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Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints

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Abstract To evaluate the importance of developmental constraints in the determination of the relative importance of seed size and emergence time, early seedling performance of two woody species with contrasting growth phenology were observed under competitive conditions with tall herbs in an early successional habitat. The oak, *Quercus mongolica* var. *grosseserrata*, with determinate shoot development (a single leaf flush), showed a marked influence of seed size on subsequent seedling height growth and survival. Because of determinate growth, emergence time had negligible effects. The walnut, *Juglans ailanthifolia*, which continued to produce new leaves throughout the growing season (indeterminate development), showed a marked influence of time of emergence on seedling performance, because it affected the amount of growth that could be achieved; seed size, however, had negligible effects as the seedlings grew. These results suggest that relative importance of seed size and emergence time for early seedling performance is closely associated with developmental constraints (growth phenology).

Key words Oak · Walnut · Seed size · Emergence time · Phenology

Introduction

Seed size is important in seed dispersal, persistence in soil, seedling establishment, and fitness in plants (e.g., Salisbury 1942; Harper et al. 1970; Venable and Brown 1988; Westoby et al. 1992; Thompson et al. 1993; Seiwa and Kikuzawa 1996). Most studies of intraspecific variation in seed mass have demonstrated the advantages of large seeds over smaller seeds in the early stages of seedling establishment. Large seeds give rise to better competitors, particularly under resource-limited or competitive conditions (e.g., Weis 1982; Gross 1984; Stanton 1984; Weller 1985; Winn 1985; Wulff 1986a; Tripathi and Khan 1990; Bonfil 1998; but see Hendrix et al. 1991).

Timing of emergence also plays a critical role in seedling establishment in plant species, particularly under competitive conditions (e.g., Bush and Van Auken 1991; Miller et al. 1994). The rank order of emergence greatly contributes to the establishment of a competitive hierarchy (Ross and Harper 1972). Earlier germinators usually show an advantage over later ones among herbs (e.g., Black and Wilkinson 1963; Cook 1980; Mack and Pyke 1983; Miller et al. 1994) as well as tree seedlings (Bush and Van Auken 1991; Jones et al. 1997; Seiwa 1997, 1998), by (1) capturing a disproportionate share of environmental resources such as light, nutrients, and water compared with late-emerging neighbors in grasslands or old fields (Ross and Harper 1972; Bush and Van Auken 1991; Miller et al. 1994), (2) receiving ephemeral light for longer before canopy closure (Jones et al. 1997; Seiwa 1997, 1998), and (3) reducing pathogen and predator load, which are less active in early spring in temperate deciduous forests (Seiwa 1997, 1998).

It has often been observed that substantial variations in seed size and emergence time occur concurrently among seeds of a single population. Although there has been extensive investigation of the effects of either seed size or emergence time on seedling performance, few studies have considered the relative importance of these two factors (but see Howell 1981; Dolan 1984; Stanton 1985). Several studies have yielded contrasting results: some have found that seedling performance is affected by only emergence time (Ross and Harper 1972; Naylor 1980; Howell 1981; Miller et al. 1994; Jones et al. 1997), while others have found it to be affected only by seed size (Dolan 1984; Stanton 1985). There are three possible reasons for this apparent discrepancy:

1. Variation in one factor much smaller than that of the other, resulting in a negligible effect on seedling performance (see Dolan 1984; Jones et al. 1997).

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2. If seedling growth rate is positively correlated with either seed size (e.g., Weis 1982; Gross 1984; Bonfil 1998; but see Schaal 1980; Zimmerman and Weis 1983) or emergence time (Miller et al. 1994), the one dominant factor would remain important in later growth stages. On the other hand, if growth rate is independent of either seed size (e.g., Wulff 1986a) or emergence time, seedling performance may be directly affected by the factor.
3. If early timing of emergence gives a longer favorable period of growth before environmental resources diminish (e.g., light), an early start may be important to seedling establishment, since earlier growth into a higher stratum is advantageous for the seedling to avoid being shaded by neighboring herbs, particularly in early successional habitats where light conditions would be improved by increasing seedling height (e.g., Ross and Harper 1972; Givnish 1982; De Steven 1991).

Thus, a solid piece of empirical work to document the relative importance of seed size and emergence time on seedling establishment in field experiments is necessary.

In temperate regions, growth phenology, or the seasonal timing of shoot growth and leaf emergence, is closely related to successional status, and has been classified into two typical patterns (*flush* and *succeeding* types) for both seedlings and adults of deciduous broad-leaved tree species (e.g., Kozlowski and Ward 1957; Marks 1975; Bicknell 1982; Kikuzawa 1983, 1991; Koike 1988; Seiwa 1998, 1999; Seiwa and Kikuzawa 1991, 1996). In the flush type, leaf production and height growth occur simultaneously in a short period irrespective of the availability of environmental resources, while in the succeeding type, vertical growth under favorable conditions continues indeterminately for a longer time accompanied by successive leaf emergence, as is usually observed for late-successional species (e.g., *Aesculus turbinata*, *Quercus mongolica* var. *grosseserrata*, *Prunus sargentii*, *Acer mono, A. japonicum*, and *A. palmatum* var. *matsumurae*) as well as early-successional species (e.g., *Castanea crenata*, *Juglans ailanthifolia*, *Alnus hirsuta*, *Betula platyphylla* var. *japonica, B. ermanii*), respectively. Analogous types have been also reported in tropical forests (Shukla and Ramakrishnan 1984; Lawman 1992). Since seedlings of the flush type usually complete shoot elongation and annual leaf production as a flush in spring by utilizing seed nutrient reserves (Seiwa and Kikuzawa 1991, 1996), height growth of flush-type seedlings would be more strongly affected by seed size than by emergence time. It is thus hypothesized that such flush-type tree seedlings would show size-dependent growth, and consequently size-dependent survival, if they show size-dependent mortality in early successional habitats. In contrast, height growth of succeeding-type seedlings would be more strongly affected by emergence time than seed size, if they have the ability to grow much taller by utilizing the longer favorable period afforded by early germination. It is thus hypothesized that such succeeding-type tree seedlings would show emergence-time-dependent growth and survival. To test these hypotheses, I conducted a field experiment in which I sowed two species with contrasting growth phenology, *Quercus mongolica* var. *grosseserrata* (flush type) and *Juglans ailanthifolia* (succeeding type), which differ substantially in seed size and emergence time.

In this study, the following questions were posed:

1. To what extent are seedling growth and survival of *Quercus* and *Juglans* affected by seed size and emergence time under an early successional competitive conditions?
2. How is the relative importance of seed size and emergence time influenced by growth phenology?

Materials and methods

Study species

Both study species, *Q. mongolica* var. grosseserrata and *J. ailanthifolia*, are common in the temperate regions of northern Japan. *Quercus* is a relatively shade-tolerant species, regenerating in a wide range of deciduous forest types and under various light conditions ranging from forest understorey to large gaps or abandoned fields (Kanazawa 1983; Ishizuka and Sugawara 1986; Koike 1988; Seiwa and Kikuzawa 1996). *Juglans* is a shade-intolerant species, regenerating in relatively favorable light conditions such as large gaps, abandoned fields, and river sides (Ishizuka and Sugawara 1986; Koike 1988). Acorns of *Quercus* and nuts of *Juglans* are usually dispersed by small mammals (i.e., Japanese squirrels and wood mice) (Miyaki and Kikuzawa 1988; Hayashida 1991; Tamura and Shibasaki 1996). Acorns of *Quercus* are also dispersed by jays (Nakamura 1984).

Study site

This study was conducted along the edge of a broad-leaved deciduous forest in the experimental forest of the Hokkaido Forest Research Institute in Shintoku (43°5’N, 142°49’ E), Japan. Trees at the study site had been re-established after a fire about 65 years ago. The tall tree layer is dominated by *Q.mongolica* var. *grosseserrata*, *Ostrya japonica*, *Ulmus davidiana* var. *japonica* and *J. ailanthifolia* (Seiwa 1998). The study site was abandoned for 2–3 years following cultivation of Japanese white radish. The soil type is andosol (FAO-UNESCO 1974), silty and freely draining. The mean annual temperature 1989–1993 was 6.0–7.3°C, and annual rainfall was 1040–1350 mm, of which 13–19% was snow. Snow cover usually lasted from mid-December to late March. Mean monthly temperature ranged from –4.9°C to 19.7°C.

Field experiments

To minimize genetic differences among individual seedlings, acorns of *Quercus* and nuts of *Juglans* were each collected from single trees within 7 km of the study area. The seeds were floated in water to determine viability. Seeds with obvious insect damage were discarded. In both species, there were wide variations in seed mass, which permitted the categorization of seeds into three mass classes. For *Quercus*, there were small (mean 1.68 g, range 1.00–2.24 g), medium (mean 2.75 g, range 2.25–3.24 g) and large (mean 4.31 g, range 3.25–5.24 g) and for *Juglans*, there were small (mean 7.19 g, range 4.00–8.99 g), medium (mean 10.0 g, range 9.00–10.99 g) and large (mean 11.98 g, range 11.00–13.99 g). Seeds were sown at a depth of 4 cm, since seedling emergence is usually improved when large seeds such as acorns are buried or placed under litter by seed dispersers (e.g., Shaw 1968; Seiwa and Kikuzawa 1996).

To reduce intraspecific interactions, the sowing interval was greater for the large-seeded species, i.e., *Juglans*, than for the small-seeded species, i.e., *Quercus*. For *Quercus*, 50 seeds of each size-class were sown at 20-cm intervals on a square grid (5 rows×10 columns) on a 100×200 cm quadrat on 16 October 1990. For *Juglans*, 10 seeds (5 rows×2 columns) each of the large and small size-classes and 12 seeds of the medium size-class (6 rows×2 columns) were sown at 30-cm intervals on a square grid on 80×240 cm quadrats on 30 October 1990. Six quadrats of the three seed size-classes of the two study species were randomly located in a plot (7×7 m) after removal of herbs, shrubs, *Sasa senanensis*, and litter. This plot was replicated at five randomly selected locations along the forest edge. A total of 750 and 160 seeds were sown for *Quercus* and *Juglans*, respectively. In the plots, a number of herbaceous species grew throughout the experiment. *Chenopodium album* var. *centorubrum* and *Artemisia montana*, which reached 1 m in height, were sparse during the first year, but increased in density with time. *Polygonum longisetum*, *Trifolium pratense*, and *Commelina communis*, which reached 20–50 cm in height in the 1st year, were dense throughout the 4-year study period. Although the same seed size-classes were planted within a quadrat in the study, interspecific competition was more severe than intraspecific competition for both the species studied.

Measurements

During germination, the position of each emerging seedling was numbered with a wire marker. To evaluate the duration of height growth, which coincided with leaf emergence in these study species (Seiwa and Kikuzawa 1991, 1996), the number of leaves present and those already fallen were determined for all seedlings. Duration of leaf emergence was defined as the period from the appearance of the shoot apex on the soil surface to the date when the last leaf began to expand. Measurements of seedling emergence and leaf phenology began on 14 March, and were repeated at 7- to 9-day intervals until August, and then every 2 weeks for the remainder of the growing season, in both 1991 and 1992. Days to emergence was defined as the period from the date of snow melt (2 April) to the date of seedling emergence. The seedlings were categorized into early- and late-emerging cohorts on the basis of emergence time; each of them included the seedlings emerging before and after 28 May in *Quercus*, and before and after 11 June 1991 and before and after 22 June 1992 in *Juglans*, since *Juglans* seedlings emerged over a period of 2 years. Seedling survival and height were recorded in July and October 1991, and yearly in October 1992, 1993 and 1994 for *Quercus*, and yearly in October 1991, 1992 and 1993 for *Juglans*. Since all *Juglans* seedlings were accidentally cut in November of 1993, the measurement stopped at the end of the 3rd growing season. Seedling height was measured as the distance from the soil surface to the shoot apex. There was no evidence of cotyledon removal, which has significant negative effects on subsequent seedling survival and growth (Bonfil 1998).

Statistical analysis

Percent emergence and days to emergence were compared among the three seed size-classes using one-way ANOVA. Tukey-Kramer HSD tests were used to compare differences among means when the ANOVA showed a significant effect. To examine the effects of seed size and timing of seedling emergence on seedling survival and seedling height, and to test how long the effects continued, two-way ANOVAs were conducted for different growth stages from 1991 to 1994 in *Quercus*. For *Juglans*, three-way ANOVAs including effects of emergence year were conducted, because germination occurred over a period of 2 years. Data were log- or (for percentage values) arcsine-transformed to meet assumptions of the ANOVA (Bartlett test).

Results

Emergence time

In *Quercus*, seedling emergence began in mid-May and continued until the end of July in all seed size-classes (Fig. 1). Percent emergence was greater for the large seeds than either the medium or small seeds (Fig. 1; ANOVA, $F=28.6$, $P<0.0001$). Although the number of days from snowmelt to seedling emergence was different among seed-size-classes (ANOVA, $F=4.21$, $P=0.015$), the absolute differences were very small (within 3.4 days). In *Juglans*, seedling emergence occurred over a period of 2 years (Fig. 1). It began in early June and continued until mid-August in all seed size-classes in both 1991 and 1992. In both years, percent emergence did not differ among seed-size-classes (ANOVA, $F<0.230$, $P>0.798$). The number of days from snow-melt to seedling emergence did not differ among seed size-classes in *Juglans* (Kruskal-Wallis test, $\chi^2=2.943$, $P=0.230$).

Growth phenology of current year seedlings

In *Quercus*, all the seedlings grew in a single flush, starting with the elongation of the shoot, followed by leaf expansion comprising all the annual leaf production, immediately after

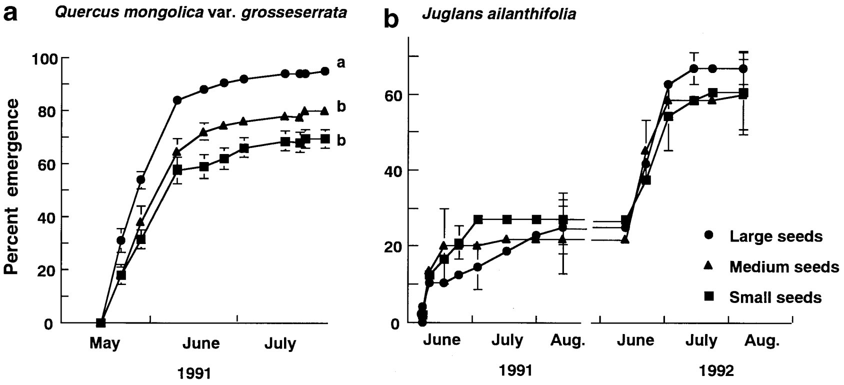

Fig. 1 Cumulative seedling emergence (mean±SE) from large, medium, and small seeds in a seed population from a single tree of **a** *Quercus mongolica* var. *grosseserrata* and **b** *Juglans ailanthifolia*. Values that do not share a common *letter* are significantly different from each other at $P<0.05$; Tukey-Kramer HSD after one-way ANOVA

Table 1 Two-way ANOVA of the effects of seed size and emergence time on the duration of leaf emergence (i.e., duration of height growth) of current year seedlings of *Quercus mongolica* var. *grosseserrata* and *Juglans ailanthifolia*. Data were log-transformed prior to calculation

Source of variation	*Quercus mongolica* var. *grosseserrata*		*Juglans ailanthifolia*		
	1991		1991		1992
	df	*F* ratio	*df*	*F* ratio	*F* ratio
Seed size (SS)	2	2.12	2	0.17	0.98
Emergence time (ET)	1	42.75^{*4}	1	10.63^{*2}	11.84^{*2}
SS×ET	2	3.51^{*1}	2	1.02	0.19

$^{*4}P<0.0001$, $^{*2}P<0.01$, $^{*1}P<0.05$

Table 2 Two-way ANOVA of the effects of seed zise and emergence time on seedling height and survival in *Quercus mongolica* var. *grosseserrata* in different growth stages. Data of seedling height and survival (%) were log- and arcsin-transformed prior to calculation, respectively

	Source of variation	*F* ratio				
		df	1991	1992	1993	1994
Seedling height	Seed size (SS)	2	124.4^{*4}	50.53^{*4}	28.42^{*4}	6.67^{*2}
	Emergence time (ET)	3	65.2^{*4}	3.04	1.79	0.90
	SS×ET	6	2.89	0.92	1.96	0.40
Seedling survival	Seed size (SS)	2	1.74	13.18^{*4}	15.17^{*4}	29.09^{*4}
	Emergence time (ET)	3	0.01	0.8	0.11	0.02
	SS×ET	6	0.71	0.04	0.29	0.08

$^{*4}P<0.0001$, $^{*2}P<0.01$

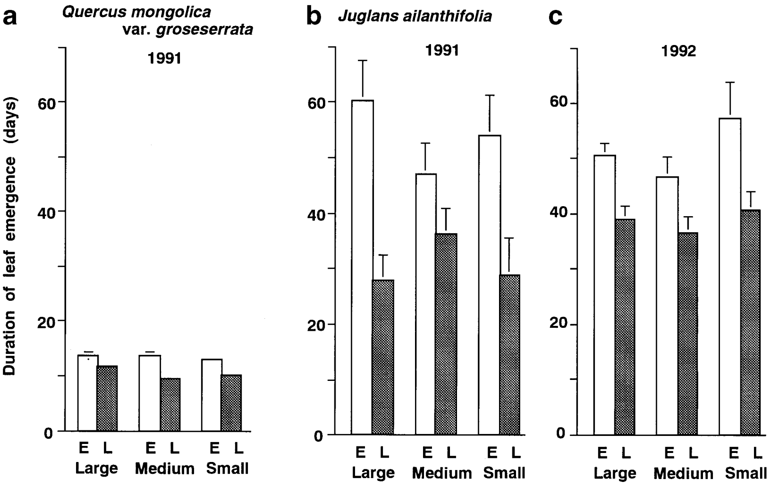

Fig. 2 Duration of leaf emergence (=duration of height growth) of current-year seedlings of early- (*E*) and late-emerging (*L*) cohorts from large, medium, and small seeds for **a** *Q. mongolica* var. *grosseserrata* in 1991 and *J. ailanthifolia* in **b** 1991 and **c** 1992

emergence, and no second flush occurred. In contrast, seedlings of *Juglans* grew continuously for a long time, accompanied by sequential unfolding of the leaves. Annual height growth stopped for all emerging seedlings at the end of July in *Quercus*, and in early September in *Juglans*. In both *Quercus* and *Juglans*, the duration of leaf emergence (=duration of height growth) was affected by emergence time but not by seed size (Table 1). Although the duration was longer for early emerging cohorts than late emerging ones for both the species, the absolute differences were large for *Juglans*, but very small for *Quercus* (Fig. 2).

Height growth

In *Quercus*, mean height of current-year seedlings was greatest for large-seeded seedlings and lowest for small-seeded ones within cohorts of different emergence times. Early-emerging cohorts were taller than late-emerging ones within each seed-size-class (Fig. 3, Table 2). Even early emergence of smaller seeds, however, did not result in seedling height exceeding those of seedlings from larger seeds. Figure 3 also shows very similar relative growth rates in seedling height (RHGR) among seedlings from different seed sizes throughout the experiment. The only exception was medium-seeded seedlings where late emergence resulted in a higher growth rate than early emergence. Thus, in *Quercus*, the initial positive effect of seed size on seedling height persisted until the end of the study period (Table 2), while the initial effect of emergence time on seedling height vanished from the 2nd year onwards (Table 2).

In *Juglans*, seedling height was significantly affected by year of emergence (Fig. 3, Table 3). The cohorts

Table 3 Three-way ANOVA of the effects of emergence year, seed size and emergence timing on seedling height of *Juglans ailanthifolia* in different growth stages. Data were log-transformed prior to calculation

	1991		1992		1993	
Source of variation	*df*	*F* ratio	*df*	*F* ratio	*df*	*F* ratio
Emergence year (EY)			1	0.75	1	9.08^{*2}
Seed size (SS)	2	1.25	2	1.32	2	0.46
Emergence timing (ET)	1	8.82^{*2}	1	3.27^{+}	1	6.07^{*1}
EY×SS			2	0.09	2	3.43^{*1}
SS×ET	2	0.05	2	0.60	2	0.95
ET×EY			1	11.75^{*2}	1	2.17
EY×SS×ET			2	0.35	2	0.21

$^{*2}P<0.01$, $^{*1}P<0.05$, $^{+}P<0.10$

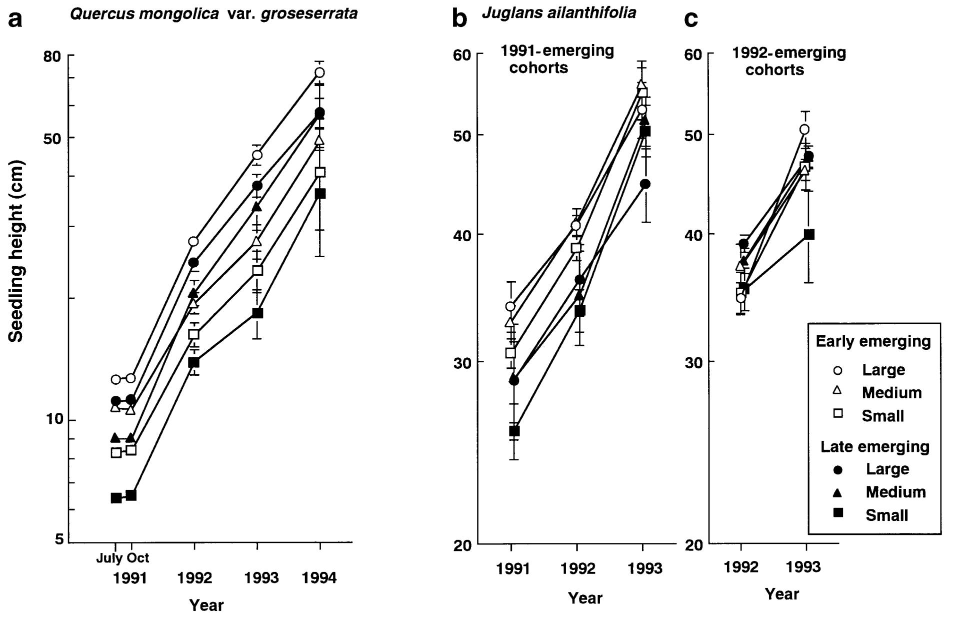

Fig. 3 Height growth (mean±SE) of seedlings which emerged from large (*circles*), medium (*triangles*), and small (*squares*) seeds for **a** *Q. mongolica* var. *grosseserrata* and **b,c** *J. ailanthifolia*. *Open* and *closed symbols* represent early- and late-emerging cohorts, respectively

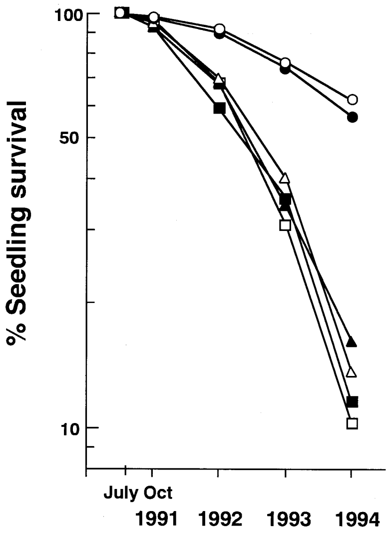

Fig. 4 Survivorship from July 1991 to October 1994 of *Q. mongolica* var. *grosseserrata* seedlings from large (*circles*), medium (*triangles*), and small (*squares*) seeds. *Open* and *closed symbols* represent early- and late-emerging cohorts, respectively

emerging in 1991 were taller than those emerging in 1992 and 1993. In the cohorts emerging in 1991, mean height of current-year seedlings was greatest for large-seeded seedlings and lowest for small-seeded ones within cohorts of different emergence time, although the difference was not significant (Table 3). Early-emerging cohorts were taller than late-emerging ones within each seed size-class (Fig. 3, Table 3). But even larger seeds that emerged late did not reach a seedling height exceeding that of early-emerging seedlings, as shown by the fact that duration of leaf emergence was positively correlated with seedling height in data pooled across all the seedlings with different emergence time and seed sizes in the cohort emerging in 1991 (Spearman rank correlation coefficient, $r_s=0.343$, $P=0.038$). In the cohort emerging in 1992, however, the correlation was not significant ($r_s=-0.099$, $P=0.457$), resulting in no clear relationship between seedling height and seed size or emergence time (Fig. 3). Figure 3 also shows similar RHGRs among seedlings of different emergence time and seed size-classes throughout the experiment for cohorts emerging in 1991. The exceptions were large-seeded seedlings, which showed lower RHGR than small- and medium-seeded seedlings in both early- and late-emergence. However, RHGRs of late-emerging seedlings did

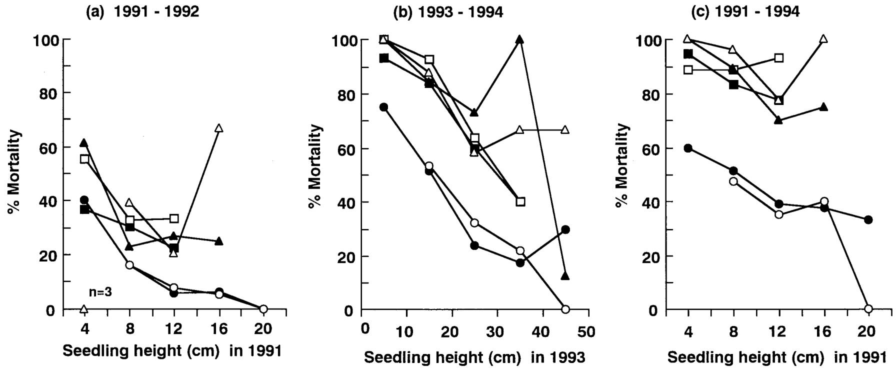

Fig. 5 Relationships between initial seedling height and seedling mortality (%) for early- and late-emerging cohorts of large (*circles*), medium (*triangles*), and small (*squares*) seedlings **a** from 1991 to 1992, **b** from 1992 to 1994, and **c** from 1991 to 1994 in *Q. mongolica* var. *grosseserrata*. *Open* and *closed symbols* represent early- and late-emerging cohorts, respectively

not exceed those of early-emerging seedlings (Fig. 3). Thus, the effect of emergence time on seedling height persisted until the end of the study period (Table 3), while the initial effect of seed size on seedling height vanished from the 2nd year onward (Table 3).

Seedling survival

In *Juglans*, during the 3-year study period, only one seedling died in 1993; the dead seedling was a late-emerging, small-seeded one which had emerged in 1991. In *Quercus*, although there was little mortality in the first year for all seed-size-classes, the mortality rate increased with time, particularly for medium- and small-seeded seedlings (Fig. 4). This has the effect of amplifying the effect of seed size on seedling survival with time (Table 2). In contrast, little difference was observed in seedling survival between early- and late-emerging cohorts over the 4-year study period in each seed-size-class (Fig. 4, Table 2).

In *Quercus*, seedlings with a shorter initial height showed greater mortality in both early- and late-emerging cohorts of each seed size-class in each growth stage (Fig. 5a–c). Percent mortality of large-seeded seedlings was usually lower than that of medium- and small-seeded seedlings in the 1st and last 2 years of the study period. Little difference in mortality was observed between early- and late-emerging cohorts in each seed size-class. The exception was early-emerging medium-seeded seedlings in which greater mortality was observed for seedlings of taller initial height in the first 2 years.

Discussion

The growth and survival of *Q. mongolica* var. *grosseserrata* seedlings were strongly influenced by seed size but less so by emergence time. In contrast, the growth of *J. ailanthifolia* seedlings was strongly affected by emergence time but only slightly by seed size. The strong effect of one factor compared with another was not due to greater variation in the former than the latter, because substantial variations were observed in both seed size and emergence time in both the species.

In all current-year seedlings of *Quercus* the shoot elongated in a single flush of growth and no secondary flush occurred, irrespective of seed-size and emergence time. Growth in height in the first year would be expected to depend strongly on seed size, as initial height growth would be closely related to the food reserve. The proportion of protein and carbohydrate reserves increases with increasing seed mass in acorns (Tripathi and Khan 1990; Bonfil 1998), which probably provides readily available energy that enhances emergence and initial vertical growth. It is worth noting that the seed reserve remaining immediately after leaf flush did not differ among seeds of different sizes (31–35% of initial seed reserve) in this species (Watanabe et al. 1996). Given the limitation of determinate growth form, annual height growth was independent of the emergence time. Thus, large-seeded seedlings, even those that emerged later, were always taller than small-seeded seedlings, even though they emerged earlier. After the second growing season, height growth rates among oak seedlings from seeds of different size and emergence time were almost identical (Fig. 3). This is probably because all seedlings had a single flush, as well as to size-dependent posterior growth. Therefore, the positive effects of seed size on seedling height persisted until the end of this experiment. In contrast, the effect of emergence time on seedling height soon diminished. In *Quercus*, when emergence times were compared among individuals of different height (age) in the experimental forest, timing of leaf emergence was earliest in the 1-year-old seedlings and shifted slightly later with the increase in height (age); the latest were the current-year seedlings (K. Seiwa, unpublished work). The difference in emergence time between early and late emergence also became smaller with increasing height (age). Such a low level of carryover effects of emergence time would explain the diminishing effect of emergence time on seedling height with time.

In contrast, in *Juglans*, early-emerging seedlings, even from small seeds, attained greater height than later-emerging ones, even those from larger seeds. Since seedling emergence of *Juglans* started approximately 3 weeks later than in *Quercus* and continued until mid-August, when herbs attained maximum height and mean daily temperature started to decrease rapidly, while environmental conditions such as light and temperature at the forest edge deteriorated with time (Seiwa 1998), particularly for late-emerging cohorts. In contrast, early-emerging seedlings would be able to utilize the longer period of favorable light and temperature conditions to grow taller before being crowded by neighboring herbs and being exposed to lower temperature. Therefore, seedling height was strongly affected by emergence time but little by seed size. Over the course of one growing season, early-emerging small seeds were able to compensate for their initial small size by longer duration of growth. Such compensatory growth would be possible for species with succeeding growth phenology, because they could continue to grow taller using current photosynthesis independent of seed reserve as long as environmental conditions remained favorable (Seiwa and Kikuzawa 1991, 1996; Watanabe et al. 1996). These findings suggest that the relative importance of the effects of seed size and emergence time on seedling growth is closely associated with growth phenology. Seedling growth greatly depends on seed size in the flush type but on emergence time in the succeeding type.

At early successional sites, such as abandoned fields or forests after cutting or fire, tree seedlings are negatively affected by severe competition for light, water and nutrients (Bush and Van Auken 1991; De Steven 1991; Myster 1993; Burton and Bazzaz 1995). Therefore, marginally taller seedlings from larger seeds can confer significant competitive advantage, as demonstrated by *Quercus*. Oak seedlings may have a greater ability to acquire resources compared with herbaceous neighbors due to their greater vertical growth and longer root system which passes through the zone of greatest competition (Myster 1993). At the end of the fourth growing season, the number of oak seedlings overtopping neighboring herbs (maximum height of herbaceous species was approximately 100 cm) was greatest for large-seeded seedlings (n=28) compared with medium- (n=3) and small-seeded seedlings (n=2). Initial size-dependent height growth and the capture of size-dependent resources enhance strongly seed-size-dependent competitive ability against neighboring herbs, resulting in proportionally greater survival of large-seeded seedlings in *Quercus*. At early successional sites, seedlings from large seeds have also shown greater reproductive success compared with those from small seeds in several herbaceous species (e.g., Gross 1984; Stanton 1984, 1985; Weller 1985; Marshall 1986; Wulff 1986b; Kalisz 1989; Cipollini and Stiles 1991; but see Schaal 1980). This 4-year observation of an oak species also showed that large-seeded seedlings may have a greater probability of growing to reproductive size than small-seeded ones at the forest edge. In *Juglans*, very few seedlings died, although observation was conducted for only 3 years. Greater seed size in *Juglans* than in *Quercus* resulted in seedlings of greater height than those of *Quercus* throughout the observed years, leading to greater competitive ability even in the small-seeded, late-emerging cohorts.

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