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Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest

R. S. Tripathi and M. L. Khan

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There is large variation in seed weight within the two species of *Quercus* (*Q. dealbata* L. and *Q. griffithii* Hk. f. & Th.) selected for the present study. Effects on germination and survival of oak seedlings were studied in relation to variation in seed weight and microsite characteristics. Germination showed a strong correlation with seed weight. Heavy seeds germinated earlier and showed better germination than light seeds and seedlings produced from the former survived and grew better. The differences in growth of the seedlings emerged from the seeds having different weights persisted in the second year also.

Emergence, survival and growth of the seedlings were highest in the plots devoid of litter and herbaceous cover and lowest in the control plots which were not cleared. Seedling emergence, survival and growth were more adversely affected by herbaceous cover than litter.

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Introduction

Variation in seedling fitness may be caused by differences in initial seed mass, microsite characteristics and/or genotypic variations. Harper and Obeid (1967) and Stanton (1984) argue that larger reserve in seeds may allow more pre-photosynthetic growth of seedlings and this in turn, may contribute to better growth and survival of seedlings that emerge from heavy seeds. Differences in the early juvenile stage could be an important determinant of the relative success of individuals in later phases of the life cycle. Several studies carried out on weeds and crops have revealed that seedling size is usually directly related with food reserves and energy content of seeds (Harper 1977, Rai and Tripathi 1982, 1987, Zimmerman and Weis 1983, Winn 1985, Keddy and Constabel 1986, Wulf 1986a, b, Roach 1987). However, in the case of tree species, similar studies are rather few and scattered (Ghosh et al. 1976,

Howe and Richter 1982, Dunlop and Barnett 1983, Stoehr and Farmer 1986).

Heterogeneity of physico-chemical and biotic factors divides a habitat into a mosaic of microsites (Harper et al. 1961, Grubb 1977). Apart from intrinsic features of seeds, variations in microsite characteristics also influence the size and fitness of the seedling population. Gross (1984) reported that within a species, seed size-classes of *Daucus carota* and *Oenothera biennis* showed differences in percentage emergence depending on the microhabitat into which they were sown. Snow (1971) suggested that large seeds produce seedlings that are competitive in the forest understorey where light is limiting, while small seeds with rapid germination colonize the openings. Several workers have emphasized the significance of herbaceous ground cover (Eis 1981, Maguire and Forman 1983, Khan and Tripathi 1989) and litter (Grime 1979, Willis 1980, Burton and Mueller-Dombois 1984, Connell et al. 1984, Winn 1985) in de-

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Tab. 1. Seed weight classes of the two species of *Quercus* along with their proportion in seed sample, viability and contents of ash, energy and storage compounds.

	Weight range (mg seed ⁻¹)	Proportion (%)	Viability (%)	Ash (mg seed ⁻¹)	Protein (mg seed ⁻¹)	Carbohydrate (mg seed ⁻¹)	Lipid (mg seed ⁻¹)	Energy (calories seed ⁻¹)
<i>Q. dealbata</i>								
Weight class								
W ₁	283–450	26.3	58.4 ^{a*}	20.46 ^a	28.63 ^a	179.66 ^a	71.05 ^a	1699.51 ^a
W ₂	550–750	40.7	60.0 ^a	34.28 ^b	54.24 ^b	273.66 ^a	237.82 ^b	3494.15 ^b
W ₃	980–1283	33.0	62.3 ^a	64.88 ^c	94.81 ^c	510.61 ^c	429.09 ^c	6510.78 ^c
<i>Q. griffithii</i>								
Weight class								
W ₁	245–450	22.2	68.6 ^a	6.77 ^a	28.15 ^a	159.47 ^a	94.61 ^a	1660.72 ^a
W ₂	560–850	48.3	71.3 ^a	20.76 ^b	60.60 ^b	288.19 ^b	225.44 ^b	3498.59 ^b
W ₃	930–1080	29.5	86.2 ^b	37.43 ^c	81.50 ^c	482.34 ^c	385.54 ^c	5707.29 ^c

* Means within a column followed by a common letter are not significantly different ($p = 0.05$) as determined by Tukey's multiple range test.

termining emergence, survival and growth of tree seedlings.

Quercus dealbata L. and *Q. griffithii* Hk. f. & Th., the two important components of sub-tropical wet hill forests of Meghalaya state in north-east India show enormous variation in seed weight. The forest floor has generally a thick accumulation of litter, while in a few places it is quite bare. The herbaceous vegetation also presents a mosaic of dense and poor patches. The variation in microsite characteristics in these forests and the common occurrence of the two species of *Quercus* showing wide differences in seed weight offer an excellent opportunity to address two basic questions: (1) do the differences in seed weight affect their germinability; and (2) do the seedling populations derived from seeds having different weights react differentially to microsite characteristics?

Materials and methods

Seed source

Mature acorns of *Quercus griffithii* and *Q. dealbata* were collected in October 1983 and March 1984, respectively from a sub-tropical wet hill forest at Upper Shilong (25°34'N, 91°56'E; altitude 1955m) in Meghalaya. In both species there was wide variation in seed weight, which permitted the categorisation of seeds into three distinct weight classes, light (W₁), medium-weight (W₂) and heavy (W₃) (see Tab. 1). Seed weight was determined by weighing 20 samples of 20 seeds each from each of the three categories. Seeds were stored separately in sealed plastic bags at room temperature (min. 10°C, max. 22°C) for future use.

Analysis of seed reserves

In order to know whether the amount of food reserves and energy content vary with the seed weight, protein,

lipid, ash and carbohydrate content and caloric values of seeds of the three weight classes were determined for both species. For the determination of average seed weight, five replicates of 20 seeds each were weighed. Protein was estimated by the method outlined by Bradford (1970) while lipid and carbohydrate were determined by the procedures described by Kochert (1976). Ash content was determined by combustion at 500°C for 2 h. To determine the caloric content a Parr Oxygen bomb calorimeter was used in which samples were ignited at an oxygen pressure of 32 atm. The calorimeter was standardised with benzoic acid tablets.

Seed germination and seedling growth

Laboratory conditions

The viability of seeds was determined by tetrazolium solution before testing them for germination. Seeds of each of the three weight classes were separately soaked for 24 h in distilled water at room temperature (22 ± 2°C). The soaked seeds were placed on moist blotting paper underlain with cotton in plastic trays (30×25 cm) for germination. In order to maintain moist condition a small quantity of water was added to the trays regularly. Each tray containing 20 seeds served as a replicate and for each weight class there were five replicates. Germination of the three categories of seeds was studied at room temperature. Seeds were considered as germinated when the radicle protruded about 1 mm beyond the seed coat. Germination was recorded daily for a period of 45 d after which germination practically ceased. Differences between viability and germinability of seeds show that some of the viable seeds did not germinate and got degenerated.

Natural conditions

The effects of seed weight and microsite characteristics were studied on germination, survival and growth of the oak seedlings in the natural habitat (forest) at Upper

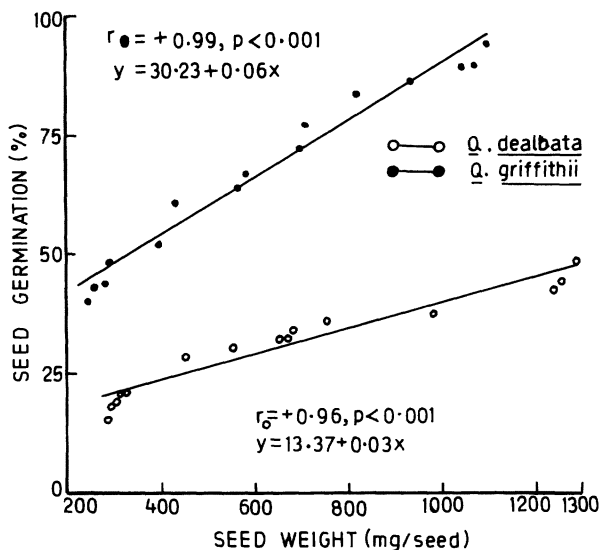


Fig. 1. Relationship between seed weight and germination of the seeds. x represents the seed weight and y seed germination.

Shillong. For this purpose, seeds of the three weight classes were sown in four different types of plots (T_1 to T_4 as described below) of 2×2 m size:

- T_1 – Control plots, where the herbaceous vegetation was allowed to grow and litter was left undisturbed.
- T_2 – Herbaceous vegetation was allowed to grow, but litter was removed.
- T_3 – Herbaceous vegetation was cleared but litter was left intact.

T_4 – Both litter and herbaceous vegetation were removed.

The forest stand where the field experiment was conducted is predominantly composed of broad-leaved tree species viz., *Quercus dealbata*, *Q. griffithii*, *Schima khasiana* Dyer., *Manglietia insignis* (Wall., Bl.) and *Myrica esculenta* Buch. Ham with *Rhododendron arboreum* Sm., *Eurya japonica* Thunb., *Myrsine semiserrata* Wall., *Lindera pulcherrima* Benth. and *Symplocos* sp. forming the under-storey. *Litsea elongata* Wall., *Daphne shillong* Banerjee, *Lantana camara* L. and *Cinnamomum* sp. are the common shrubs and *Osbeckia crinata* Benth., *Eupatorium adenophorum* Spreng., *Coffea khasiana* L., *Rubus* sp. and some ferns and mosses represent the herbaceous ground flora. The average tree density in the forest was 613 ha^{-1} . The density of herbaceous vegetation was 78 and 20 plants m^{-2} in rainy and winter seasons respectively. Average depth of litter was 19.5 mm. The forest canopy is sparse due to selective tree felling and burning. The mean light intensity on the forest floor was 11.8×10^3 lux. The soil is lateritic, sandy loam and acidic (pH 5.3) with low contents of organic matter (2.9%) and nitrogen (0.17%).

Five 2×2 m plots were established for each of the above mentioned treatments and 100 seeds of each of the three weight classes were separately sown in each plot in 2 cm deep pits, with 20 cm gap in between. The experimental design consisted of four treatment plot for three weight classes for both species, each replicated five times. Seedling emergence was recorded at 2-d intervals over a period of 60 d after which no emergence occurred. Seedling survival was monitored at two-month intervals over a period of two years (from June,

Tab. 2. Germination behaviour of seeds of different weight classes of two species of *Quercus* under laboratory conditions.

Species	Seed weight class	Period taken for initiation of germination (d)	Percentage germination over a 45-d period
<i>Q. dealbata</i>	W ₁	19 ^{a*}	22 ^a
	W ₂	17 ^b	38 ^b
	W ₃	16 ^b	41 ^b
<i>Q. griffithii</i>	W ₁	17 ^a	51 ^a
	W ₂	14 ^b	69 ^b
	W ₃	12 ^c	84 ^c

Analysis of Variance

	Source of variation	MS	df	F value	MS	df	F value
<i>Q. dealbata</i>	Seed weight	11.67	2	14.0**	521.67	2	100.97**
	Error	0.83	12		5.17	12	
<i>Q. griffithii</i>	Seed weight	29.4	2	40.09**	1286.67	2	75.69**
	Error	0.73	12		17	12	

* Means followed by a common letter are not significantly different ($p = 0.05$) as determined by Tukey's multiple range test.
 ** Significant at the 0.001 level.

Tab. 3. Effects of seed weight and treatment plots on germination of two species of *Quercus* in the forest stand at Upper Shillong.

Species	Seed weight class	Treatment plots [†]			
		T ₁	T ₂	T ₃	T ₄
<i>Q. dealbata</i>	W ₁	8.2	13 ^{a*}	14 ^a	18.2
	W ₂	15	20.2 ^a	20.8 ^a	24.8
	W ₃	23	31 ^a	32 ^a	35
<i>Q. griffithii</i>	W ₁	23.8	30 ^a	27 ^a	40.2
	W ₂	30	43.4 ^a	41.2 ^a	51.2
	W ₃	51.6	58.2 ^a	55 ^a	68

Analysis of variance

Source of variation		MS	df	F value	P
<i>Q. dealbata</i>	Weight	1445.12	2	353.91	0.001
	Plot	289.2	3	70.82	0.001
	Weight x plot	3.65	6	0.894	NS
	Error	4.08	48		
<i>Q. griffithii</i>	Weight	3955.27	2	858.27	0.001
	Plot	747.18	3	172.98	0.001
	Weight x plot	11.62	6	2.52	0.05
	Error	4.61	48		

[†] Symbols T₁ to T₄ explained under Materials and method.

* Means in the rows followed by letter 'a' do not differ significantly from each other, while the others (both in rows and columns) are significantly different (p = 0.05) from one another as determined by Tukey's multiple range test.

Tab. 4. Effects of seed weight and treatment plots on seedling survival (%) of two species of *Quercus* in the forest stand at Upper Shillong after a period of two years.

Species	Seed weight class	Treatment plots [†]			
		T ₁	T ₂	T ₃	T ₄
<i>Q. dealbata</i>	W ₁	9	11	15	18
	W ₂	15	19	25	30
	W ₃	19	22	27	35
<i>Q. griffithii</i>	W ₁	13 ^{a*}	15 ^a	18	21
	W ₂	18 ^a	21 ^a	28	33
	W ₃	25 ^a	28 ^a	32	39

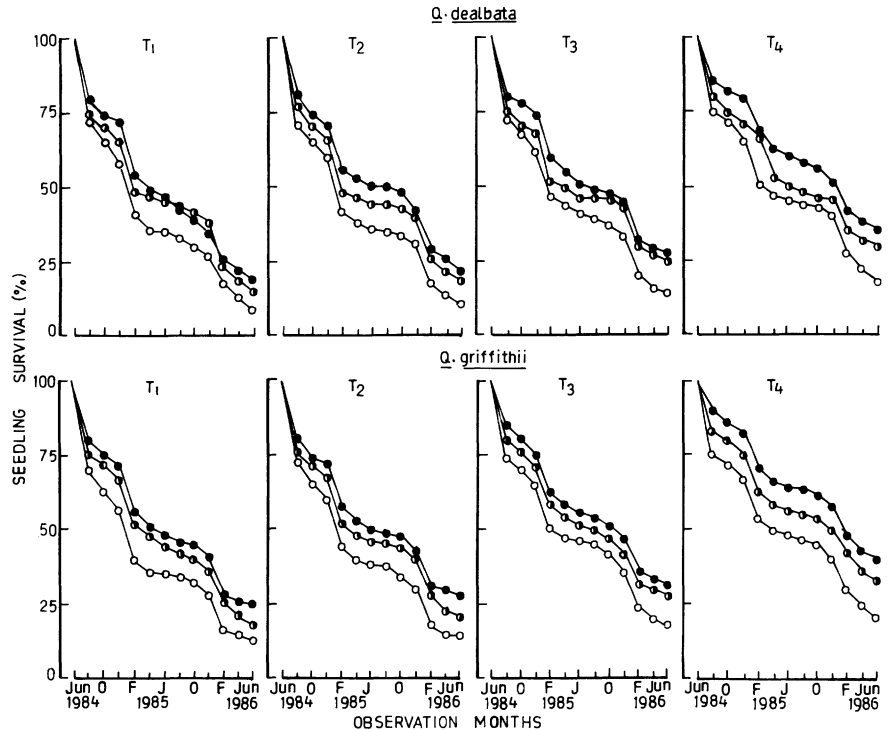
Analysis of variance

Source of variation		MS	df	F value	P
<i>Q. dealbata</i>	Weight	831.67	2	266.13	0.001
	Plot	513.75	3	164.40	0.001
	Weight x plot	14.99	6	4.78	0.001
	Error	3.125	48		
<i>Q. griffithii</i>	Weight	1023.75	2	299.63	0.001
	Plot	441.52	3	129.23	0.001
	Weight x plot	16.53	6	4.84	0.001
	Error	3.42	48		

[†] Symbols T₁ to T₄ explained under Materials and methods.

* Means in the rows followed by letter 'a' do not differ significantly from each other, while the others (both in rows and columns) are significantly different (p = 0.05) from one another as determined by Tukey's multiple range test.

Fig. 2. Survival (%) of seedlings emerged from the seeds of three weight classes in four different types of plots (T₁-T₄, described in Materials and methods) ○, ● and ● represent the seedlings emerged from heavy, medium and light seeds respectively.



1984 to June, 1986). Three lots of 10 seedlings of the respective species derived from each of the three seed-weight classes were harvested from each type of plot after 1 and 2 yr from the date of sowing and their dry matter yield was determined to find out whether differences in seedling growth due to seed weight did persist. The seedlings were excavated from each plot and washed thoroughly with water to remove the soil particles adhering to the root system. Dry matter yield was determined by drying the plant material in an oven at 60°C to constant weight. Data were analysed by two way analysis of variance and by applying Tukey's multiple range test.

Results

Seed reserves

Quercus dealbata and *Q. griffithii* showed wide variation in seed weight based on which three distinct seed weight classes could be recognized. Seed viability did not vary with seed weight (Tab. 1). Seeds of *Q. dealbata* were slightly heavier than those of *Q. griffithii*. Protein, lipid, ash, carbohydrate and energy contents of *Q. dealbata* seeds were also greater than *Q. griffithii*; however, the differences were statistically insignificant except for ash content ($P = 0.05$). The food reserves, ash content and caloric values increased significantly ($P = 0.05$) with seed weight in both species (Tab. 1).

Seed germination

Germination was highly correlated ($P < 0.05$) with seed weight in both species (Fig. 1). The heavy seeds (W_3) germinated earlier and their germination percentage was significantly ($P < 0.001$) higher than the lighter seeds (Tab. 2). Seed germination was greater in *Q. griffithii* than in *Q. dealbata* (Tabs 2 and 3).

Differences in seed germination due to plot types were highly significant ($P < 0.001$, Tab. 3). Seeds of all weight classes showed maximum germination when sown in the plots devoid of litter and herbaceous vegetation, while minimum germination was observed in the control plots. Seedling emergence in the plots containing litter did not differ significantly from that in the plots with herbaceous vegetation (Tab. 3).

Survival and growth of seedlings

Seedling survival was significantly affected by seed weight and plot types (Tab. 4). In both species seedlings that emerged from the heavy seeds (W_3) survived better than those from the lighter seeds. Further, survival of seedlings was maximum in T₄ and minimum in T₁ plots. Survival was more adversely affected by the herbaceous cover than by the accumulated litter (Tab. 4 and Fig. 2). Survivorship curves suggest greater mortality of seedlings during the juvenile stage and during December to February, the period characterised by high soil moisture

Tab. 5. Dry matter yield (g/seedling) of 1- and 2-yr old seedlings produced by the seeds having different weight and sown in different treatment plots.

Species	Seed weight class	1-yr old seedlings treatment plots†				2-yr old seedlings treatment plots†			
		T ₁	T ₂	T ₃	T ₄	T ₁	T ₂	T ₃	T ₄
<i>Q. dealbata</i>	W ₁	0.42	1.0 ^{a*}	1.35 ^a	1.82	1.08	2.28	2.82	3.3
	W ₂	1.0	1.6 ^a	2.0 ^a	2.4	2.26	3.88	4.84	5.58
	W ₃	2.46	2.74 ^a	3.0 ^a	3.4	5.4	5.8	7.16	8.68
<i>Q. griffithii</i>	W ₁	1.06	1.94 ^a	2.5 ^a	3.0	2.82 ^a	3.36 ^a	5.0	5.48
	W ₂	2.58	2.84 ^a	3.12 ^a	3.54	5.1 ^a	5.46 ^a	6.28	6.98
	W ₃	3.22	3.44 ^a	3.62 ^a	4.1	6.08 ^a	6.44 ^a	8.44	9.26

Analysis of variance									
	Source of variation	MS	df	F value	P	MS	df	F value	P
<i>Q. dealbata</i>	Weight	15.88	2	238.08	0.001	97.79	2	1004.78	0.001
	Plot	3.98	3	59.63	0.001	23.81	3	244.65	0.001
	Weight x plot	0.073	6	1.09	NS	0.98	6	10.11	0.001
	Error	0.067	48			0.097	48		
<i>Q. griffithii</i>	Weight	10.98	2	182.17	0.001	57.52	2	537.15	0.001
	Plot	4.26	3	70.68	0.001	22.16	3	206.91	0.001
	Weight x plot	0.37	6	6.18	0.001	0.69	6	6.47	0.001
	Error	0.06	48			0.107	48		

† Symbols T₁ to T₄ explained under Materials and methods.

* Means in the rows followed by letter 'a' do not differ significantly from each other, while the others (both in rows and columns) are significantly different (p = 0.05) the from one another as determined by Tukey's multiple range test.

stress and low temperature in Meghalaya (Yadav and Tripathi 1981).

Dry matter yield was also significantly affected by seed weight and plot types (P<0.001) (Tab. 5). Seedlings emerged from heavy seeds (W₃) and grown in plots devoid of litter and herbaceous vegetation produced the highest biomass, while those resulting from the lighter seeds (W₁) and grown in the control plots produced least dry matter. The differences in dry matter yield of seedlings due to litter and herbaceous cover were insignificant up to 1 yr of age, however, after 2 yr the differences were significant (P = 0.05). In general, herbaceous vegetation influenced seedling growth more adversely than did litter (Tab. 5). The differences in growth of the seedlings from the seeds of different weight classes persisted in the second year also (Tab. 5).

Discussion

The results reveal that germination, survival and growth of seedlings in *Quercus dealbata* and *Q. griffithii* are influenced to a large extent by the food reserves and energy content of seeds, which increased significantly with seed weight (Tab. 1). Rapid and better germination of the heavier seeds (Tab. 2, Fig. 1) attributable to larger food reserves of these seeds is in agreement with the earlier reports by Griffin (1972), Ghosh et al.

(1976), Howe and Richter (1982) and Dunlop and Barnett (1983) in other tree species. An increased proportion of protein and carbohydrate, as suggested by Flint and Palmblad (1978), provides the readily available energy which stimulates germination. Better survival and growth of the oak seedlings which emerge from heavy seeds are linked with larger protein, lipid, carbohydrate and energy contents of these seeds as compared with light seeds.

In a study on *Lithospermum caroliniense*, Weller (1985) reported that nutlet mass was positively correlated with emergence, survival and seedling size. Initial size hierarchies related to differences in nutlet mass were maintained as the seedlings grew. Likewise, the differences in growth of the oak seedlings persisted through the second year. Rai and Tripathi (1987) argued that better survival and growth of seedlings resulting from seeds rich in food reserves confer competitive advantage on plants. Better growth of the oak seedlings emerging from the larger seeds leads to the conclusion that the ecological fitness of the oak species under study is presumably linked with greater maternal carry-over effects.

The treatment plot in which litter and herbaceous vegetation were left intact, differed a great deal from those where one or both of these were absent. Therefore, seeds sown in the different treatment plots are

expected to respond differently and the effect of microsite characteristics on seed germination and seedling population responses may be modified by the food and energy content of the seeds. In general, the litter and herbaceous cover inhibited emergence, survival and growth of the oak seedlings. The heavy seeds (W_3) gave rise to a larger number of seedlings than the light seeds. This may be due to better germination of the former (Tab. 2 and 3) and/or to the differential response of the seeds differing in food and energy content to accumulated litter and herbaceous vegetation. Winn (1985) reported that in *Prunella vulgaris*, germination of small seeds is inhibited more by the litter and herbaceous cover than that of heavier seeds. In field experiments with four biennial species, Gross and Werner (1982) showed that species with smaller seeds could establish only on the bare ground, while those with larger seeds germinated and survived both on bare ground and in established vegetation. Crawley and Nachapong (1985) observed that in *Senecio jacobaea* primary shoots produce large seeds and regrowth shoots produce small seeds. When sown in dense, unaltered vegetation, neither kind of seed produced many seedlings, whereas in cut-grass plots, where plant competition was reduced but still was substantial, seeds from primary shoots produced just as many seedlings as they did in cultivated, competition-free soil. In contrast, the smaller seeds from regrowth shoots produced virtually no seedlings when sown in similar cut-grass plots. The seedlings emerging from the seeds produced by regrowth shoots were less competitive than those from the seeds produced by primary shoots. The overall implication of these findings is that individuals with larger mean seed size have a reproductive advantage in competitive habitats. Howe and Richter (1982) also suggested that large-seeded plants have an advantage when seedlings have to compete.

McGinley et al. (1987) argued that whenever the environment consists mostly of the favourable habitat, a parent does best by producing only small offspring. If conditions are reversed, production of larger offspring could be more advantageous. In general, greater availability of safe microsites may render the seed size difference to be of lesser adaptational significance. In the case of oak species, observed differences in seed germination, seedling survival and growth in different plot types due to seed size do indicate that the oak seeds of different sizes differ considerably in their safe-microsite requirement, which may ensure successful colonisation of a mosaic of habitats within the forested ecosystem where they are dispersed. Far greater risk of predation on light and medium-weight seeds (40% and 50% respectively) than on heavy seeds (25%; M. L. Khan and R. S. Tripathi, unpubl. data) reveals that relatively smaller seeds are presumably preferred by predators whereby the predation pressure on the heavy seeds tends to decrease. Such a situation may certainly confer advantage on the heavy seeds and the production of a

high proportion of light (W_1) plus medium-weight (W_2) seeds (up to 67% in *Q. dealbata* and 70.5% in *Q. griffithii*) may be indirectly helpful in protecting the heavy seeds against predation. In the case of levelled topography most of the seeds, irrespective of size, disperse around the parental plant with an average dispersal distance of 20 m. However, the small seeds are carried to longer distances by run-off water (M. L. Khan and R. S. Tripathi, unpubl. data) thus indicating that in a place like Meghalaya where rainfall is heavy and the terrain is mostly hilly, the production of smaller seeds may help in dispersal. The ratios between dry matter yield of seedlings produced by heavy seeds and by lighter seeds in different treatment plots indicate that in the plots devoid of litter and herbaceous vegetation the growth differences due to seed size were narrowed down considerably compared with the plots having litter and/or herbaceous vegetation. A similar trend is discernible when seed germination differences owing to seed weight in different treatment plots is considered. This suggests that even small seeds of the two oak species performed well in such situations where litter and herbaceous vegetation were not present to cause suppression in seed germination and seedling growth.

Improvement in seed germination and survival and growth of seedlings attributable to larger seed weight particularly in the plots where litter had accumulated and herbaceous plant species offered competition, indicates that sufficient energy contained in large seeds enhances the emergence of seedlings and sustain them until they grew high enough to support themselves photosynthetically. Thus the microsites that are unfavourable for the light seeds, could be successfully exploited by the heavier seeds. The occurrence of seeds of different weight showing large variation in food reserves and energy content in *Q. dealbata* and *Q. griffithii* and differential response of these seeds and seedlings produced by them to microsite characteristics may be viewed as an important regenerative strategy.

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