on seedling survival 1 month after (*a*) exposure to spring frost, and (*b*) after the first winter. Data from both samples were combined. Seedling size was estimated from leaf length measurements on (*a*) May 16 and (*b*) Sept 17. Positive effects are indicated by solid lines, and negative effects by broken lines. Thick arrows indicate significant path coefficients ($P < 0.05$).



seedling size (Fig. 4*a*) even though seedling size was, in part, determined by acorn size. ANOVA also indicated that overwintering survival was associated with both acorn and seedling size, but path analysis (Fig. 4*b*) revealed that the effect of acorn size on overwintering survival was indirect, mediated by its significant relation to seedling size. The path coefficient measuring the effect of acorn size on overwintering survival was not significant (Fig. 4*b*), suggesting a direct influence of seedling size (or some physiological variable closely correlated with it) on overwintering survival.

Discussion

Acorn size in *Q. rubra* had a direct, positive influence on the short-term survival of young seedlings exposed to spring freeze (Fig. 4). To our knowledge, this is the first report of either a direct or indirect association between seed size and seedling frost tolerance. Overwintering survival was indirectly influenced by acorn size through its effect on seedling size at the end of the growing season (Fig. 4). By this time of the year, seedling size was a function not only of acorn size but also of exposure to spring freeze and other factors.

In the 1st month after emergence, when the leaves were still expanding, *Q. rubra* seedlings were highly susceptible to freezing damage. Exposure to −3°C for 8 h caused partial to complete necrosis of the aerial shoot and expanding leaves, and a 10-fold increase over background mortality. One explanation for our finding that survival of these seedlings was partially dependent on initial acorn size (irrespective of the size of the seedling before treatment) is that they had lost much or all of their photosynthetic capacity through freezing injury. Recovery is likely to be, in part, dependent on the amount of reserves remaining in the cotyledons and (or) translocated from the cotyledons to the roots. Interestingly, frost exposure of 1-month-old seedlings produced similar mortality rates to those reported elsewhere for artificially defoliated, unshaded red oak seedlings (McGraw et al. 1990). A similar frost treatment applied 1 month later caused little damage and no differential mortality between frost-exposed and control seedlings (results not shown), indicating that a degree of frost tolerance is acquired by red oak seedlings in the 2nd month of growth.

Armstrong and Westoby (1993) argued that seedlings from large seeds exhibit higher survival rates because of a greater concentration of mobilizable metabolic reserves in their tissues that might be associated with a slower relative growth rate (Shipley and Peters 1990). We did not find any significant correlation between RGR and acorn size for either sample or size measure to support this explanation for differences in survival among red oak seedlings.

The results of Nielson and Wullstein (1983) indicate that the risk of oak seedling damage from spring freeze can increase from south to north even though germination and seedling emergence will occur later in the north. To date, we have been unable to test this hypothesis for *Q. rubra* because of a lack of published information on seedling emergence dates throughout its range. These data, as well as a more comprehensive experiment with seedling exposure to different subzero temperatures (cf. Maruta 1983), are needed to better evaluate latitudinal variation on selection intensity. Nevertheless, our results suggest that the selective advantage of large acorn size should increase with latitude because of the positive relationship between acorn size and seedling survival following exposure to spring frost, and to the indirect contribution of acorn size to winter survival (Fig. 4). All else being equal, production of larger acorns at higher latitudes would be predicted. However, as we previously reported, *Q. rubra* and many other oaks produce, on average, smaller acorns at high latitudes (Aizen and Woodcock 1992). One possible explanation for this observation is that small acorn size is adaptive at high latitudes because it allows frost avoidance through delayed emergence. The 4-day differential in days to emergence for the range of acorn sizes in this study (comparable to the size range across red oak's distribution) reduces the probability of seedling frost exposure in May in Amherst by 10%. Possibly this effect could compensate for the cumulative effects of decreased stress resistance of seedlings from small acorns, though it seems unlikely.

Constraints imposed by the length of the growing season on patterns of seed maturation could be an overriding source of variation in seed size both on a geographic scale and within a single plant. In recent empirical and experimental work, Galen and Stanton (1991, 1993) found that a decline in *Ranunculus adoneus* seed size along a snow-melting gradient can be explained as a plastic response to the number of days available for seed filling. Clinal variation in acorn size could reflect a similar mechanism. The experimental evidence we report here supports the view that a negative phenotypic clinal variation in acorn size in *Quercus* species (Aizen and Woodcock 1992) might be molded by factors other than natural selection operating at the seedling establishment level.

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