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Effect of seed weight, light regime and substratum microsite on germination and seedling growth of *Quercus semiserrata* Roxb.

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Abstract: Seeds of *Quercus semiserrata* Roxb. vary widely in weight, and can be classified into small (<5 g), intermediate (5 to 8 g) and heavy (>8 g) classes. Heavy seeds contain greater reserves of protein, carbohydrate, lipid and energy than intermediate-weight and small seeds. Seed weight has a strong effect on germination. Heavy seeds germinate early and show better germination than small seeds both under laboratory as well as greenhouse conditions. Further, the seedlings from heavy seeds survive better and yield greater dry mass than those from small seeds. Of the four substratum microsites tested (above moss layer, above litter, under litter and above soil surface), maximum germination occurred on moss. The position under litter produced significantly better results than above litter, but did not vary in comparison to soil surface. Of the three light regimes tested (90%, 52% and 28% of full light), 52% light resulted in maximum germination, seedling survival and dry mass production. However, the results between 90% and 28% light did not vary significantly. An interaction of seed weight, microsite and light appears to lay optimal conditions for seed germination and early seedling growth.

Resumen: Las semillas de *Quercus semiserrata* Roxb. Varían ampliamente en peso, y pueden ser clasificadas como pequeñas (<5 g), intermedias (5 a 8 g) o pesadas (>8 g). Las semillas pesadas contienen reserves más grandes de proteína, carbohidratos, lípidos y energía que las semillas de peso intermedio y las pequeñas. El peso de las semillas tiene un fuerte efecto sobre la germinación. Las semillas pesadas germinan más temprano y muestran una germinación major que las semillas pequeñas, tanto en condiciones de laboratorio como de invernadero. Además, las plántulas formadas a partir de semillas pesadas tienen una major supervivencia y tienen un rendimiento mayor de peso seco que las derivadas de semillas pequeñas. De los cuatro micrositios de sustrato que fueron investigados (sobre una capa de musgos, sobre el mantillo, bajo el mantillo y sobre la superficie del suelo), la máxima germinación tuvo lugar sobre el musgo. La posición bajo el mantillo produjo resultados significativamente mejores que sobre el mantillo, pero no varió en relación con la superficie del suelo. Los resultados obtenidos bajo el mantillo fueron significativamente diferentes de los obtenidos sobre el mantillo, pero de los obtenidos en la superficie del suelo. De los tres regimens lumínicos probados (90%, 52%, y 28% de la luz total), 52% de luz produjo los máximos de germinación, supervivencia de plantas y producción de biomasa seca. Sin embargo, los resultados entre 90% y 28% de luz no variarion significativamente. La interacción del peso de la semilla, el micrositio y la luz parece ofrecer condiciones óptimas para la germinación de semillas y el crecimiento temprano de las plántulas.

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Resumo: As sementes da *Quercus semisserata* Roxb. variavam fortemente em peso, e foram classificadas nas classes de pequenas (<5 g), intermédias (5 a 8 g) e pesadas (>8 g). As sementes pesadas contêm maiores reservas em proteínas, hidratos de carbono, lípidos e energia do que as sementes intermédias e as mais pequenas. O peso das sementes tem um efeito marcado na precocidade da germinação e mostraram uma melhor germinação do que as sementes pequenas, quer em laboratório, quer em estufa. Além disso, as plântulas das sementes pesadas apresentaram uma melhor sobrevivência e produziram uma massa seca maior do que as provenientes de sementes pequenas. Dos quatro substratos das micro estações testadas (sobre uma camada de musgo, sobre folhada, sob folhada e sobre a superfície do solo), a germinação máxima verificou-se no musgo. A posição sob folhada produziu resultados significativamente melhores do que sobre o mesmo substrato, mas não variou em comparação com a superfície do solo. Dos três regimes de luz testados (90%, 52% e 28% de luz plena) o regime dos 52% produziu uma germinação máxima, uma maior sobrevivência e uma maior produção de massa seca. Contudo, os resultados entre os 90% e os 28% de luz não variaram significativamente. As condições óptimas para a germinação das sementes e para o crescimento precoce estão contudo relacionadas com a interacção entre o peso da semente, a micro estação e o regime de luz.

Key words: Germination, India, light regime, oak, *Quercus semiserrata*, seedling growth, seed weight, substratum microsite.

Introduction

Oaks show wide variation in seed size within a species. Seedlings emerging from seeds of varied sizes exhibit differential competitive performance due to variation in emergence time and growth rate (Barik *et al.* 1996; Garrison & Augspurger 1983; Tripathi & Khan 1990). Large and heavy seeds have better seedling survival and growth than small seeds (Armstrong & Westoby 1993; Bonfil 1998; Vera 1997). However, small seeds confer the advantage of greater dispersal efficiency (Ganeshaiah & Uma Shaanker 1991; Hegde *et al.* 1991). Thus conflicting selection pressures for two components of fitness, namely, seedling establishment and dispersal efficiency, have the potential to maintain variability in seed size. Pre-dispersal predation of seeds may determine seed number per acorn in oaks (Garrison & Augspurger 1983). Selection due to predation of seeds may also favour large or small size seeds depending on the predator's preference (Harper *et al.* 1970).

Extrinsic factors such as substratum microsite and light may substantially affect seed germination and seedling survival (Bargali *et al.* 1998; Everham *et al.* 1996; Khan & Tripathi 1989a; Myster 1994; Nyandiga & Mcpherson 1992; Rao *et al.* 1997). Small-scale heterogeneity of physical and biotic factors divides a habitat into a mosaic of microsites, only some of which are suitable for germination of the seeds (Grubb 1977) and establishment of seedlings (Khan & Tripathi 1989b). When only a few favourable microsites are available, seed number may be maximised to ensure dispersal to favourable sites. On the other hand, if favourable sites are plentiful, the advantages of producing a large number of seeds may be outweighed by the higher probability of emergence associated with larger seeds (Winn 1985). Most species in closed canopy tropical forests appear to depend on gaps for successful regeneration (Whitmore 1978). The intensity of light available to seeds for germination depends on the size of the gap (Popma & Bongers 1991).

This study pertains to *Quercus semiserrata* Roxb., a late successional, evergreen tree reaching up to 25 m height and occupying dense canopy to small and medium size gaps (Haridasan & Rao 1987). The seeds mature at the end of rainy season (November) and germinate soon after fall. The germinated seeds and small seedlings may face a prolonged winter drought since precipitation during winter (November to February) is very little or absent in some years. A mosaic of microsites is available for seeds to fall, germinate and establish on the forest floor. These microsites include litter, moss and exposed soil. We test here that (a) heavy seeds will confer greater seed germination and seedling survival by the virtue of greater food reserves, (b) moss will provide a better substratum than litter or bare soil since moisture stress may prevail during winter, and (c) high intensity light will not favour seed germination and seedling growth since it may create moisture stress.

Materials and methods

Seed source and reserves

After shedding, we collected about 6,000 mature acorns of *Q. semiserrata* in October-November, 1996 from a sub-tropical wet hill forest in Namdapha National Park (27°51′ - 28°51′ N latitude, 95°45′ - 97°30′ E longitude, and 200-400 m altitude) in Arunachal Pradesh, India. The healthy, non-predated seeds were weighed individually and classified into three weight classes, namely, 'small' (<5 g), 'intermediate' (5 to <8 g) and 'heavy' (≥8 g). Mean seed weight for each class was determined by averaging the weights falling in each category. The relative proportion of three weight classes was calculated by dividing the number of seeds in each class by the total seeds. Observations on predated seeds were taken while weighing the seeds, and the proportion of predated seeds in each weight class was calculated by dividing the number of predated seeds by the total seeds in each weight class. Mainly an unidentified moth larva predated the seeds. The predated seeds were discarded in further study. Seeds were stored in sealed plastic bags at room temperature (22 ± 8°C) and sown within a week to avoid the loss of viability.

Fifty seeds from each of the three weight classes were used for testing viability by 5% tetrazolium solution for 24 h. To understand whether food and energy reserves vary in three weight classes, ash, protein, carbohydrate, lipid and caloric value were determined by drawing 20 seeds from each of the three weight classes. Ash content was determined by combustion at 500°C for 2 h. Protein was estimated according to Bradford (1970). Carbohydrate and lipid were determined by the procedures described by Kochert (1976). Caloric content was determined by a Parr oxygen bomb calorimeter wherein samples were ignited at 32 atm oxygen pressure and standardised with benzoic acid tablets.

Germination in laboratory

Seeds from the three weight classes were separately soaked for 24 h in distilled water at room temperature (25 ± 2°C). The soaked seeds were placed on moist blotting paper underlain with cotton in plastic trays (30 x 25 cm) for germination. To maintain the moist condition, a small quantity of distilled water was added to the trays daily. A tray containing 10 seeds served as one replicate and there were five replicates for each weight class. Seeds were considered as germinated when the radical had protruded about 1 mm beyond the seed coat. Germination was recorded daily for 45 days when it had practically ceased.

Seed germination and seedling growth in greenhouse

The effect of seed weight, light regime and substratum microsite on germination was studied under greenhouse conditions at the North Eastern Regional Institute of Science and Technology campus, Itanagar (27°07′ N latitude, 93°22′ E longitude, 100 m altitude). The experiment was set up in a factorial design comprising 3 weight classes, 3 light regimes, 4 substratum microsites and five replicates. Three light regimes were created separately in 3 greenhouses. The first greenhouse was covered with a double-layered black muslin cloth to reduce the light intensity to about 28%, and was labelled as L_1. The second greenhouse was covered with a single layered white muslin cloth to reduce the light intensity to about 52% and was labelled as L_2. The third greenhouse had polythene roofing to reduce the light intensity to about 90% and was labelled as L_3. The three light regimes correspond to that available respectively in a small, intermediate and large gap in a natural forest. In order to minimise water splashing during rainy season, four sides of a greenhouse were covered up to a height of 70 cm with a polythene sheet.

The four substratum microsites included a moss layer of 10 mm and seeds sown on it, a litter layer of 20 mm from a mixture of tree species and seeds sown on it, a litter layer of 20 mm from a mixture of tree species and seeds sown under it, and a soil surface and seeds sown on it. Fifteen plots of 45 x 60 cm in each greenhouse were established for each of the four substratum microsites. Thus a total of 60 plots were established in each greenhouse. Five plots of each substratum microsite in each greenhouse were used for each of the three seed weight classes. Ten seeds were sown in each plot. The seeds within a row were 10 cm apart from each other and the interval between the two rows was 15 cm. Thus a total of 600 seeds from each weight class were sown. The plots for each treatment were randomly placed, but were not moved to minimise site effects within the greenhouses. The plots were watered at weekly interval, and an equal amount of water was added to each plot in all the three greenhouses. The soil used for the experiment is a lateritic sandy loam, with pH 5.2, 0.3% nitrogen and 3.8% organic matter. Seedling emergence was recorded at 3-day interval for 90 days when it had ceased.

Further study on seedling survival and dry matter yield was continued only on bare soil, and discontinued on the other three substrata. Seedling survival and dry matter yield were determined after one year of growth. The survived seedlings, not more than five, from each treatment were harvested by excavation and washed thoroughly with water to remove the adhered soil particles. Dry matter yield was determined by weighing the dried plant material at 60°C to constant weight in an oven.

Data were statistically analysed through one-way, two-way and three-way analysis of variance using SYSTAT 6.0 to determine significant differences caused due to seed weight, substratum microsite and light regimes. Non-linear regression (modified exponential model) was done to determine the relationship between seed weight and germination percentage as well as emergence time.

Results

Seed source and reserves

The relative proportion of intermediate-weight class was maximum and amount to nearly one-half of the total population. The proportion of predated seeds declined ($p<0.01$), but seed viability increased significantly ($p<0.05$) with the seed weight (Table 1). The ash content and the reserves of protein, carbohydrate, lipid and energy increased significantly ($p<0.05$) with the seed weight (Table 1).

Seed germination

Germination in laboratory was good, since all the seed weight categories achieved more than 50% germination (Table 2). The analysis of variance yielded a significant ($p<0.01$) effect of seed weight on germination percentage, and on the time taken for germination (Table 2). The germination percentage was exponentially correlated ($r = 0.996$, $df = 13$, $p<0.001$) with seed weight (Fig. 1a) and emergence time ($r = 0.965$, $df = 13$, $p<0.001$, Fig. 1b). The heavy seeds took lesser time (2 weeks) for emergence than the small seeds (4 weeks, Table 2).

The percentages of seed germination in greenhouse were lower than in laboratory. Differences in seed germination due to a 3-way factorial design, namely, seed weight ($F = 15169.2$, $df = 2$), light regime ($F = 370.3$, $df = 2$) and substratum microsite ($F = 512.9$, $df = 3$) were significant ($p<0.001$). The effect of seed weight was the strongest, followed by substratum microsite and light regime. Heavy seeds yielded greater germi-

Table 1. Physical and chemical characteristics of *Q. semiserrata* seeds. The values are mean ± sd. The F-ratio was obtained from the analysis of variance. The values with an asterisk are significant at $p<0.05$, and others at $p<0.01$.

Parameters	Seed weight class			F-ratio
	Small	Intermediate	Heavy	
Mean seed weight (g)	4.05 ± 0.31	6.58 ± 0.46	10.56 ± 0.69	350.5
Relative proportion (%) of the weight class	20.6 ± 5.0	47.0 ± 6.5	32.4 ± 6.6	47.8
Proportion of predated seeds (%)	44.1 ± 4.2	35.7 ± 3.7	20.2 ± 3.4	105.4
Viability of healthy seeds (%)	65.2 ± 4.0	73.6 ± 5.2	84.6 ± 2.1	30.3*
Ash (g seed^{-1})	0.12 ± 0.02	0.20 ± 0.02	0.31 ± 0.02	99.9
Protein (g seed^{-1})	0.35 ± 0.03	0.55 ± 0.04	0.85 ± 0.03	311.9
Carbohydrate (g seed^{-1})	1.69 ± 0.04	2.70 ± 0.04	4.46 ± 0.06	5101.8
Lipid (g seed^{-1})	1.30 ± 0.03	2.14 ± 0.02	3.49 ± 0.03	9212.8
Energy (kcal seed^{-1})	19.5 ± 0.2	32.8 ± 0.3	53.6 ± 0.3	27837.4

Table 2. Germination of *Q. semiserrata* under laboratory conditions. The values are mean ± sd. The F-ratio was obtained from the analysis of variance and found significant at p<0.01.

Seed weight Class	Days taken for initiation of germination	Germination achieved (%)
Small	31.2 ± 2.6	51.2 ± 2.9
Intermediate	21.0 ± 1.6	70.2 ± 4.0
Heavy	14.8 ± 0.8	87.0 ± 3.7
F-ratio	128.7	103.9

nation percentages than small or intermediate seeds on all substratum microsites, and under all light regimes (Fig. 2). The 52% light yielded significantly greater germination percentage than 28% or 90% light on all substratum microsites and in all weight categories. However, the germination percentages between 28% and 90% light did not differ in any of the cases.

Differences in seed germination due to substratum microsite were highly significant ($F = 512.9$, $df = 3$, $p<0.001$). Seeds of all weight classes under all light regimes showed maximum germination on moss layer, while minimum on litter surface (Fig. 2). Seeds sown under litter yielded greater germination than on the litter surface.

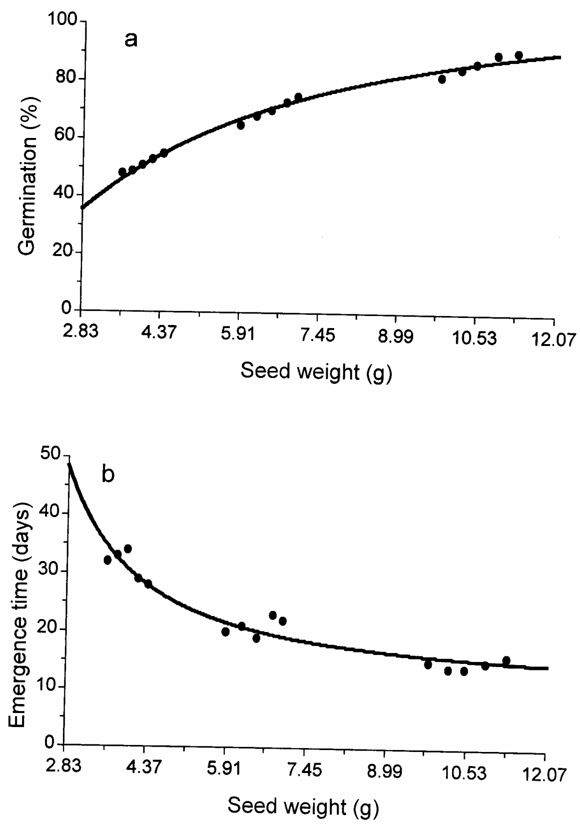

Fig. 1. The relationship of seed weight classes with germination (a) and emergence time (b). The relationships followed modified exponential model $Y = ae^{b/x}$ with $r = 0.996$ for germination, and $r = 0.965$ for emergence time. The degrees of freedom in each case are 13.

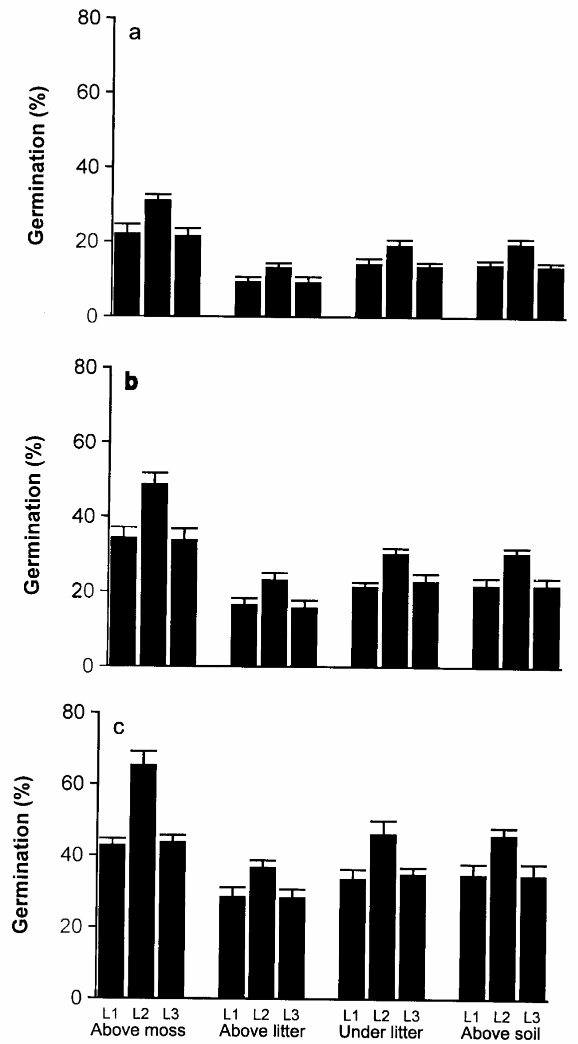

Fig. 2. Germination percentage in greenhouse conditions for small (a), intermediate (b) and heavy (c) seed weight classes on four substratum microsites and three light regimes. L1 is 28% light, L2 is 52% light and L3 is 90% light.

But the germination percentages under litter and on soil surface did not vary significantly (p>0.05). Germination of small seeds on soil surface was about 1.5 times of that above litter under all the three light conditions (Fig. 2). It declined to about 1.3 for intermediate-weight seeds and to about 1.2 for heavy seeds. Similarly, the efficiency of moss layer in alleviating germination also declined from 1.6 times for small to 1.3 for heavy seeds.

Survival and growth of seedlings

Two-way analysis of variance showed that the seedling survival was significantly affected by seed weight and light regime (p<0.001). Seedlings that emerged from heavy seeds survived better than those from small seeds under all light regimes (Fig. 3). However, survival of seedlings was maximum in 52% light for all weight classes, and did not differ between 28% and 90% light.

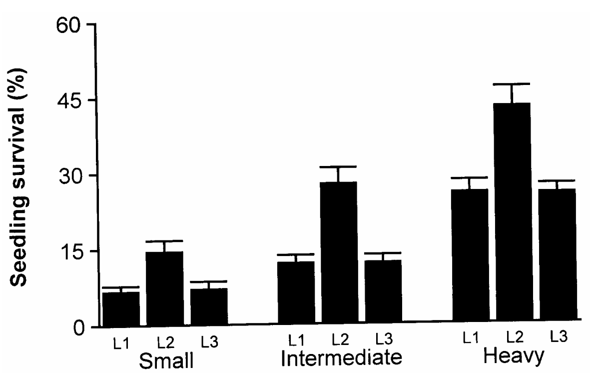

Fig. 3. Survival of seedlings raised from small, intermediate and heavy seeds after one year of growth on bare soil under three light conditions.

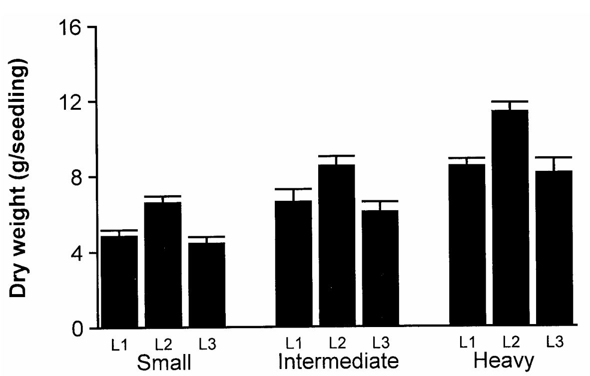

Fig. 4. Dry mass production of seedlings raised from small, intermediate and heavy seeds after one year of growth on bare soil under three light conditions.

Two-way analysis of variance also showed that the dry matter yield was also significantly affected by seed weight and light regime (p<0.001, Fig. 4). Seedlings that emerged from heavy seeds and grown under 52% light produced the maximum dry mass, while those resulting from small seeds and grown under 90% light produced least dry mass (Fig. 4). The yield under 28% light was almost similar (p>0.05) to that under 90% light.

Discussion

Effects on germination

Variation in seed weight clearly influences germination in *Q. semiserrata*. Heavy seeds germinate early and achieve grater germination percentage than small seeds under laboratory as well as greenhouse conditions. Greater stocks of food and energy in heavy than small or intermediate-weight seeds provide readily available energy to stimulate germination (Flint & Palmblad 1978). Earlier and better germination of heavy seeds has been reported in oaks (Barik *et al.* 1996; Bonfil 1998; Singh 1998; Tripathi & Khan 1990), pines (Dunlop & Barnett 1983) and other species (Hegde *et al.* 1991; Howe & Richter 1982; Vera 1997).

Moss was a better substratum than litter or soil surface for seed germination. For high moisture retention capacity, moss probably forms a better microenvironment for germination and seedling emergence than litter (Cross 1981). In a similar experiment on the forest floor, Barik *et al.* (1996) noted higher germination on moss than above-or under-litter or on soil surface in two oaks. In the present study, seed germination on soil surface was significantly better than above litter, but did not differ with that under litter. Thus, it could safely be concluded that the presence of litter and established vegetation may inhibit germination, whereas moss underneath may provide a better substratum for germination and growth. Furthermore, litter has more inhibitory effect on germination of small than heavy seeds that is in conformity to Gross & Werner (1982), Myster (1994) and Winn (1985).

The seeds germinate differentially with respect to relative light exposure. The seeds under 52% light yielded maximum germination in all weight classes, and on all substratum microsites. Since *Q. semiserrata* is a late successional species, its preference for 52% light for the best germination performance is expected. In other words, the species is light dependent for germination and may prefer small to intermediate-sized gaps with sparse light. Emergence may be inhibited by the lack of threshold radiation for photosynthesis in low light (Fetcher *et al.* 1983; Khan & Tripathi 1989a). Since equal amount of water was added at weekly interval to the plots, presumably higher evaporation of moisture under 90% than 28% and 52% may have caused water stress or allowed high temperatures to kill the seeds (Koller 1972). Ashton & Larson (1996) also argued that the forest gaps exposed to long periods of direct radiation have very dry surfaces, creating an inhospitable environment for germination and growth. Dependence on light for germination is correlated with seed size, and germination in darkness declines progressively as seed size decreases (Grime *et al.* 1981).

Effects on seedling survival and growth

Heavy seeds not only have a competitive advantage of early and greater germination, but also have greater seedling survival and dry mass produced after one year of growth that may be linked with the large reserves of nutritive substances (Dunlop & Barnett 1983; Kang *et al.* 1992; Tripathi & Khan 1990). The effect of light on seedling survival and dry matter accumulation was marked. Intermediate light level (52%) suited most to all seed weight categories. Cornelissen (1992) found the best seedling growth of a gap-dependent, evergreen tree, *Gordonia acuminata* in 33% light. Subsequently, he found a similar response in a deciduous tree, *Cornus controversa* (Cornelissen 1993). Under elevated CO_2 conditions, seedling growth of a late successional red oak increased more in low than high light (Bazzaz & Miao 1993).

Interactive effects

A strong interactive effect of seed weight, light and substratum microsite appears to regulate the success of germination, survival and early growth of *Q. semiserrata*. Heavy seeds perform better at all substratum microsites and in all light conditions. Thus maintenance of the population of heavy seeds is of critical importance. Higher predation on small and intermediate-weight than heavy seeds suggests that the small seeds, by the virtue of their preference to the predators, reduce predation risk on heavy seeds. It has also been suggested that only relatively large seeds possess sufficient stored energy to survive until they reach high enough into the canopy to support themselves photosynthetically (Harper *et al.* 1970). While large amount of reserves in heavy seeds improves germination and growth, dispersal efficiency decreases with the increase in seed weight (Ganeshaiah & Uma Shaanker 1988). *Q. semiserrata* seems to require some light for germination and early growth irrespective of the substratum microsite. Thus dispersal of seeds in gaps may produce good results. The better germination on moss indicates that the species may favour moister sites for dispersal. In fact the seeds of this species mature in November when rainy season comes to a close. The seeds thus face a prolonged dry spell in the field (winter drought). However, moss is more abundant under shaded conditions than in gaps. Seeds thus compete for greater reserves, intermediate light and moister microsite for germination and early growth.

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