ROLE OF LIGHT, MOISTURE AND NUTRIENT AVAILABILITY IN REPLACEMENT OF *QUERCUS LEUCOTRICHOPHORA* BY *PINUS ROXBURGHII* IN CENTRAL HIMALAYA

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BARGALI, K. 1997. Role of light, moisture and nutrient availabillity in replacement of *Quercus leucotrichophora* by *Pinus roxburghii* in Central Himalaya. In large areas of Central Himalaya, *Quercus leucotrichophora* forests are being replaced by *Pinus roxburghii.* To determine the role of light, moisture and nutrient availability in this replacement, seedlings of these two species were planted separately and in mixture and the performance of each in the presence of the other was examined. It was found that in all conditions, *P. roxburghii* had more dry mass yield over *Q. leucotrichophora* and this became more pronounced in higher resource availability. Competition effect and relative crowding coefficient also indicated that *P. roxburghii* is superior in obtaining resource. This competitive superiority of *P. roxburghii* also increased with increasing resource availability. Relative yield total also showed some niche differentiation between these two species. Continual man-made disturbances, which allow more light and nutrient availability, have enabled *P. roxburghii* to invade *Q. leucotrichophora* forest and to establish stable stands.

Keywords: Central Himalaya - *Quercus* - *Pinus* - competition - relative yield

BARGALI, K. 1997. Peranan cahaya, kelembapan dan ketersediaan nutrien bagi menggantikan *Quercus leucotrichophora* dengan *Pinus roxburghii* di Himalaya Tengah. Di kawasan yang luas di Himalaya Tengah, hutan *Quercus leucotrichophora* digantikan dengan hutan *Pinus roxburghii.* Untuk menentukan peranan cahaya, kelembapan dan ketersediaan nutrien dalam penggantian ini, anak benih kedua-dua spesies ditanam berasingan dan secara campuran, dan prestasi setiap spesies dengan kehadiran spesies yang satu lagi juga dikaji. Dalam semua keadaan, *P.roxburghii* didapati mempunyai hasil jisim kering yang lebih banyak berbanding dengan *Q. Leucotrichophora* dan ini menjadi semakin nyata dengan ketersediaan sumber yang lebih tinggi. Kesan persaingan dan koefisien kerumun relatif juga menunjukkan bahawa *P.roxburghii* terbaik untuk mendapatkan sumber. Saingan *P.roxburghii* yang terbaik juga bertambah dengan bertambahnya ketersediaan sumber. Jumlah hasil relatif juga menunjukkan beberapa perbezaan di antara kedua-dua spesies ini. Gangguan manusia secara berterusan yang menyebabkan lebih banyak cahaya dan ketersediaan nutrien membolehkan *P.roxburghii* menceroboh hutan *Q.leucotrichophora* dan untuk menubuhkan dirian yang stabil.

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Introduction

A failure of two species to cohabit in nature may be due to the effect of each in its own habitat to exclude the other (Tripathi & Harper 1973). In large areas of Central Himalaya (along an elevational gradient of 1200-2200 m) with increased disturbances, *Quercus leucotrichophora* A. Camus (banj oak) is failing to regenerate while *Pinus roxburghii* Sarg. (chir pine) is rapidly encroaching upon these sites. To determine the factors that enable successful establishment of chir pine in banj oak forest, it is important to examine the performance of these two species in mixture comparing with their performances in pure culture. Habitat preference by these species suggests that the efficiency of light and nutrient utilisation by them could be an important aspect of their competitive abilitiy. While *Q. leucotrichophora* is associated with more mesic and nutrient-rich sites and is a shade-loving species, *P. roxburghii* grows on sites which are deficient in nutrient and water and is a light-demanding species. The former is a major late successional species of this region (Central Himalaya), whereas the latter is an early successional species which can form stable stands only under the influence of tree cutting and burning (Bisht 1990). Harper (1977) stated that resource availability, disturbance regime and competition are factors important in controlling community structure and composition. So, the appropriate way to recognise essential ecological differences between pairs of species is to grow them together under a variety of resource levels because the mutual interference of species that do not commonly occur together may be of considerable ecological significance (Tripathi & Harper 1973).

The present paper deals with the effects of light, moisture and nutrient availability on competition between *Q. leucotrichophora* and *P. roxburghii*, with the aim to determine if these factors are important in the replacement of *Q. leucotrichophora* by *P. roxburghii.*

Materials and methods

Mature and seemingly healthy seeds were collected from trees at the time of peak seedfall and stored immediately in polythene bags in the laboratory. Soil was collected from a *Q. leucotrichophora* forest stand (to a depth of 15 cm). The soil was air dried and sieved through wire mesh (mesh size 1 mm) to remove gravel and plant parts. After sieving, the soil had 0.375% N, 0.093% P and 0.113% K. For light and moisture treatments, the soil was filled in polythene bags with drainage holes (approx. 1.5 kg per bag), and for nutrient treatments, the soil in the bags was mixed with fine commercial sand (having undetectably low nutrients) in 1:3 ratio. Seedlings were raised from collected seeds and maintained two per polythene bag. In one set of bags each bag contained two seedlings of one species only (pure culture) and numbered 6 bags per species per treatment. In another set of bags each bag contained one seedling of each species (mixed culture) and numbered 12 bags per treatment. Subsequent to germination the plants were allowed to establish for one month before different treatments were imposed. After establishment the seedlings were kept under the following conditions.

Light

Low (L_1), intermediate (L_2) and high (L_3) light levels were achieved by placing screens covered with three, two or one layer of muslin cloth over and around the bags. In addition, seedlings were also placed in the open as very high (L_4) light level. The irradiance under the screens measured by means of a lux meter was 25%, 50%, 70% and 100% full sunlight respectively. These values were checked from time to time during the progress of the experiment and the bags were irrigated to keep the soil at field capacity.

Moisture

Seedling were subjected to four watering frequencies, i.e. 21days, 14 days and 7 days intervals and daily. These treatments were referred to as low (W_1), intermediate (W_2), high (W_3) and very high (W_4) moisture levels respectively. This experiment was carried out under glasshouse conditions from September 1986 to September 1988, with mean minimum and maximum temperatures of 5 °C (December-January) and 36 °C (June) respectively.

Nutrient

Nutrient gradient was produced by adding 0, 144, 264, 384 and 504 mg of 12:32:16 NPK fertiliser mixture to bags containing approx. 1 kg of soil and commerial sand mixture. Seedlings were irrigated with distilled water to prevent addition of nutrients. This experiment was also carried out under glasshouse conditions.

In September 1988, six seedlings (two years old) of both species were harvested for each treatment. Roots were washed with tap water and plant material was separated into different components, dried at 60 °C in an oven for 48 h and weighed. ANOVA was calculated for seedling growth following Snedecor and Cochran (1980) to evaluate the effect in interspecific competition. Competition between species was further evaluated by comparing pure culture yield to yield in mixed culture. Yield for each species and total yield of both species as a function of the light moisture and nutrient availability were presented in the form of a replacement figure (de Wit 1960).

Relative dry mass yield (g plant^{-1}) totals were calculated as (RYT) = (yield of species i in mixture/yield of species i in pure culture) + (mean yield of species j in mixture/ yield of species j in pure culture). RYT > 1 indicates niche differentiation with respect to the yield measure, i.e. species differ in their resource use pattern; RYT = 1 indicates that no competition is occurring (or use of the same resources); RYT < 1 indicates mutually antagonistic relationship between the two species. Relative crowding coefficients (RCC) were calculated, i.e.

$$\text{RCC} = \frac{\text{mean yield of } i \text{ in mixture/mean yield of } j \text{ in mixture}}{\text{mean yield of } i \text{ in pure culture/mean yield of } j \text{ in pure culture}}$$

RCC > 1 indicates that species *i* is competitively superior to species *j*, and vice versa when RCC < 1. In the present study, *i* is *Q. leucotrichophora* and *j* is *P. roxburghii.*

Results

Both species responded similarly to light or moisture availability but not to nutrient availability (Figure 1). Nutrient (N), light (L), moisture (M) and competition (C) (pure vs. mixture) and all their interactions (i.e. N × L, N × M, N × C, etc.) significantly affected the dry mass yield of both species ($p < 0.01$). Except for L_2 light, W_3 and W_4 moisture, and N_2 nutrient levels at each resource gradient, the dry mass yield of *P. roxburghii* was generally greater in the mixed culture than in the pure culture, while growth of *Q. leucotrichophora* was greater in the pure culture except at L_4 light level. Thus the presence of *P. roxburghii* reduced the dry mass of *Q. leucotrichophora,* particularly towards the higher side of each resource (Figure 1). In the mixed culture, the dry mass of *P. roxburghii* was about twice greater at very high light (L_4) and very low moisture (W_1) levels and about five times greater at very high nutrient level (N_5) than *Q. leucotrichophora* (Figure 2). At low and intermediate light levels (L_1 and L_2), *Q. leucotrichophora* had about twice greater dry mass than *P. roxburghii* (Figure 2). Mean separation test indicates significant difference between species at these resource levels (*t*-test, $p < 0.05$).

Replacement diagrams show that *P. roxburghii* makes up a greater proportion of dry mass in a resource-rich state (i.e. high light, high moisture and high nutrient) (Figure 3). Relative yield totals indicate some differences in resource use pattern (or niche differentiation) of the two species (RYT > 1) (Figure 3) at each resource gradient. Relative crowding coefficients suggest that *P. roxburghii* is competitively superior to *Q. leucotrichophora* at each resource gradient (RCC<1) (Figure 3), and this competitive superiority of *P. roxburghii* increased with increasing resource availability.

Analysis of dry mass data (g seedling^{-1}) for competition effect (McGilchrist 1965) indicates that at the nutrient and light gradients, the competitive ability of *P. roxburghii* increased with increasing resource availability, while at the moisture gradient it showed greater competitive superiority at the lowest moisture level (W_1). *Quercus leucotrichophora* showed a reverse pattern (Table 1).

Discussion

The competitive ability of *P. roxburghii* increased with increasing resource availability while that of *Q. leucotrichophora* decreased. This is in conformity to the hypothesis of Grime (1977) that the ability of a species to compete for a given

Table 1. Analysis of data on dry mass production (g seedling^{-1}) showing competition effect in 2-y-old seedlings of *Q. leucotrichophora* and *P. roxburghii* under different conditions of light, moisture and nutrients

Species	Light level				Moisture level				Nutrient level				
	L_1	L_2	L_3	L_4	W_1	W_2	W_3	W_4	N_1	N_2	N_3	N_4	N_5
Q. leucotrichophora	- 0.09	0.30	0.49	- 0.32	- 0.02	- 0.31	- 0.56	- 0.59	- 0.030	- 0.21	- 0.36	- 0.41	- 0.49
P. roxburghii	- 0.02	- 0.07	0.40	0.59	1.71	1.07	- 0.14	- 0.04	- 0.28	- 0.06	0.79	0.78	0.76

$$\text{Competition effect} = \frac{\text{dry mass (g plant}^{-1}\text{) of sp. in mixture - dry mass of sp. in pure culture}}{\text{dry mass of sp. in pure culture}}$$

resource might be expected to change according to its availability. Competitive reduction in *Q. leucotrichophora* was higher when light, moisture and nutrients, were in abundance than when they were limited. Zangerl and Bazzaz (1983) also suggested greater competitive influence in resource-rich states. According to the resource-ratio hypotheses of Tilman (1980, 1982), these two species can be separated along a gradient of light and nutrients as they are inversely ranked in their competitive abilities for these resources.

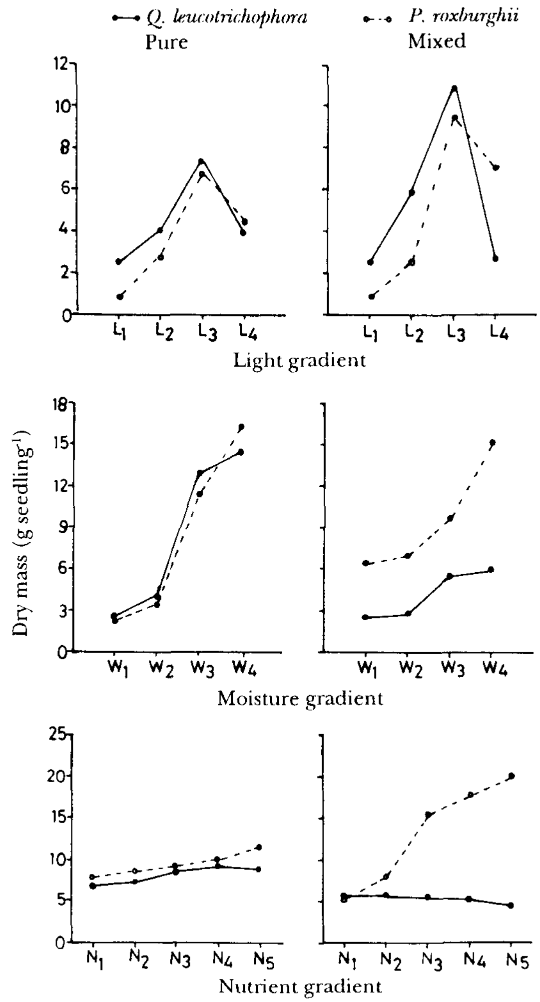

Figure 1. Dry mass yield (g) per seedling of *Q. leucotrichophora* and *P. roxburghii* at different gradients of light, moisture and nutrients

When dry mass data were observed visually, then generally model 2 of competitive outcome (de Wit 1960, Harper 1977) was found, i.e. with one species accumulating more biomass in mixture than in pure culture while the other species accumulated more in pure culture. Parrish and Bazzaz (1982) suggested that when two competing individuals are of the same species, each may be affected equally by the presence of the other because of the great similarity in their genetic identity and consequent limitation in variation in capabilities of using a given resource. On the other hand, when the individuals are of different species, it is likely that in competition one will be considerably better than the other at obtaining resources. As a result, in competition, a clear winner and loser may be expected.

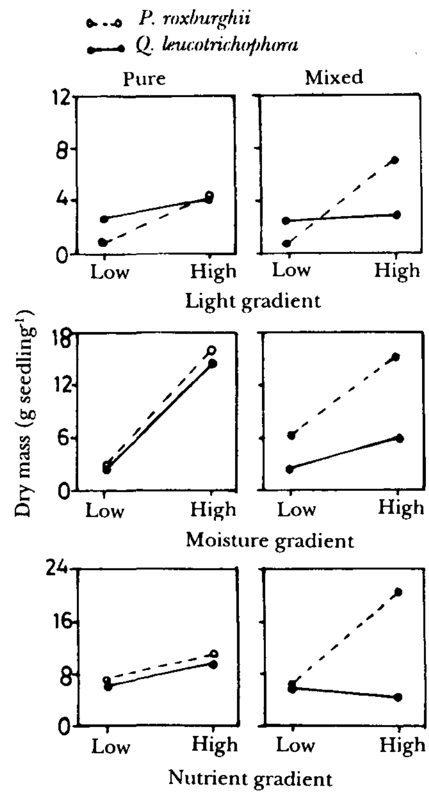

Figure 2. Light x competition, (pure vs. mixed), moisture x competition and nutrient x competition plots for *Q. luecotrichophora* and *P. roxburghii*

The data on dry mass production show that generally *P. roxburghii* had better growth yield over *Q. leucotrichophora* and this became more pronounced toward the higher resource availability. However, towards lower light intensities (i.e. L_1 and L_2), *Q. leucotrichophora* had some advantage over *P. roxburgii.* Tilman (1985), Singh and Bisht (1992), and Bargali (1993) also reported that plants that are superior competitors for nutrients may be poorer competitors for light. If any soil resource (nutrient, water, etc.) is limiting, increase in its availability should lead to increased plant productivity and above-ground biomass. The increased biomass would lead to increased light interception. Thus as nutrient or any limiting soil resource increases in availability, light should become relatively less available, especially for shorter plants such as seedlings. The plant species are known to differ in their competitive abilities for a limiting soil resource and light, with each species being a superior competitor for a particular ratio of the resources. As various biogeochemical processes increase the availability of the limiting soil resources, the availability of light at the soil surface decreases creating a gradient through time in the soil resource, a light ratio. This changing ratio leads to a replacement of one plant by another (Tilman 1985). In view of the fact that during succession in this region nutrients in the soil increase, *Q. leucotrichophora* should be superior to *P. roxburghii* in such nutrient-rich conditions as it replaces *P. roxburghii* in normal succession (unaffected by tree cutting and burning). The data for seedling growth (Figure 1) do not support this hypothesis. However, *P. roxburghii* which is a superior competitor for nutrients is an inferior competitor for light. Therefore it must replace *Q. leucotrichophora* in lighted condition. Continual man-made disturbances, by allowing high light availability, have enabled *P. roxburghii* to invade *Q. leucotrichophora* forests and to establish stable stands.

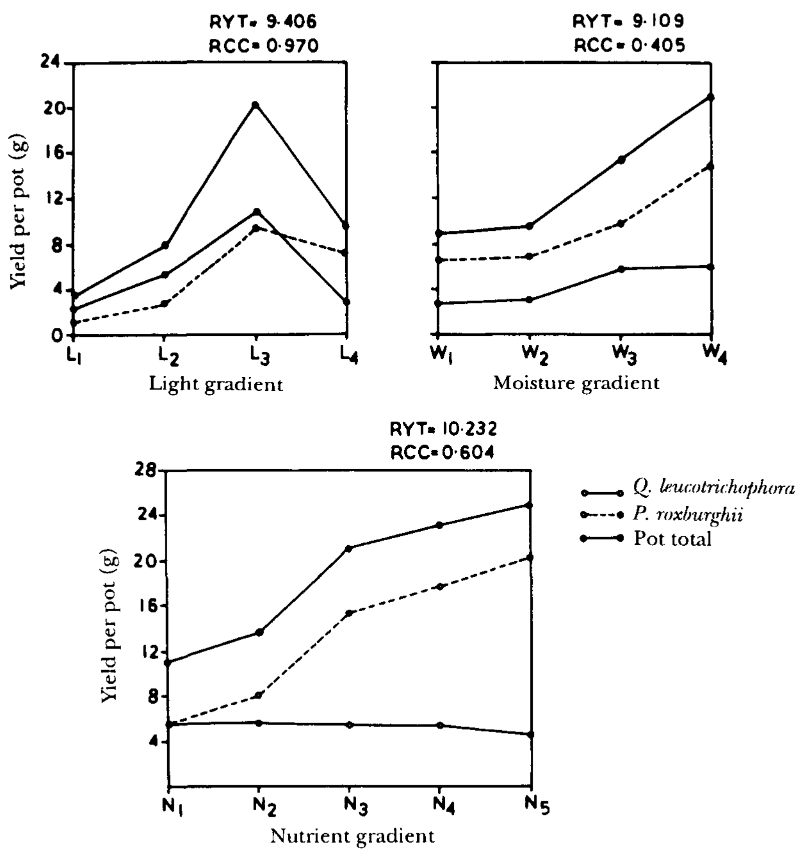

Figure 3. Replacement diagrams for three resources conditions including light, moisture and nutrients. RYT = relative yield totals and RCC = relative crowding coefficient.

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