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The responses of *Pinus roxburghii* and *Quercus leucotrichophora* to nutrient applications

K. BARGALI
Department of Botany, Kumaun University, Nainital - 263 002 India

Abstract. Seedling growth of *Pinus roxburghii* Sarg. an early successional species, and *Quercus leucotrichophora* A. Camus a late successional species; was compared at five levels of nutrient application. Seedlings of the two species were grown in mixture (interspecific competition) and in monoculture (intraspecific competition). Nutrients were applied at five levels (0, 144, 264, 384 and 504 mg) of a 12:32:16 NPK fertilizer once each of the two growing season. The dry phytomass yield of *P. roxburghii* was greater than that of *Q. leucotrichophora* under all experimental conditions and the difference between the two species was greater in mixture. In monoculture dry phytomass of *Q. leucotrichophora* seedlings generally increased with the amount of applied nutrients, but in competition with *P. roxburghii* it decreased. The Relative Yield (RY), Relative Yield Totals (RYT) and Relative Crowding Coefficient (RCC) indicate that *P. roxburghii* is a better competitor than *Q. leucotrichophora*. A comparison of replacement rates between *Q. leucotrichophora* and *P. roxburghii* implies that *Q. leucotrichophora* is a poorer competitor at all the nutrient levels except for the lowest one.

Key words: Dry phytomass, seedling growth, competition, RY, RYT, RCC, relative replacement rate

Introduction

Pinus roxburghii Sarg. and *Q. leucotrichophora* A. Camus are the two most important forest species in the Central Himalaya at 1,000-2,000 m a.s.l. Both are evergreen species with similar periodicities of leaf production, leaf fall and leaf longevities (a little over one year; Ralhan *et al.* 1985). *Q. leucotrichophora* is regarded as a major late succesional species, while *P. roxburghii* is among the colonizers of barren areas created by landslide, cutting and burning of forests (Bisht 1990). An exceptional ability to occupy the driest and rockiest slopes suggests that the basic strategy of *P. roxburghii* is that of stress-tolerance. This is generally a trait of later seral species, but its ability to colonize disturbed sites rapidly is typical of an early successional species (Grime 1977). Soil nutrients are markedly higher in the *Q. leucotrichophora* forest (0.28-0.58% total N, Singh and Singh 1986), than in the *P. roxburghii* forest (0.15-0.18% total N, Singh and Singh 1987). In large areas of Central Himalaya the fire-intolerant *Q. leucotrichophora* is failing to regenerate and the fire resistent *P. roxburghii* is rapidly encroaching upon those sites subsequent to disturbance i.e. tree cutting and burning (Tewari 1982; Bisht 1990). It has been suggested that the greater nutrient conservation efficiency of *P. roxburghii* and the associated reduction of nitrogen availability in the forest floor makes it difficult for *Q. leucotrichophora* a nutrient demanding species, to invade sites once occupied by *P. roxburghii* (Singh *et al.* 1984). An important question is how *P. roxburghii* with a low nutrient demand, outcompetes the more nutrient demanding *Q. leucotrichophora* on nutrient-rich *Q. leucotrichophora* sites after disturbance. While *Q. leucotrichophora* is more shade tolerant than *P. roxburghii*, neither performs significantly better than the other in the open i.e. full sunlight (Rao and Singh 1989).

The present paper reports the results of an experiment designed to assess a) the growth of *P. roxburghii* and *Q. leucotrichophora* seedlings at five levels of nutrient application and b) the interaction between nutrient application and competition in seedling growth. The objective was to elucidate the characteres that enable *P. roxburghii* to replace *Q. leucotrichophora* in nutrient-rich sites.

Material and Methods

Experimental design

The responses of *P. roxburghii and Q. leucotrichophora* seedlings to five levels of nutrient application was studied both in mixture as well as monoculture. Seedlings were grown in polyethylene bags, each containing 1 kg of 1 : 3 mixture of sieved *Q. leucotrichophora* forest soil (0-15 cm) with 0.275% N, 0.093% P and 0.113% K, and fine sand with indetectably low nutrients. pH of the mixture ranged from 6.2 to 6.4, which is within the range recorded for soils in *P. roxburghii* and *Q. leucotrichophora* forests (5.7-6.8; Khanna 1986). A gradient of nutrient availability was produced by adding 0, 144, 264, 384 and 504 mg of 12:32:16 NPK fertilizer per bag once each growing season, altogether two times. These five levels of nutrient application are called very low (VL), low (L), intermediate (I), high (H) and very high (VH), respectively. In one set of six bags two seedlings of the same species were planted. A second set of twelve bags was planted with one seedling of either species in each bag.

The experiment was carried out in an unshaded greenhouse where the mean minimum and mean maximum temperatures were 1 to 5° C higher than outside greenhouse. The bags were watered regularly, at least three times each week, with deionized water to prevent an additional input of nutrients. Each bag was placed on 12 x 12 cm plastic tray to prevent transfer of nutrients from a nearby bag. Two harvests (H_1 and H_2) were taken one and two years after the start of the experiment, respectively. Roots were washed and the components were separated and oven dried at 60° C to constant weight. The amount of leaves fallen during the period of experiment was also measured (Hickman 1975).

Data analysis

Effect of species (*Q. leucotrichophora* VS *P. roxburghii*), competition (pure VS mixed), and nutrient application (VL-VH) on dry phytomass yield were analysed using analysis of variance (Snedecor and Cochran 1968). The response of dry phytomass was calculated using the equation of Levins (1968; see Zangerl and Bazzaz 1983):

$$B = \frac{1}{(\sum_{i=1}^{S} P i^2)}$$

in which, B is response breadth, Pi is the proportion of dry phytomass response of a species in state i and S is the total number of states (i.e. nutrient levels). The resulting measure B is a scale from 0 to 1 with 1 being widest breadth. The degree of similarity between the two species was calculated according to the equation of Schoener (1970; see Zangerl and Bazzaz 1983).

$$PSij = 1 - 1/2 \sum_{h=1}^{S} (Pih - Pjh)$$

in which, PSij is the degree of similarity between species i and j and Ph is the proportion of response of species i or j in state h. These values also ranged from 0 to 1 with 1 being maximum similarity.

The results for seedling phytomass were examined visually for fit to one of the four possible outcome or "models" of competition between two species (de Wet 1960; Harper 1977) to determine whether the outcome varied with nutrient level or harvest time. These four possible outcome of pairwise interspecific competition are (1) both species perform as they do in intraspecific competition; (2) one species grows larger in interspecific competition than it does in intraspecific competition, while the other species grows larger in intraspecific competition; (3) both the species accumulated less biomass in interspecific competition than they do in intraspecific competition; (4) both species grow larger in interspecific competition than in intraspecific competition.

Relative Yield Totals (RYT) were also calculated: RYT = (mean pot yield of a species i in a mixture/mean pot yield of a species i in a pure culture) + (mean pot yield of a species j in a mixture/mean pot yield of a species j in a pure culture). An RYT>1 indicates growth in mixture exceeds the average growth of each species growing alone; i.e. niche differentiation with respect to growth; RYT = 1 indicates the use of identical amount of resource i.e. that competition is not occuring; RYT < 1 implies a mutually antagonistic relationship between the two species. Relative Crowding Coefficients (RCC) were calculated as a measure of competitive ability, or aggressivity of one species toward the other; RCC= (mean yield of a species i in a mixture/mean yield of a species j in a mixture)/ (mean yield of a species i in a pure culture/mean yield of a species j in a pure culture). Value of RCC >1 indicates that species i is competitively superior to species j. The opposite is true when RCC<1.

The relative replacement rates (Van der Bergh 1968) were calculated as follows:
Relative replacement rate of species (i) in relation to species (j) =

$$\frac{\dfrac{\text{Relative yield of species (i) at } n^{th} \text{ harvest}}{\text{Relative yield of species (j) at } n^{th} \text{ harvest}}}{} \quad \% \quad \frac{\text{Relative yield of species (i) at } m^{th} \text{ harvest}}{\text{Relative yield of species (j) at } m^{th} \text{ harvest}}$$

Between harvests, a relative rate > 1 implies that a species i is gaining an advantage over a species j and values < 1 imply the opposite.

In the present study, the species i is *Q. leucotrichophora* and the species j is *P. roxburghii*, and all data are based on dry phytomass per seedling (g).

Results and Discussion

Dry phytomass

Under monoculture (intraspecific competition) both species showed a positive correlation between phytomass and the amount of applied nutrients, except for *Q. leucotrichophora* at the very high (VH) nutrient level (Fig. 1). Under mixture (interspecific competition), this trend was reversed for *Q. leucotrichophora* while it was accentuated for *P. roxburghii*. Analysis of variance indicates that dry phytomass of seedling was significantly affected by species, competition, nutrient application and all their interactions (P<0.05 or 0.01). Under interspecific competition, at the second harvest the maximum *P. roxburghii* phytomass was about five times greater than that for *Q. leucotrichophora*, indicating that *Q. leucotrichophora* was a poorer competitor than *P. roxburghii* in this experiment. The utilization of resources according to their availability as shown by *P. roxburghii* in the present experiment is a characteristic opportunistic trait of early succesional species (Zangerl and Bazzaz 1983). At the first harvest *Q. leucotrichophora* had greater phytomass yield than *P. roxburghii* at all the nutrient levels except for the highest one. However, at the second harvest *P. roxburghii* had greater yield than *Q. leucotrichophora* under all experimental conditions. This indicates that the higher seed reserve of *Q. leucotrichophora* favoured dry phytomass production in the initial stage, as seed weight of *Q. leucotrichophora* was 17 to 18 times greater than *P. roxburghii* (Bisht 1990). The reduced growth of *Q. leucotrichophora* seedling at high levels of nutrient application is likely to be the result of competition for light with *P. roxburghii* seedlings, which owing to their high rates of growth shaded those of *Q. leucotrichophora*. It is assumed that at high levels of nutrient application in the bags, neither nutrient nor moisture were limiting the growth of either species in the mixture experiment.

The data on dry phytomass per seedling were analysed for competition and depression effects (Table 1) following McGilchrist (1965; see Tripathi and Harper 1973). The values for increase in a species in mixture over its yield in monoculture (competition effect) suggest that *P. roxburghii* is a successful competitor at higher nutrient levels. The depression effect (reduction caused by a species in the yield of its associate in mixture) suggests that the presence of *Q. leucotrichophora* tended to increase the dry phytomass of *P. roxburghii* while the presence of *P. roxburghii* caused a decrease in the dry phytomass of *Q. leucotrichophora* (Table 1).

When the data of dry phytomass yield were visually analysed for similarity to competitive models given by de Wet (1960) and Harper (1977). I found two types of outcome. At the first harvest (H_1) up to intermediate nutrient level (I), both species showed better performance in interspecific competition (model 4). At the high (H) and very high (VH) levels at the first harvest and at all the nutrient levels at the second harvest, *P. roxburghii* showed better performance in interspecific competition (model 2). Parrish and Bazzaz (1982) have explained that in intraspecific competition, individuals, very likely have great similarity in their genetic identity and consequent limitation in variation in capabilities of using a given resource. However, in interspecific competition individuals are of different species; it is likely that in competition one will be considerably better than the other at obtaining resource. As a result a clear winner or loser may be expected. In present study when *P. roxburghii* was grown with *Q. leucotrichophora*, *P. roxburghii* grew larger than when paired with *P. roxburghii* but *Q. leucotrichophora* not as large as with *Q. leucotrichophora*.

Species	Nutrient level	Competition effects H_1	Competition effects H_2	Depression effects H_1	Depression effects H_2
Pinus roxburghii					
	VL	0.58	-0.28	-2.72	0.20
	L	0.39	-0.06	-1.25	1.52
	I	0.17	0.79	-0.60	3.04
	H	0.04	0.78	1.82	3.81
	VH	0.22	0.76	2.59	4.52
Quercus leucotrichophora					
	VL	0.97	-0.03	-1.59	2.11
	L	0.29	-0.21	-1.24	0.48
	I	0.13	-0.36	-0.64	-6.85
	H	-0.30	-0.41	-0.18	-7.76
	VH	-0.46	-0.49	-1.09	-8.73

Table 1. Analysis of data on dry phytomass yield (g seedling^{-1}) showing "competition" and "depression" effects at the first (H_1) and second (H_2) harvests. Nutrient level increased from VL to VH.

Response breadths (B) and proportional similarities (PS)

Both the species showed broader responses on the gradient of nutrient application showing more similarity to each other in intraspecific competition than in interspecific competition (Table 2). *P. roxburghii* had broader response than *Q. leucotrichophora* at first harvest, while it had narrower response than *Q. leucotrichophora* at the second harvest. According to previous observations (Parrish and Bazzaz 1982; Rao and Singh 1989) it should have been broader for the early successional *P. roxburghii* than for the late successional *Q. leucotrichophora* under both interspecific and intraspecific competition. Zangerl and Bazzaz (1983) suggested that Levins's B and other response breadths are more often estimates of response equatibility in plants. Species that utilized nutrient in proportion to their availability show fluctuating growth responses which correspond to narrow response by Levins's calculations. They further suggested that Levins's B is preferrable measure of oportunism. In accordance with this, the narrower Levins's B for *P. roxburghii* showed again that it is more opportunistic than *Q. leucotrichophora* in interspecific competition. Interspecific competition decrease the proportional similarity between the species from 0.95 to 0.86 at first harvest and from 0.93 to 0.78 at second harvest (Table 2).

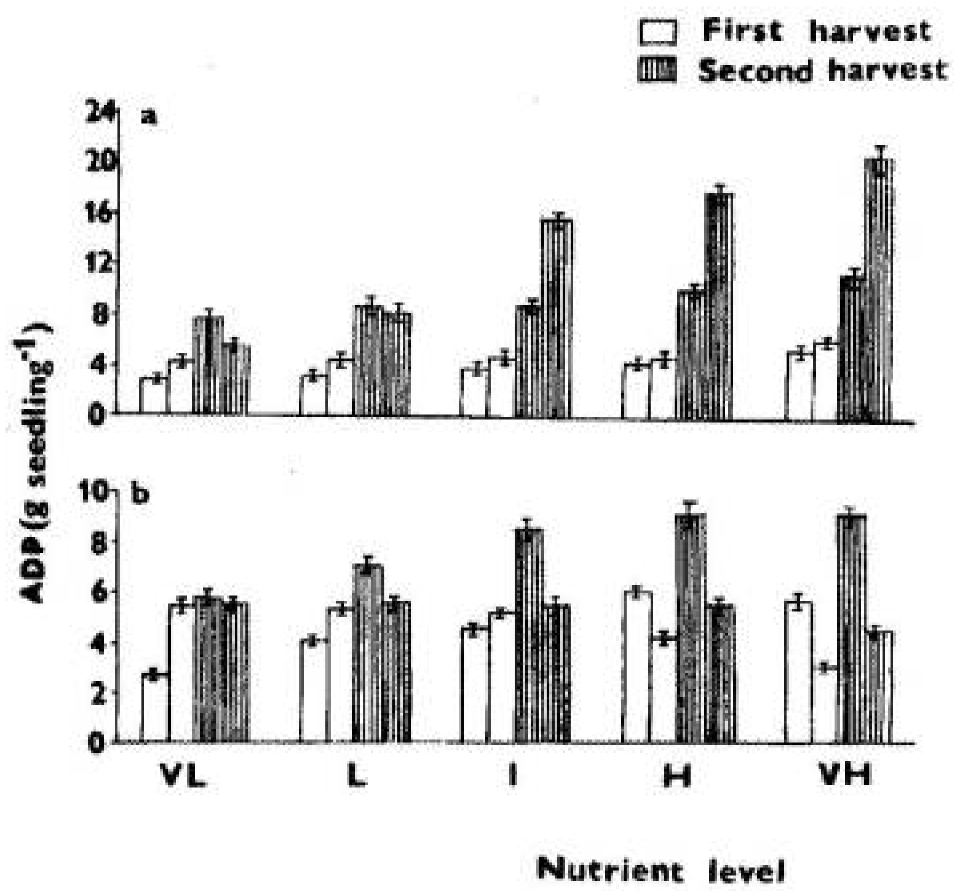

Fig. 1. The average dry phytomass - ADP (g) per seedling of *Pinus roxburghii* (a) and *Quercus leucotrichophora* (b) at the first harvest (open columns) and at the second harvest (bared columns). For each harvest at each nutrient level, the left one represents the performance of the species in monoculture (intraspecific competition) and the right one represents its performance in mixture (interspecific competition). Bar represents standard error (i±SE).

Root : Shoot ratio and leaf weight ratio

The higher leaf weight ratio (0.30-0.60) and lower root:shoot ratios (0.33-0.67) of *P. roxburghii* are indicative of an early successional species (Grime 1977, Abrahamson 1979). Both the ratios had an inconsistent pattern along the gradient of nutrient application (Table 3). However, under interspecific competition the root:shoot ratio of *P. roxburghii* increased towards highest nutrient level, in *Q. leucotrichophora* it showed a decrease. It seems that the competitive success of *P. roxburghii*, measured by dry phytomass yield, increases with reduced root production in *Q. leucotrichophora*; root play an important role in competition for nutrients. LWR represents leaf mass (g) required to produce one gram of total dry seedling phytomass. At second harvest interspecific competition was correlated to higher LWR of *Q. leucotrichophora* at all levels, *P. roxburghii* up to intermediate level than intraspecific competition. At higher nutrient levels, *Q. leucotrichophora* required greater leaf mass to produce the same amount of dry phytomass than *P. roxburghii*, perhaps causing a lower dry phytomass yield of *Q. leucotrichophora* in interspecific competition.

Species	Intra-specific competition		Inter-specific competition	
	H_1	H_2	H_1	H_2
Pinus roxburghii	0.97	0.98	0.98	0.85
Quercus leucotrichophora	0.94	0.99	0.97	0.99
PSij between *Pinus roxburghii* and *Quercus leucotrichophora*	0.95	0.96	0.86	0.78

Table 2. Levin's B and proportional similarity (Psij) for total seedling phytomass yield of *Pinus roxburghii* and *Quercus leucotrichophora* on gradient of nutrient application at the first (H_1) and second (H_2) harvests.

The relative performance of species in mixture

The relative yield (the yield of a particulaler species in a mixture over its yield in monoculture) of *P. roxburghii* remained higher than *Q. leucotrichophora* under all experimental conditions (Table 4). The quotient of relative yield (*Q. leucotrichophora*/*P. roxburghii*) decreased from very low (L) to very high (VH) level of nutrient application; the changes were particularly marked at second harvest (Table 4). This indicates that the aggressiveness of *P. roxburghii* increases with increasing nutrients. Under all experimental conditions, RYT>1 indicating the niche differentiation with respect to growth (Table 4). Values of RCC were<1 except at very low (VL) nutrient level, indicating that *P. roxburghii* was a better competitor than *Q. leucotrichophora* (Table 4).

The relative replacement rate indicates that *P. roxburghii* is gaining an advantage over *Q. leucotrichophora* at all levels of nutrient application except at very low (VL) level. It seems that at very low (VL) nutrient level, nutrients are present in low amounts that species fail to manifest their genetic differences (Parrish and Bazzaz 1982) and competition is of little importance. Zangerl and Bazzaz (1983) also reported competitive superiority of early successional species in resource-rich environments.

Conclusion

This is an unusual case where a species, which generally occurs on nutrient-rich sites is outcompeted by a species normally associated with nutrient-poor sites. Usually the opposite is true a species adapted to nutrient-poor soils is likely to be excluded from nutrient-rich sites by species adapted to nutrient-rich habitats (Goldberg 1982). It would seem that *P. roxburghii* is not specifically adapted to nutrient-poor soils, but that it's dominance causes a reduction in availability of nutrient in the soil (Singh *at al.* 1984). Similarly, instead of being specifically adapted to nutrient-rich soils, *Q. leucotrichophora* enriches the sites which it dominates through its nutrient-rich leaf litter. The greater competitive ability of *P. roxburghii* as evidenced by present study enables it to regenerate in *Q. leucotrichophora* forests, and it may enable it to gain an advantage in competitive interaction with *Q. leucotrichophora* in the long term. The advantage of *P. roxburghii* over *Q. leucotrichphora* is probably important in gaps created immediately after cutting of *Q. leucotrichophora* forests in which the soil is still relatively nutrient-rich. These conclusions were reached for seedlings under experimental conditions; competition between adult trees in the field may be different.

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Species	Nutrient level	Intraspecific competition R : S H1	H2	LWR H1	H2	Interspecific competition R : S H1	H2	LWR H1	H2
Pinus roxburghii									
	VL	0.35	0.58	0.52	0.29	0.66	0.56	0.45	0.54
	L	0.45	0.66	0.54	0.30	0.45	0.65	0.46	0.42
	I	0.46	0.48	0.51	0.31	0.47	0.34	0.43	0.41
	H	0.46	0.52	0.55	0.56	0.49	0.34	0.47	0.41
	VH	0.21	0.45	0.60	0.41	0.67	0.48	0.38	0.41
Quercus leucotrichophora									
	VL	1.61	1.66	0.25	0.21	0.97	0.67	0.34	0.37
	L	1.21	1.26	0.31	0.31	1.01	0.87	0.31	0.35
	I	0.99	1.94	0.28	0.16	1.52	0.85	0.28	0.35
	H	1.19	1.19	0.29	0.22	1.31	1.23	0.34	0.38
	VH	1.25	1.59	0.31	0.20	0.98	0.54	0.24	0.24

Table 3. Root:shoot ratio (R:S) and leaf weigh ratio (LWR) of *Pinus roxburghii* and *Quercus leucotrichophora* seedlings at five levels of nutrient application at first (H_1) and second (H_2) harvests.

Nutrient level	Harvests	RY *Q. leu.*	RY *P. rox.*	QRY *Q. leu./P.rox.*	RYT	RCC	Relative replacement rates of *Q. leu.* with respect to *P. roxburghii*
VL	H_1	0.91	1.57	0.58	3.54	1.26	-
	H_2	0.96	0.72	1.33	1.69	1.34	2.29
L	H_1	1.29	1.39	0.93	2.69	0.93	-
	H_2	0.79	0.94	0.84	1.73	0.83	0.90
I	H_1	1.13	1.16	0.97	2.29	0.97	-
	H_2	0.64	1.79	0.36	2.43	0.36	0.37
H	H_1	0.70	1.04	0.67	1.74	0.67	-
	H_2	0.59	1.78	0.33	2.36	0.33	0.49
VH	H_1	0.54	1.22	0.44	1.76	0.44	-
	H_2	0.50	1.76	0.28	2.26	0.28	0.63

Table 4. Relative yield (RY), Quotient of Relative Yield (QRY), Relative Yield total, Relative Crowding Coefficient (RCC) and Relative replacement rates (reference harvest first) H_1 and H_2 refer to first and second harvest respectively. All the data are based on dry phytomass per seedling (g). For further details see text.

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