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NUTRIENT UTILISATION EFFICIENCIES OF TWO CENTRAL HIMALAYAN TREE SPECIES

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BARGALI, K. & BARGALI, S. S. 2000. Nutrient utilisation efficiencies of two Central Himalayan tree species. The nutrient utilisation efficiencies of two Central Himalayan species, one from nutrient-rich sites, *Quercus leucotrichophora*, and another from nutrient-poor sites, *Pinus roxburghii*, were compared at different nutrient and moisture levels. For this, seedlings of these two species were grown at four soil nutrient levels and each nutrient level was kept under four watering frequencies. *Pinus roxburghii* showed greater relative growth rate and greater relative retranslocation of nutrients before leaf senescence; however, nutrient concentrations in mature leaves were always higher for *Q. leucotrichophora*. *Pinus roxburghii* also had greater uptake, recovery and use efficiency for each nutrient examined compared to *Q. leucotrichophora*. However, in both species, nutrient uptake, recovery and nutrient use efficiency decreased with increasing nutrient availability. It seems that greater nutrient utilisation efficiencies of *P. roxburghii* should not only enable its seedlings to rapidly invade nutrient-rich *Q. leucotrichophora* forest sites, but also help to resist reinvasion of the site by *Q. leucotrichophora* as reported for large areas for Central Himalaya.

Key words : *Quercus leucotrichophora* - *Pinus roxburghii* - nutrient - moisture - relative growth rate - uptake efficiency - recovery efficiency - use efficiency

BARGALI, K. & BARGALI, S. S. 2000. Kecekapan penggunaan nutrien dua spesies tumbuhan Himalaya Tengah. Kecekapan penggunaan nutrien dua spesies Himalaya Tengah, satu dari tapak kaya nutrien (subur), *Quercus leucotrichophora*, dan satu lagi dari tapak kurang nutrien (tidak subur), *Pinus roxburghii*, dibandingkan pada tahap nutrien dan kelembapan yang berbeza. Untuk tujuan ini kedua-dua spesies ditanam di tanah yang mempunyai empat aras nutrien yang berbeza dan setiap aras nutrien diletakkan di bawah empat kekerapan siraman yang berbeza. *Pinus roxburghii* menunjukkan kadar pertumbuhan relatif yang lebih besar serta translokasi semula relatif yang lebih tinggi sebelum penuaan daun; bagaimanapun, kepekatan nutrien dalam daun matang sentiasa lebih tinggi bagi *Q. leucotrichophora*. *Pinus roxburghii* juga menunjukkan kecekapan pengambilan nutrien, pemulihan dan penggunaan yang lebih tinggi untuk setiap nutrien yang dikaji berbanding dengan *Q. leucotrichophora*. Bagaimanapun, kecekapan pengambilan nutrien, pemulihan dan penggunaan nutrien kedua-dua spesies berkurangan apabila ketersediaan nutrien bertambah. Kelihatannya kecekapan penggunaan nutrien *P. roxburghii* bukan sekadar membolehkan anak benihnya mengambil alih tapak hutan *Q. leucotrichophora* yang kaya nutrien, tetapi juga membantu menentang pengambilalihan semula tapak oleh *Q. leucotrichophora* seperti yang dilaporkan berlaku di kawasan yang luas di Himalaya Tengah.

Introduction

Nutrient availability frequently limits plant growth in natural communities and the nutrition of plants is related in many ways, directly and indirectly, to soil moisture. Even if the availability of only one nutrient is varied experimentally, complex and

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partially indirect effects on plant growth are encountered. However, plant species show marked differences in physiological and ecological responses along nutrient gradients. The artificial condition imposed in a experiment do effect the interpretation of results and their application to a natural condition. However, differences between species that appear on an artificially produced gradient strongly suggest differences in resource use at a given site in the field (Parrish & Bazzaz 1982).

Quercus leucotrichophora A. Camus and *Pinus roxburghii* Sarg. are the two dominant forest forming species of Central Himalaya at 1000–2000 m elevation. The former is associated with more mesic and nutrient-rich sites, while the sites of the latter are often deficient in water and nutrients. With increasing site disturbances, *Q. leucotrichophora* is failing to regenerate in many areas and *P. roxburghii* is rapidly encroaching upon the *Q. leucotrichophora* forests subsequent to tree cutting and burning (Saxena *et al.* 1985). The present study analyses the nutrient utilisation efficiencies of these two species on a two dimensional gradient of nutrient and moisture. The main objectives were (i) to see how the nutrient utilisation pattern of these two species changes with changes in nutrient and/or moisture availability, and (ii) to relate nutrient availability to total uptake and to the recovery of nutrient from senescing leaves.

Materials and methods

Mineral soil material to a depth of 15 cm was collected from a *Q. leucotrichophora* forest. The soil was air dried and sieved through wire mesh screen (mesh size 1 mm) to remove all plant parts. The soil was mixed with fine sand (ratio soil: sand = 1:3) and put into polyethylene bags (1 kg per bag). Seedlings of *P. roxburghii* and *Q. leucotrichophora* were obtained from the current year seed crop and maintained singly in polyethylene bag. Twelve bags for each species were placed under each treatment (Table 1).

The experiment was carried out in a glasshouse. Ambient temperature was minimum during December–January (5 °C) and maximum during June (36 °C). A layer of cotton gauze in the bottom of each bag prevented soil from being washed out of the bags during watering and plants were watered with deionized water to prevent addition of nutrients. At the start of the experiment ten individuals of each species were harvested for determination of the average initial biomass and N, P and K contents of each component. After one year all the seedlings were harvested, separated into components, over dried and weighed. After weighing the plant material was ground and analysed for nutrients. Nitrogen was determined using Kjeldahl Auto VS-KTP Nitrogen Analyzer, phosphorus by a spectrophotometer and potassium by a flame photometer following Bisht (1990). Differences in nutrient concentration were used to calculate an index of nutrient use efficiency that is the result of the reabsorption of nutrients before leaf abscission (*NUER*) following Schlesinger *et al.* (1989):

$$NUER = \frac{\text{concentration in mature leaves - concentration in senescent leaves}}{\text{concentration in mature leaves}} \, [\%] \quad (1)$$

Because the plants were grown in a glasshouse and watered at the soil surface foliar leaching was assumed to be negligible.

Table 1. List of treatments

Nutrient treatment		
Nutrient level	Abbreviation	Amount of NPK applied (mg)
Low	L	144
Intermediate	I	264
High	H	384
Very high	HH	504
Moisture treatment		
Watering level	Abbreviation	Watering frequency
Low	W1	21 days interval
Intermediate	W2	14 days interval
High	W3	7 days interval
Very high	W4	daily

The biomass data were used to calculate relative growth rate (*RGR*; Evans 1972), for which significant differences were determined by analysis of variance ($p < 0.05$), following Snedecor and Chochran (1968). Efficiency of nutrient uptake *Eu* was calculated as

$$Eu = \frac{\text{increase in plant nutrient mass}}{\text{nutrient mass available}} \qquad [\text{g mg}^{-1}] \qquad (2)$$

For any time interval, nutrient availability was defined as the amount of nutrient added to each bag (Shaver & Melillo 1984). Efficiency of nutrient recovery (*Er*) was calculated from the parameters of a linear regression of nutrient mass per g in mature leaves vs. senescent leaves. $D = a + bM$ where M and D are mass values per seedling respectively and

$$Er = 1 - b - (a/M) \qquad [\text{g g}^{-1}] \qquad (3)$$

Similarly, efficiency of nutrient use (*Euse*) was also calculated from the parameters of a linear regression of nutrient mass (g) per seedling vs. total dry mass (g) per seedling : $D = a + bN$ where, N and D are nutrient and dry mass values per seedling respectively, and

$$Euse = 1 - b - (a/\text{N}) \qquad [\text{g g}^{-1}] \qquad (4)$$

Results and discussion

Relative growth rate

The *RGR* of *P. roxburghii* was significantly higher than that of *Q. leucotrichophora* at all the treatments, particularly towards lower nutrient and moisture levels (Table 2). In both species *RGR* increased with increasing nutrient and/or moisture level. Gray and

Table 2. Relative growth rates for *Quercus leucotrichophora* and *Pinus roxburghii* seedlings under different nutrient and water regimes. All data are means ± 1 SE, n=12.

Nutrient level	Moisture level	Relative growth rate ($g\ g^{-1}\ d^{-1}$)	
		Q. leucotrichophora	*P. roxburghii*
L	W_1	0.005 ± 0.0005	0.007 ± 0.0006
	W_2	0.007 ± 0.0004	0.008 ± 0.0005
	W_3	0.008 ± 0.0006	0.008 ± 0.0006
	W_4	0.008 ± 0.0007	0.009 ± 0.0005
I	W_1	0.005 ± 0.0007	0.006 ± 0.0003
	W_2	0.007 ± 0.0005	0.008 ± 0.0006
	W_3	0.008 ± 0.0002	0.009 ± 0.0010
	W_4	0.009 ± 0.0004	0.009 ± 0.0008
H	W_1	0.005 ± 0.0006	0.007 ± 0.0002
	W_2	0.008 ± 0.0008	0.008 ± 0.0002
	W_3	0.008 ± 0.0007	0.010 ± 0.0008
	W_4	0.009 ± 0.0007	0.010 ± 0.0006
HH	W_1	0.005 ± 0.0006	0.007 ± 0.0003
	W_2	0.008 ± 0.0005	0.008 ± 0.0002
	W_3	0.008 ± 0.0009	0.010 ± 0.0007
	W_4	0.009 ± 0.0007	0.010 ± 0.0006

Schlesinger (1983) also reported *RGR* to increase with increases in nutrient and moisture availability. However, toward the higher nutrient levels *P. roxburghii* showed small variations in *RGR*. Many species that occupy nutrient-poor sites show little change in *RGR*, when grown under nutrient-rich condition (Chapin *et al.* 1986). Grime and Hunt (1972) suggested that relative growth rate of plants is simultaneously subject to genetic and environmental controls and high *RGR* is often associated with success in potentially productive situations. Thus, the higher *RGR* of *P. roxburghii* suggests that in similar situations this species is more productive than *Q. leucotrichophora*.

Foliar nutrient concentrations and relative retranslocation of nutrients

Our foliar concentration data confirm earlier results (Ralhan & Singh 1987, Singh & Bisht 1992) of lower nutrient concentration in leaves of species from infertile sites as compared to species from fertile sites (Table 3). In Central Himalaya, *P. roxburghii* forests occupy less fertile soils than *Q. leucotrichophora* forests (Singh & Singh 1992). Therefore relatively lower concentrations of N, P and K in the foliage of *P. roxburghii* than in the foliage of *Q. leucotrichophora* were expected. With increasing nutrient levels nutrient concentrations in the foliage of both species increased. This is consistent with the reported tendency of nutrient content to increase with nutrient availability (Bisht 1990). However, the nutrient content generally decreased with increasing watering frequencies (though differences were not significant), possibly due to the dilution effect of water supply (Table 3). There existed a significant positive correlation ($p < 0.05$) between foliar nutrient concentration and concentration of nutrient in the soil for each nutrient examined.

The relative retranslocation of nutrients in both species was lower towards higher nutrient levels as well as higher watering frequencies (Table 3). It seems that in a

Table 3. Comparison of foliar nutrient concentrations and nutrient reabsorption in *Q. leucotrichophora* and *P. roxburghii* under different nutrient and water regimes. Concentration data are means ± 1 SE with n= 5, and *t*-test (p < 0.05) are used to distinguish differences between species and nutrients.

Nutrient treatment	Water treatment	Concentration						Fractional reabsorption					
		Q. leucotrichophora			*P. roxburghii*			*Q. leucotrichophora*			*P. roxburghii*		
		N	P	K	N	P	K	N	P	K	N	P	K
L	W_1	2.25 ±0.018	0.14 ±0.002	0.71 ±0.002	1.85 ±0.006	0.11 ±0.001	0.67 ±0.002	0.178	0.107	0.063	0.216	0.182	0.111
	W_2	2.25 ±0.014	0.14 ±0.001	0.70 ±0.002	1.80 ±0.004	0.11 ±0.001	0.67 ±0.001	0.195	0.107	0.054	0.222	0.167	0.099
	W_3	2.12 ±0.014	0.14 ±0.001	0.68 ±0.001	1.80 ±0.002	0.10 ±0.00	0.67 ±0.002	0.151	0.128	0.044	0.233	0.190	0.094
	W_4	1.95 ±0.012	0.13 ±0.002	0.68 ±0.002	1.75 ±0.001	0.10 ±0.001	0.66 ±0.001	0.154	0.077	0.051	0.228	0.189	0.090
I	W_1	2.46 ±0.018	0.15 ±0.002	0.74 ±0.002	2.03 ±0.011	0.12 ±0.001	0.68 ±0.004	0.186	0.10	0.081	0.222	0.176	0.120
	W_2	2.40 ±0.019	0.15 ±0.002	0.72 ±0.003	2.03 ±0.010	0.12 ±0.002	0.67 ±0.002	0.187	0.10	0.053	0.231	0.172	0.116
	W_3	2.34 ±0.012	0.14 ±0.001	0.71 ±0.002	2.02 ±0.010	0.12 ±0.002	0.67 ±0.005	0.188	0.071	0.041	0.224	0.117	0.107
	W_4	2.27 ±0.011	0.13 ±0.001	0.70 ±0.002	2.02 ±0.011	0.11 ±0.001	0.67 ±0.005	0.185	0.038	0.034	0.227	0.110	0.104
H	W_1	2.72 ±0.010	0.16 ±0.002	0.75 ±0.001	2.24 ±0.014	0.14 ±0.002	0.70 ±0.003	0.099	0.075	0.034	0.127	0.142	0.084
	W_2	2.65 ±0.012	0.16 ±0.001	0.74 ±0.002	2.23 ±0.015	0.14 ±0.004	0.70 ±0.003	0.094	0.087	0.027	0.121	0.142	0.084
	W_3	2.60 ±0.011	0.15 ±0.001	0.74 ±0.001	2.22 ±0.001	0.13 ±0.001	0.69 ±0.002	0.108	0.067	0.027	0.101	0.128	0.075
	W_4	2.48 ±0.012	0.14 ±0.002	0.72 ±0.002	2.22 ±0.021	0.13 ±0.002	0.69 ±0.004	0.093	0.057	0.014	0.099	0.107	0.079
HH	W_1	2.83 ±0.014	0.18 ±0.002	0.76 ±0.003	2.43 ±0.015	0.15 ±0.013	0.72 ±0.005	0.064	0.10	0.019	0.111	0.144	0.034
	W_2	2.78 ±0.015	0.17 ±0.001	0.76 ±0.004	2.42 ±0.016	0.15 ±0.012	0.72 ±0.003	0.065	0.070	0.026	0.101	0.133	0.028
	W_3	2.65 ±0.012	0.17 ±0.001	0.75 ±0.002	2.42 ±0.017	0.15 ±0.002	0.72 ±0.005	0.075	0.088	0.020	0.090	0.126	0.022
	W_4	2.60 ±0.011	0.16 ±0.002	0.74 ±0.001	2.41 ±0.012	0.14 ±0.001	0.71 ±0.002	0.058	0.062	0.013	0.089	0.122	0.021

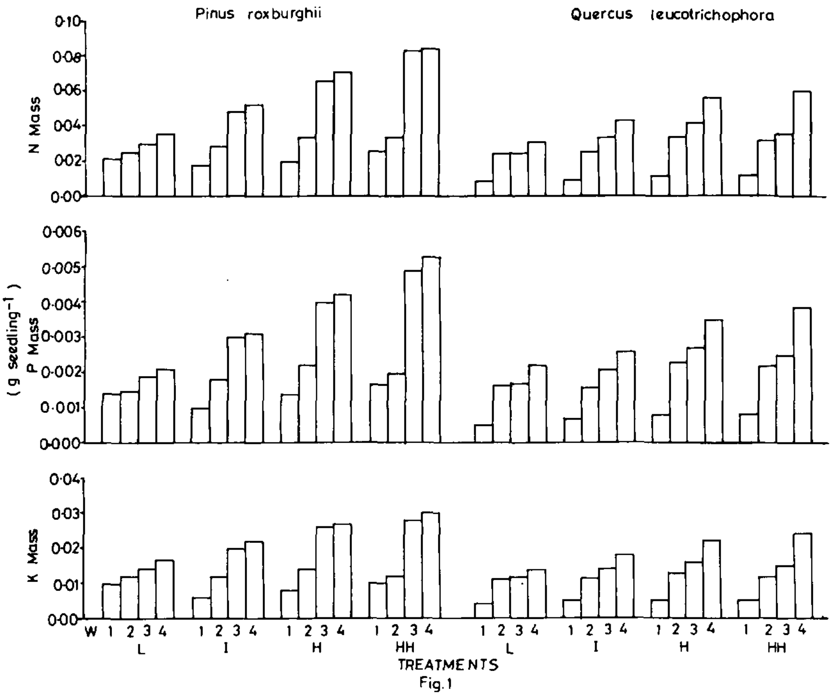

Figure 1. Total nutrient content (g) per seedling (open columns) for *Quercus leucotrichophora* and *Pinus roxburghii* under different nutrient and water regimes. Nutrient level increases from L to HH and water level from 1 to 4.

resource-rich condition plants have better accessibility to soil nutrient and intra-nutrient cycling becomes less important. At each treatment relative retranslocation was higher for *P. roxburghii* than for *Q. leucotrichophora.* Vitousek (1982) also reported that conifers generally show higher reabsorption efficiency than broad-leaved species. High relative retranslocations are often associated with nutrient-poor sites, conferring a greater efficiency of nutrient use in these species (Waring & Schlesinger 1985). Relative retranslocation of nutrients showed a negative correlation with soil nutrient concentration (though values were not always significant).

Nutrient content

Total nutrient content of seedlings increased with increasing nutrient and moisture levels in both species (Figure 1). However, at the lowest moisture level changes in nutrient content were insignificant. As soil moisture has a direct effect on the supply of nutrients to the plants, the mineral utilisation by plants might be limited by water supply. In all conditions *P. roxburghii* had higher nutrient contents than *Q. leucotrichophora* indicating that it can extract nutrients more efficiently than *Q. leucontrichophora* in such similar situations.

Nutrient uptake efficiency

Nutrient uptake efficiency decreased with increasing nutrient availability but increased with increasing moisture level at each nutrient level (Table 4). These

Table 4. Nutrient uptake efficiency (g mg^{-1}) for *Q. leucotrichophora* and *P. roxburghii* seedlings under different nutrient and water regimes

Nutrient treatment	Water treatment	*Q. leucotrichophora*			*P. roxburghii*		
		N	P	K	N	P	K
L	W1	0.0004	0.00001	0.00016	0.0012	0.00003	0.00041
	W2	0.0013	0.00003	0.00047	0.0013	0.00003	0.00049
	W3	0.0014	0.00003	0.00048	0.0017	0.00004	0.00059
	W4	0.0017	0.00004	0.00059	0.0019	0.00004	0.00069
I	W1	0.0002	0.00001	0.00009	0.0005	0.00001	0.00012
	W2	0.0007	0.00002	0.00024	0.0008	0.00002	0.00027
	W3	0.0010	0.00002	0.00032	0.0015	0.00003	0.00046
	W4	0.0013	0.00003	0.00041	0.0016	0.00004	0.00050
H	W1	0.0002	0.00001	0.00007	0.0004	0.00001	0.00013
	W2	0.0007	0.00002	0.00022	0.0007	0.00002	0.00023
	W3	0.0009	0.00002	0.00027	0.0015	0.00003	0.00043
	W4	0.0012	0.00003	0.00037	0.0016	0.00003	0.00046
HH	W1	0.0002	0.00001	0.00005	0.0004	0.00001	0.00012
	W2	0.0005	0.00001	0.00014	0.0005	0.00001	0.00014
	W3	0.0005	0.00002	0.00017	0.0013	0.00003	0.00034
	W4	0.0010	0.00002	0.00028	0.0014	0.00003	0.00037

Table 5. Linear regression statistics for the relationship of nutrient mass in mature leaves vs. senescent leaves and nutrient mass per seedling vs. dry mass per seedling

Nutrient	Species	Correlation coefficient	Intercept(*a*)	Slope(*b*)	Efficiency at minimum N, P or K	Efficiency at maximum N, P or K	Mean* efficiency
Relationship between nutrient mass in mature leaves and senescent leaves					(Efficiency of nutrient recovery)		
N	*Q. leu.*	0.959	-0.0094	1.255	0.227	0.077	0.127
	P. rox.	0.974	-0.0096	1.291	0.258	0.104	0.162
P	*Q. leu.*	0.982	-0.00009	0.965	0.107	0.089	0.092
	P. rox.	0.930	-0.00013	0.952	0.172	0.133	0.149
K	*Q. leu.*	0.933	-0.0019	1.233	0.077	0.035	0.042
	P. rox.	0.851	-0.0054	1.702	0.104	0.043	0.079
Relation between amount of nutrient and dry weight per seedling					(Efficiency of nutrient use)		
N	*Q. leu.*	0.982	0.232	52.12	77.48	54.99	58.76
	P. rox.	0.967	0.574	46.36	77.97	52.21	58.93
P	*Q. leu.*	0.983	0.223	835.7	1240.1	891.6	952.1
	P. rox.	0.958	0.550	762.9	1113.11	865.7	973.3
K	*Q. leu.*	0.993	0.055	138.3	149.4	139.6	141.6
	P. rox.	0.997	0.191	139.4	170.8	144.7	149.8

*Mean efficiency is the efficiency at the mean observed N, P and K values in the leaves or seedlings.

changes in nutrient uptake efficiency are consistent with observations from previous physiological studies on root:shoot relationship under nutrient stress. For example, Gray and Schlesinger (1983), Shaver and Mellio (1984), and Chapin *et al.* (1986) found negative relationship between nutrient uptake rate and tissue nutrient concentration for a variety of grass, sedge, herb and shrub species. The well-known tendency of plants to produce a higher root:shoot ratio under nutrient stress (Bisht 1991) would reinforce the changes at the physiological level. Patterns of uptake efficiency were the same for each nutrient and in all conditions the efficiency was greater for *P. roxburghii* than for *Q. leucotrichophora.*

Nutrient recovery and nutrient use efficiency

The relationships between availability of nutrients and nutrient recovery, and nutrient use efficiency is linked through plant nutrient contents. For both species nutrient recovery and nutrient use efficiency decreased with increasing nutrient availability, and all the minimum, maximum and mean efficiencies were greater for *P. roxburghii* than for *Q. leucotrichophora* (Table 5). Stachurski and Zimka (1975) and Ralhan and Singh (1987) also reported that as nutrient availability increases, the proportion of nutrient in mature leaves that was recovered before senescence would decrease. Similarly Singh and Bisht (1992) have suggested that as nutrient availability increases the amount of biomass produced per unit of nutrient uptake decreases, as seen in Table 5.

Conclusion

It is evident from this study that *P. roxburghii* seedlings can utilise nutrients more efficiently than *Q. leucotrichophora* seedlings. The higher growth rate of *P. roxburghii* should allow it to acquire a larger proportion of available soil nutrients and therefore suppress the growth of *Q. leucotrichophora* in nutrient-rich banj oak forest sites (Singh & Bisht 1992). The fact that nutrient uptake efficiency decreases with increasing nutrient availability suggests that as nutrient input increases, the rate of nutrient movement through an ecosystem will be less affected by nutrient uptake of plant. If the efficiency of nutrient recovery decreases, the nutrient supply to new primary production must depend more upon current uptake and less upon internal recycling. Decreases in nutrient availability results in the production of litter with a higher nutrient concentration under high nutrient availability and, vice versa, litter with lower nutrient concetration under low nutrient availability. Litter with high nutrient content decomposes faster and causes less initial nutrient immobilisation than a low nutrient litter (Upadhyay *et al.* 1989). The litter of *Q. leucotrichophora* is more nutrient-rich than the litter of *P. roxburghii.* Probably this, in conjuction with nutrient immobilisation in the microbial mass of *P. roxburghii* litter, allows *P. roxburghii* to resist reinvasion by *Q. leucotrichophora* (Singh & Singh 1992). The present study indicates that species from a nutrient-poor site is competitively superior to species from a nutrient-rich site. However, this attempt is limited by the fact that the study was focused on a short period of the life of long-lived plants.

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