

## Responses of nurse plants on the growth of forest tree species along nutrient gradients

Dr. Deepti Goel

Department of Botany,  
D.S.B. Campus, Kumaun University,  
Naini Tal – 263 002, Uttarakhand, INDIA  
Email: [deeptigoel2002@rediffmail.com](mailto:deeptigoel2002@rediffmail.com)

**Abstract:** The present study deals with the influence of 'nursing effects' of actinorrhizal plants on the growth of some important Central Himalayan species. The studied species were: *Pinus roxburghii* Sarg. (chir-pine), *Quercus floribunda* Lindl. (tilonj-oak), *Cupressus torulosa* D. Don (cypress), *Coriaria nepalensis* Wall. (makoi), and *Alnus nepalensis* D. Don (alder). For this study seedling of both nitrogen fixing and target species were grown in pure culture and mixed cultures in polyethylene bags containing sand and soil mixture in 3:1 ration. The gradients of nutrient availability were developed by adding 0, 80, 160 and 240 mg /kg ammonium nitrate to the bags (as two equal doses, one at start and other during growing season). The gradients are referred to as N1, N2, N3 and N4, respectively. In all target species, seedling growth and seedling dry mass increased with increasing nutrient levels. Our experiments indicated that when individuals of different species grow together, more than one interaction may be involved and their effects change with changing environments. [Nature and Science. 2009;7(4):35-50]. (ISSN: 1545-0740).

**Keywords:** Nitrogen fixing, nutrient gradients, Central Himalaya, target species, biomass

### INTRODUCTION

Nutrients are one of the important environmental resources for which species occurring together in a community compete with one another. Nutrient gradients are complex indirect effect if only one nutrient is used. Artificial conditions imposed in a study effects the interpretations of results and their application to field conditions. The difference between the gradient suggests neighbors affect differences in resource availability (Parrish and Bazzaz, 1982a). However, plant species do show marked differences in physiological and ecological responses along nutrient gradients, and these differences can offer valuable insights into plant community organization and competitive relations. In theory, competition should be a stronger selective factor in more persistent communities than in short lived ones, resulting in more divergence of resource use patterns in the persistent communities (Parrish and Bazzaz, 1982b). Soil nutrients are markedly higher in the oak forest (0.33 to 0.58% total nitrogen, Singh and Singh, 1986), than in the pine forest 0.15 to 0.18% total N, Singh and Singh, 1987). Singh *et al.*, (1984) suggested that the slow decomposing pine litter by promoting N-immobilization in microbes renders site nitrogen poor, and that shortage of nitrogen in combination with frequent fires has helped in expansion of pine in oak areas. The former is less nutrient demanding than the latter. Where nitrogen in soil is low in earlier stage and increase with progress of succession, the early successional (*Alnus nepalensis* and *Cupressus torulosa* D. Don.) species should grow more rapidly at low nutrient level than latter successional species (*Quercus floribunda* Lindl. and *Pinus roxburghii* Sarg.) (Tilman, 1982). A study on the Sierra Madre Mexico suggested that the evergreen species occurring in nutrient poor sites is out competed by the deciduous species of nutrient rich sites by competition when nutrient availability is increased (Goldberg, 1982).

The main objectives of this investigation are to (i) examine the facilitative effect of the nitrogen fixing actinorrhizal plants on important forest species of central Himalaya, and the way it is modified with changes in soil resources, nutrients and (ii) to discuss whether the species mixtures involving a facilitator species bring about enhancement in productivity.

### Materials and Methods

Seedlings of *Pinus roxburghii*, *Quercus floribunda*, *Cupressus torulosa*, *Alnus nepalensis* and *Coriaria nepalensis* were raised from the seeds of current crop (1998) and transferred to polyethylene bags (containing 8 kg of sand: soil mixture in 3:1 ratio) of 60 x 30 cm size. It was considered that this sand soil mixture had negligible concentration of nutrients, and the amount of soil was sufficient for an unrestricted root growth of seedlings for the duration of experiment.

To analyze the nursing effect of nitrogen fixing species on growth performance of selected non-nitrogen fixing species, seedlings of both (N-fixing and non-N-fixing) were maintained in following combinations each with six replicates:

Non-N <sub>2</sub> -fixing	N <sub>2</sub> -fixing	Non-N <sub>2</sub> -fixing	N <sub>2</sub> -fixing
1. <i>P. roxburghii</i>	with <i>A. nepalensis</i>	2. <i>P. roxburghii</i>	with <i>C. nepalensis</i>
3. <i>C. torulosa</i>	with <i>A. nepalensis</i>	4. <i>C. torulosa</i>	with <i>C. nepalensis</i>
5. <i>Q. floribunda</i>	with <i>A. nepalensis</i>	6. <i>Q. floribunda</i>	with <i>C. nepalensis</i>
7. <i>Q. floribunda</i>	with <i>C. torulosa</i>	8. <i>Q. floribunda</i>	with <i>Q. floribunda</i>
9. <i>C. torulosa</i>	with <i>C. torulosa</i>	10. <i>P. roxburghii</i>	with <i>P. roxburghii</i>
11. <i>A. nepalensis</i>	with <i>A. nepalensis</i>	12. <i>C. nepalensis</i>	with <i>C. nepalensis</i>

The polyethylene bags were moved from one place to another to avoid the self-shading of the plants. The bags were filled, each with 8 kg of sand and soil mixture in 3:1 ratio.

Ten individuals of each species were separated into their component parts and oven dried at 60°C to obtain the initial dry weight of all the six species. The experiments were performed under greenhouse conditions from October 1998 to November 2000 with temperature ranging from 5°C (minimum) in December- January to 30°C (maximum) in June.

Observations for height growth (up to shoot apex) recorded at monthly intervals. For dry mass, the plants were harvested at six months interval in the first year and finally at the end of second year. The roots were washed and the different parts of the plant (i.e. leaves, stem, roots and nodules) were separated and dried at 40°C in an oven for one week and weighed. Statistical analysis was done following Snedecor & Cochran (1968).

After establishment, seedlings of *P. roxburghii*, *C. torulosa*, *Q. floribunda*, *A. nepalensis* and *C. nepalensis* were provided with four nutrient gradients in each combination. The gradient of nutrient availability was developed by adding 0, 80, 160 and 240 mg kg<sup>-1</sup> NH<sub>4</sub>NO<sub>3</sub> to the bags (in the form of two doses) once each growing season and referred to as N1, N2, N3, N4 nutrient gradient, respectively. Other macro and micronutrients were provided in the form of Arnon nutrient solution (Tables 1 a & b). All the nutrient levels were subjected to equal, adequate and regular water supply.

**Table 1(a):** Composition of Nitrogen Free Nutrient Solution (in 500 ml of distilled water each time of irrigation):

COMPOUND	STRENGTH
Ca(OH) <sub>2</sub>	0.1 mM
MgSO <sub>4</sub>	0.7 mM
MoO <sub>3</sub>	1.88 μM
CuSO <sub>4</sub>	37.5 μM
MnSO <sub>4</sub>	1.0 mM
H <sub>3</sub> BO <sub>3</sub>	0.7 mM
K <sub>2</sub> SO <sub>4</sub>	0.25 mM
ZnSO <sub>4</sub>	0.25 mM
Ferric citrate	12.5 μM

**Table 1(b):** Composition of Complete Nutrient Solution (in 500 ml of distilled water each time of irrigation).

COMPOUND	STRENGTH
Ca (OH) <sub>2</sub>	0.1 mM
MgSO <sub>4</sub>	0.7 mM
MoO <sub>3</sub>	1.88 μM
CuSO <sub>4</sub>	37.5 μM
MnSO <sub>4</sub>	1.0 mM
H <sub>3</sub> BO <sub>3</sub>	0.7 mM
K <sub>2</sub> SO <sub>4</sub>	0.25 mM
ZnSO <sub>4</sub>	0.25 mM
Ferric citrate	12.5 μM
NH <sub>4</sub> NO <sub>3</sub>	18.75 μM

## Results

### Height growth

Height growth of 2-yr-old seedlings under different nutrient levels is presented in Fig. 2.1. In general, the height of all species tended to increase with increasing nutrient level both in pure culture and mixed culture. Across the nutrient levels, the height increment in the study period for *Pinus* was 173-313 % in pure culture, 304-411% in combination with *A. nepalensis* (hereafter referred to as *Alnus*) and 287-421% with *C. nepalensis* (hereafter referred to as *Coriaria*) (Table 2.1). The facilitative effect of symbiotic plants was measured as growth of target species individuals (oak, pine, *Cupressus*) in the presence of nurse species individuals relative to that when grown in presence of conspecific individuals. Facilitative effect of *Alnus* was maximum at the lowest nutrient level, and then tended to decrease with increasing nutrient level up to N4. Facilitative effect of *Coriaria* on *P. roxburghii* (hereafter referred to as *Pinus*) was about 30% at N1 level and then continuously decreased up to N4 nutrient level (16%) (Table 2.2). Height of *C. torulosa* (hereafter referred to as *Cupressus*) both in pure and mixed culture followed the same pattern as that of *Pinus*. Across the nutrient levels, the height increment in one-year was 866-1119% in pure culture and 986-1214% in combination with *Alnus* and 1056-1250% with *Coriaria*. Facilitative effect of *Alnus* on *Cupressus* was comparatively greater (33% at N1 level) than of *Coriaria* (25% at N1 level), and tended to decrease with increasing nutrient level (at N4 level 16% and 11% by *Alnus* and *Coriaria*, respectively). Height of *Quercus* followed the same pattern as that of *Pinus* and *Cupressus* in pure culture as well as in mixed culture. Across the nutrient levels, the height increment was 213-332% in pure culture and 264-383% in combination with *Alnus* and 264-359% with *Coriaria*. Facilitative effect of *Alnus* on oak was comparatively greater than *Coriaria*. The facilitative effect of *Alnus* and *Coriaria* was maximum at the lowest nutrient level (20% and 30%, respectively), and then tended to decrease with increasing nutrient level up to N4 (11% and 9% by *Alnus* and *Coriaria*, respectively). Response to nutrient enrichment was lower in *Pinus* than other species.

**Table 2.1:** Percent increment in seedling height of target species (*P. roxburghii*, *C. torulosa* and *Q. floribunda*) and nurse species (*A. nepalensis* and *C. nepalensis*) along the nutrient gradient in pure and mixed cultures.

Species combination	N1	N2	N3	N4
<i>P. roxburghii</i> with <i>P. roxburghii</i>	173	257	308	313
<i>P. roxburghii</i> with <i>A. nepalensis</i>	304	411.1	439	412
<i>P. roxburghii</i> with <i>C. nepalensis</i>	286	384	433	421
<i>C. torulosa</i> with <i>C. torulosa</i>	866	1128	1145	1119
<i>C. torulosa</i> with <i>A. nepalensis</i>	986	1344	1353	1214
<i>C. torulosa</i> with <i>C. nepalensis</i>	1057	1316	1345	1251
<i>C. torulosa</i> with <i>Q. floribunda</i>	828	1107	1136	1098
<i>Q. floribunda</i> with <i>Q. floribunda</i>	213	287	318	332
<i>Q. floribunda</i> with <i>A. nepalensis</i>	265	327	342	383
<i>Q. floribunda</i> with <i>C. nepalensis</i>	247	306	340	359
<i>Q. floribunda</i> with <i>C. torulosa</i>	116	194	209	235
<i>C. nepalensis</i> with <i>C. nepalensis</i>	1105	1309	806	652
<i>C. nepalensis</i> with <i>P. roxburghii</i>	901	986	637	496
<i>C. nepalensis</i> with <i>C. torulosa</i>	821	873	514	454
<i>C. nepalensis</i> with <i>Q. floribunda</i>	1020	1183	680	607
<i>A. nepalensis</i> with <i>A. nepalensis</i>	1075	901	759	660
<i>A. nepalensis</i> with <i>P. roxburghii</i>	738	787	586	445
<i>A. nepalensis</i> with <i>C. torulosa</i>	692	762	556	388
<i>A. nepalensis</i> with <i>Q. floribunda</i>	840	884	628	498

**Table 2.2:** Percent facilitation by *A. nepalensis* and *C. nepalensis* on height growth of target species (*P. roxburghii*, *C. torulosa* and *Q. floribunda*) along the nutrient gradients.

Target species	% facilitation by <i>A. nepalensis</i>				% facilitation by <i>C. nepalensis</i>			
	N1	N2	N3	N4	N1	N2	N3	N4
<i>P. roxburghii</i>	40.0	37	30	25	30.2	24.6	20.3	16.2
<i>C. torulosa</i>	32.0	30.0	27.0	16.0	25.0	21.3	19.0	11.0
<i>Q. floribunda</i>	30.0	23.0	19.1	11.9	20.4	16.9	14.1	9.3

### Total seedling dry mass

Seedling dry mass of all target and nurse species along the nutrient gradient at two years of age are presented in Fig. 3.1. In all target species, the dry mass of 2-years-old seedling increased with increasing nutrient supply. However, the difference between dry mass at N3 and N4 nutrient level was insignificant.

In *Pinus*, the seedling mass ranged from 3.23-11.62 g seedling<sup>-1</sup> when grown alone and from 7.45-18.48 g seedling<sup>-1</sup> when grown with *Alnus*. The facilitation of *Alnus* was maximum at N1 level (130%) and then continuously decreased up to N4 nutrient level (56%). The facilitation of *Coriaria* was less than the facilitation of *Alnus*, but the response to different nutrient levels was similar. In N1 nutrient level the facilitation was 115% and decreased with increasing nutrient level N4 (58%) (Table 3.1).

Across the nutrient levels in *Cupressus* the seedling biomass ranged from 6.01-15.92 g seedling<sup>-1</sup> in pure culture, from 15.16-30.28 g seedling<sup>-1</sup> with *Alnus*, and

14.50-25.00 g seedling<sup>-1</sup> with *Coriaria*. The facilitation of *Alnus* was again highest at N1 level (150%) and minimum at N4 level (88%).

In *Quercus*, the mass ranged from 2.25-9.30 g seedling<sup>-1</sup> in pure culture and 6.07-10.90 g seedling<sup>-1</sup> with *Alnus* and 5.40-11.00 g seedling<sup>-1</sup> with *Coriaria*. However, with *Cupressus* it decreased from N1-N4 nutrient level. Facilitation effect of *Alnus* was highest at N1 (129%) and sharply declined towards the higher nutrient level N4 (19%).

In the two nurse species (*Alnus* and *Coriaria*) when grown with the other species, the dry mass increased upto N2 level, and then decreased in the higher part of the nutrient gradient.

Responses of shoot and root biomass to different nutrient levels were similar to that of total seedling dry mass.

Analysis of variance for seedling dry mass at two years indicated that difference between species, level of competition, treatment as well as their interactions were highly significant ( $P < 0.01$ ; Table 3.2).

**Table 3.1:** Percent facilitation by *A. nepalensis* and *C. nepalensis* of seedling dry mass of target species (*P. roxburghii*, *C. torulosa* and *Q. floribunda*) along the nutrient gradients.

Target species	% facilitation by <i>A. nepalensis</i>				% facilitation by <i>C. nepalensis</i>			
	N1	N2	N3	N4	N1	N2	N3	N4
<i>P. roxburghii</i>	130	90	60	56	115	75	50	58
<i>C. torulosa</i>	150	114	94	88	141	95	59	51
<i>Q. floribunda</i>	169	59	21	17	129	46	25	19

**Table 3.2:** 3-factor analysis of variance for seedling dry mass of study species along the nutrient gradients.

### Tests of Between-Subjects Effects

Dependent Variable: SEEDLING

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	53894.386 <sup>a</sup>	76	709.137	1452.774	.000
TREATMEN	1053.052	3	351.017	719.113	.000
SPECIES	11428.544	4	2857.136	5853.278	.000
COMBINAT	389.992	3	129.997	266.319	.000
TREATMEN * SPECIES	1419.019	12	118.252	242.256	.000
TREATMEN * COMBINAT	16.660	9	1.851	3.792	.000
SPECIES * COMBINAT	1972.910	11	179.355	367.437	.000
TREATMEN * SPECIES * COMBINAT	161.434	33	4.892	10.022	.000
Error	74.195	152	.488		
Total	53968.581	228			

a. R Squared = .999 (Adjusted R Squared = .998)

## Discussion

In the experiments based on pot-culture of seedlings, we examined the nursing effect of two nitrogen-fixing actinorhizal plants: *Alnus nepalensis* and *Coriaria nepalensis* on some important forest species, viz., *Pinus roxburghii*, *Quercus floribunda* and *Cupressus torulosa* of central Himalaya. While *Alnus* (alder), *Coriaria* and *Pinus* (pine) are effective colonizers of the landslide and other disturbed sites, *Quercus* (oak) is important late successional species of central Himalayan forests (Singh and Singh 1992). *Cupressus* (cypress) has restricted distribution and seldom forms a large stretch of forest on steep and eroding slopes (Troup 1921). Both oak and pine are evergreen with single year leaf lifespan, alder and *Coriaria* are sub-evergreen, and cypress is evergreen with several years of leaf lifespan. On roots of alder and *Coriaria*, the actinomycetes (*Frankia*) form nodules that are capable of biological nitrogen fixation. Both have also mycorrhizal association. These features enable these plants to thrive in nutrient-poor soils and increase their potential in forestry as nurse plant (Gauthier *et al.*, 1983).

The occurrence of *P. roxburghii*, *C. torulosa*, *A. nepalensis* and *C. nepalensis* species is associated with nutrient-poor sites and that of the oak with nutrient-rich sites, indicating thereby that during the succession nutrients in soil increases and with the progress of succession community biomass increases (Chaturvedi, 1983; Rawat 1983), and availability of light to seedlings declines (Singh and Singh, 1992).

In all target species, seedling growth (height, diameter and seedling dry mass) increased with increasing nutrient level. In each experiment facilitative effect of nitrogen fixers (alder, *Coriaria*) was evident, so was the competitive effect of target species (pine, cypress and oak) on it (Figs. A-F). Since the positive effect of facilitation was more than the negative effects of competition, mixtures had higher values than the average of monocultures. The facilitative effect of alder and *Coriaria* was maximum at lowest nutrient level (N1) and then continuously decreased with increasing nutrient level. However, the effect of competition of target plant on nurse plant was maximum at the highest nutrient level (N4) and decreased with decreasing nutrient level. Bertness and Callaway (1994) hypothesized that competition increases in importance toward the more productive part of the environmental gradient, whereas facilitation is more important under harsh conditions. The facilitation of *Coriaria* was less than the facilitation of alder, possibly due to its (*Coriaria*) spreading habit. Clearly, combination of species, species number and abiotic environment interact to determine ecosystem function. Our experiments indicate that when individuals of different species grow together, more than one interaction may be involved, and their effects change with changing environment.

Since alder overtops the associated species, the negative effect on alder growth in mixture cannot be due to the competition with heterospecific individual. It seems that as soil nutrients increase, alder's ability to fix nitrogen declines, and this trend is sharpened by the presence of heterospecific individual. *Coriaria* individual is less adversely affected by the presence of heterospecific individual and whatever reduction in its growth occurs is more than compensated for by its facilitative effect resulting in more growth in mixture than in monoculture (Fig. M). Our study indicates that the growth of facilitator is reduced in the presence of species facilitated and the combined dry mass production in mixed culture is increased when facilitator species is smaller and slow growing than the species as whose growth is facilitated. Thus, the impact of species diversity depends on the interaction between individuals of species and that can vary from one combination to another.

The root:shoot ratios were relatively lower towards the higher nutrient gradients (Table 4.0). Several authors have reported a decrease in the root:shoot ratio of plants treated with N-fertilizers (Hocking, 1972; Reddy *et al.* 1976; Luxmoore, 1971; Chapin, 1980), and root and shoot allocation patterns may be adjusted to alleviate imbalances in resource availability (Chapin, 1980; Zangerl and Bazaaz, 1983). Plants from infertile

habitats maximize nutrient uptake through high root:shoot ratio (Nye and Timber, 1977). Rapidly growing species from high-nutrient habitats show considerable plasticity in root:shoot ratio generally having higher ratios at low availability and lower ratios at high availability than do species from low nutrient habitats (White, 1973; Grime and Curtis, 1976; Grime, 1979). Parrish and Bazzaz (1982a) have explained the decrease in proportion of biomass in roots of perennial species with increasing nutrient concentration in two ways. First, the plants could have some sort of feedback system enabling them to reduce root growth if a small root system could provide enough nutrient and water for shoot; and second, the higher concentration of nutrients could kill the root tips, limiting root growth.

In presence of nurse plant, root: shoot ratio of target species decreased in all nutrient levels. This may indicate that nutrient supply was greater in mixed culture due to biological nitrogen fixation by nurse plant. All the target species showed greater height and mass with increasing soil nutrient concentration.

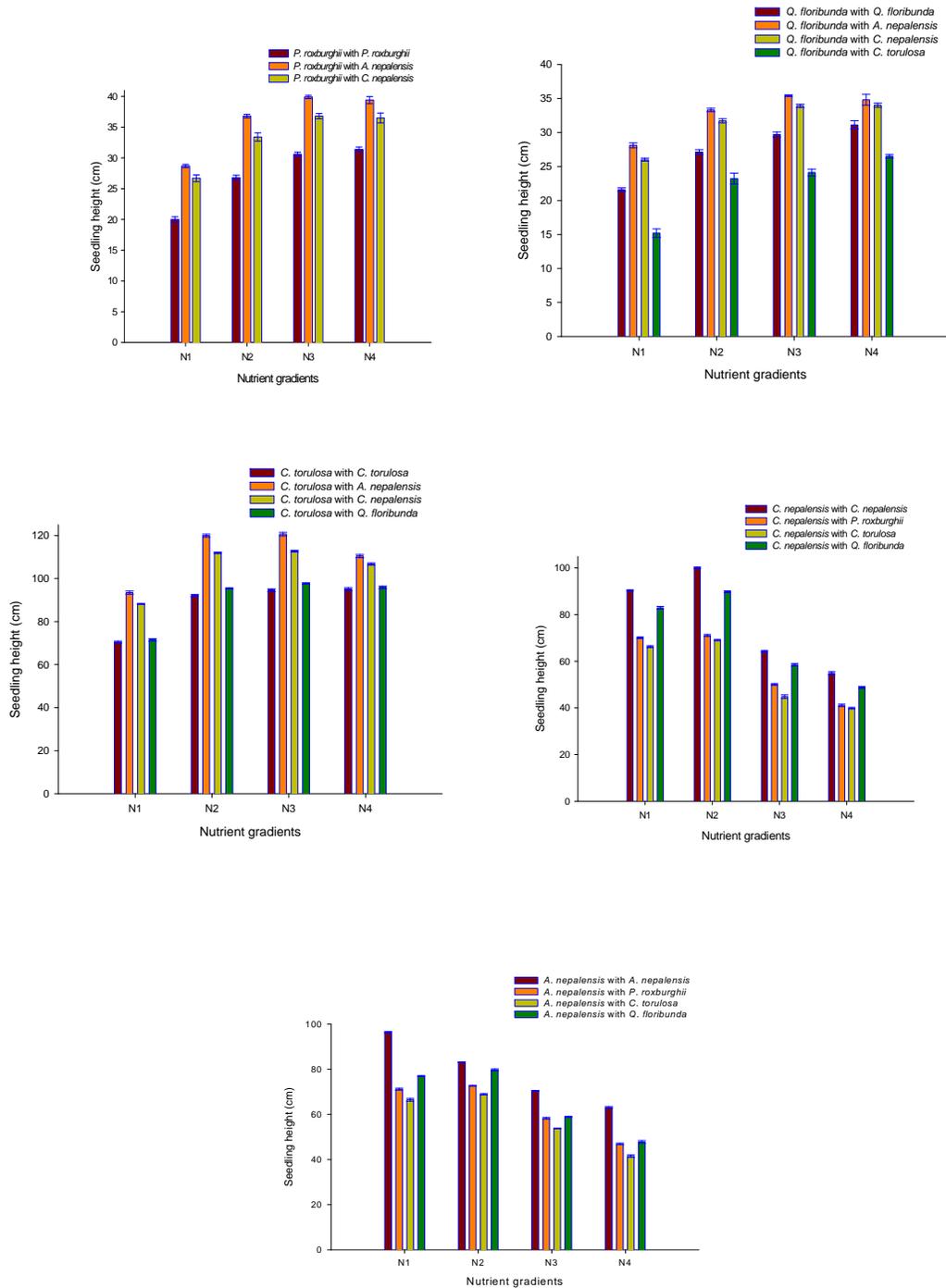
Both *Coriaria* and alder come as an early succession species in freshly exposed soil of landslide-affected sites which are often rocky and severely eroded. A relatively heavy demand for nitrogen in nitrogen-poor soil is met through biological N-fixation in alder and *Coriaria*. The production of nitrogen-rich litter and mineralization increases soil fertility. In the course of succession, these species are replaced by seral species in the natural habitats (Sharma and Ambasht, 1988). Thus, the higher fertility suppresses the growth of alder and *Coriaria* by inhibiting the nitrogen supply to these nodules forming species associated with mycorrhizal fungi. The nodule biomass declines with increasing soil fertility. The replacement of alder and *Coriaria* by target species as found in the present experiment represents the facilitation model of succession. Parrish and Bazzaz (1982b) have explained that in monoculture, individuals, very likely have similar and widely overlapping fundamental niches, and 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 resources. However, when the individuals with similar fundamental niche are of different species, as in mixed culture, it is likely that in competition one will be considerably better than the other one at obtaining resources. As a result, under competition growth of one species is reduced. The difference in individual's weight between species was lowest at the lowest nutrient level, indicating that there were not enough nutrients present for the individuals to manifest genetic differences strongly and develop competitive hierarchies (Parris and Bazzaz, 1982). Competition between species has been shown to be more intense at higher fertility level (Mahmood and Grime, 1976; Austin and Austin, 1980). The results presented here, however, should be considered only a starting step towards the understanding of role of resources in facilitation. This study shows that competitively superior species may not only suppress the growth of its competitor, it may also realize better growth in its presence. Thus, there is a scope for exploring the usefulness of forest species "as a nurse species" in forestry practices. However, there are several limitations in this study. First, experiments have focus on a short period of the life of long-lived plants. Second, different resources as adults than as seedlings may limit plants. Third, environmental conditions in poly-houses where seedlings were grown are different from those of outside. High humidity and nighttime condensation of vapours and warmer temperatures differentiate the poly-house environment for the natural one. However, results presented here clearly indicate that they may be important determinants of the sequence of replacement of species in this region.

In this experimental study based on pot cultures, we have considered tree seedlings of the Western Himalayan forest, grown in both monocultures and mixtures of two species along a nutrient gradient. We examined whether seedling mass was greater in mixture than in monoculture and how it was modified due to variation in species growth form and soil nutrient level. The species pairs only included the species that occur together in natural communities. We assume that a mixture of two species is twice as diverse a monoculture. We considered various functional types, such as

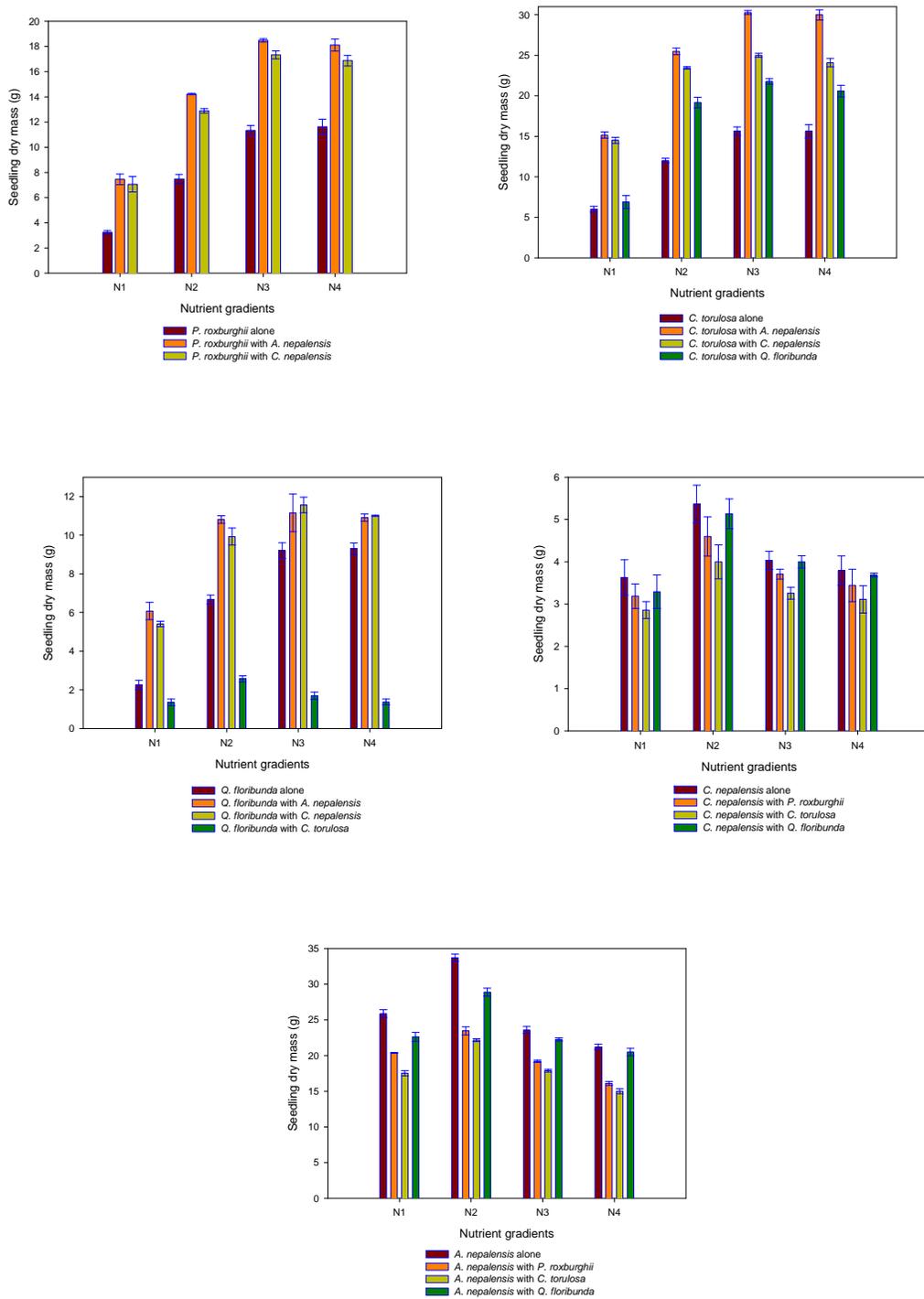
nitrogen fixing species known for their facilitating role, and broadleaved evergreen species and conifer species, considered highly competitive in behavior (Singh *et al.*, 1984). We assume that interacting individuals of species and their interaction with the abiotic conditions influence ecosystem properties. In the Western Himalayan forest generally, interactions occur among the individuals of 2-4 tree species.

**Table 4.0:** Root:shoot ratio of target species (*P. roxburghii*, *C. torulosa* and *Q. floribunda*) and nurse species (*A. nepalensis* and *C. nepalensis*) along the nutrient gradients in pure and mixed cultures.

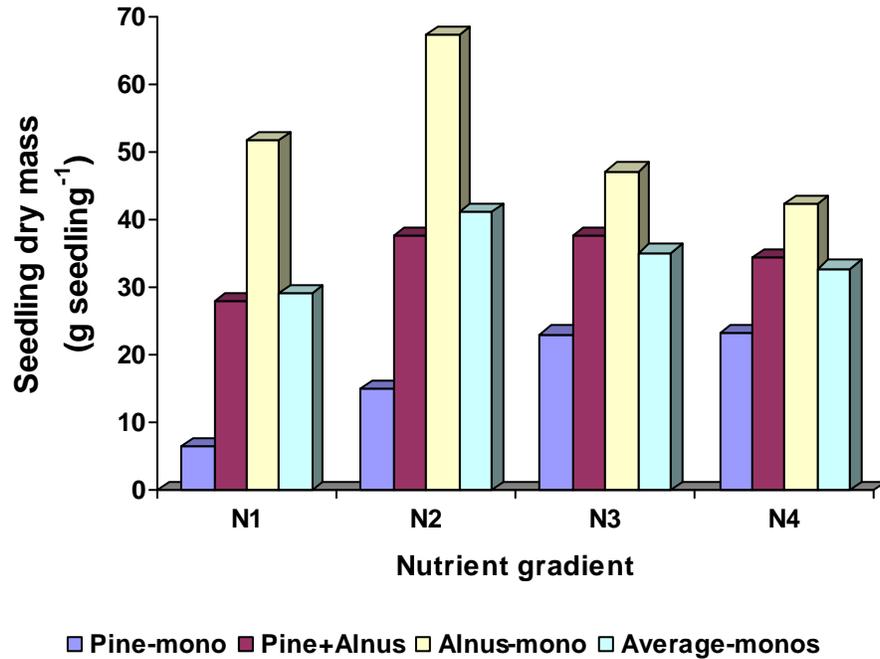
Species combination	N1	N2	N3	N4
<i>P. roxburghii</i> with <i>P. roxburghii</i>	0.598	0.442	0.401	0.392
<i>P. roxburghii</i> with <i>A. nepalensis</i>	0.574	0.380	0.302	0.282
<i>P. roxburghii</i> with <i>C. nepalensis</i>	0.570	0.363	0.329	0.317
<i>C. torulosa</i> with <i>C. torulosa</i>	0.522	0.491	0.432	0.425
<i>C. torulosa</i> with <i>A. nepalensis</i>	0.495	0.412	0.381	0.371
<i>C. torulosa</i> with <i>C. nepalensis</i>	0.401	0.379	0.312	0.301
<i>C. torulosa</i> with <i>Q. floribunda</i>	0.516	0.412	0.417	0.398
<i>Q. floribunda</i> with <i>Q. floribunda</i>	1.172	1.041	0.980	0.947
<i>Q. floribunda</i> with <i>A. nepalensis</i>	1.061	0.981	0.971	0.792
<i>Q. floribunda</i> with <i>C. nepalensis</i>	1.195	0.988	0.853	0.723
<i>Q. floribunda</i> with <i>C. torulosa</i>	0.924	1.001	1.106	0.973
<i>C. nepalensis</i> with <i>C. nepalensis</i>	0.669	0.478	0.387	0.398
<i>C. nepalensis</i> with <i>P. roxburghii</i>	0.563	0.414	0.315	0.289
<i>C. nepalensis</i> with <i>C. torulosa</i>	0.555	0.495	0.320	0.337
<i>C. nepalensis</i> with <i>Q. floribunda</i>	0.554	0.483	0.331	0.369
<i>A. nepalensis</i> with <i>A. nepalensis</i>	0.746	0.706	0.612	0.614
<i>A. nepalensis</i> with <i>P. roxburghii</i>	0.828	0.785	0.737	0.649
<i>A. nepalensis</i> with <i>C. torulosa</i>	0.802	0.737	0.676	0.606
<i>A. nepalensis</i> with <i>Q. floribunda</i>	0.791	0.714	0.665	0.687



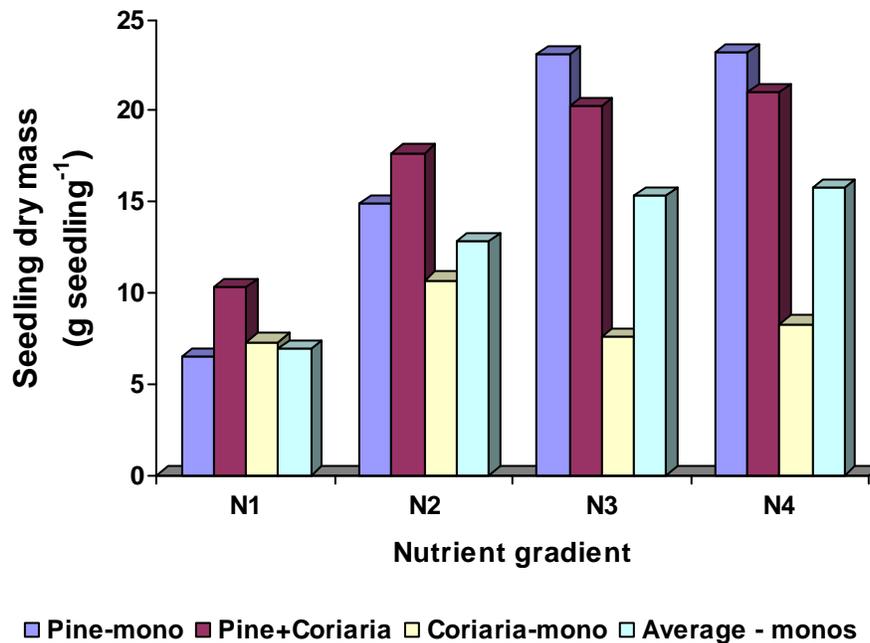
**Fig 2.1:** Average seedling height (cm  $\pm$  SE) in different combinations of target [*P. roxburghii*, *C. torulosa*, *Q. floribunda*] and nurse species [*A. nepalensis*, *C. nepalensis*] along the nutrient gradients at yr-2.



**Figs. 3.1:** Average seedling biomass ( $\text{g seedling}^{-1} \pm \text{SE}$ ) in different combinations of target [*P. roxburghii*, *C. torulosa*, *Q. floribunda*] and nurse species [*A. nepalensis*, *C. nepalensis*] along the nutrient gradients at yr-2.



**Fig. A:** The sum of dry mass in mono and mixtures of pine and *Alnus* (g seedling<sup>-1</sup>) along the nutrient gradients.



**Fig. B:** The sum of dry mass in mono and mixtures of pine and *Coriaria* (g seedling<sup>-1</sup>) along the nutrient gradients.

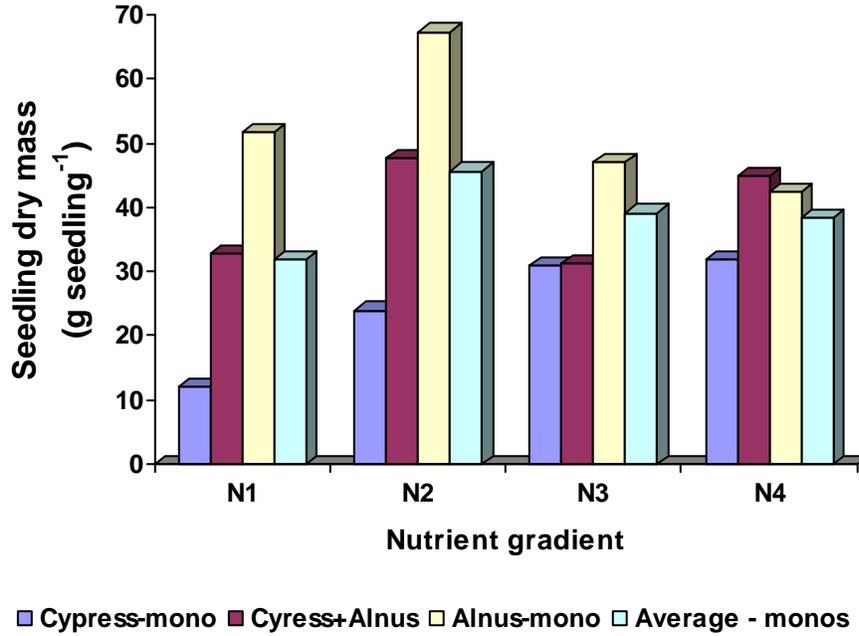


Fig. C: The sum of dry mass in mono and mixtures of cypress and *Alnus* (g seedling<sup>-1</sup>) along the nutrient gradients.

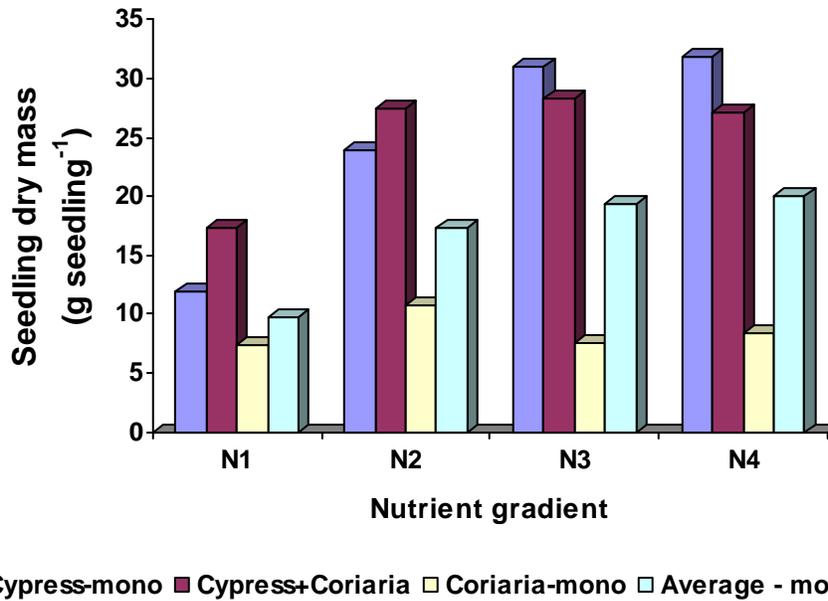
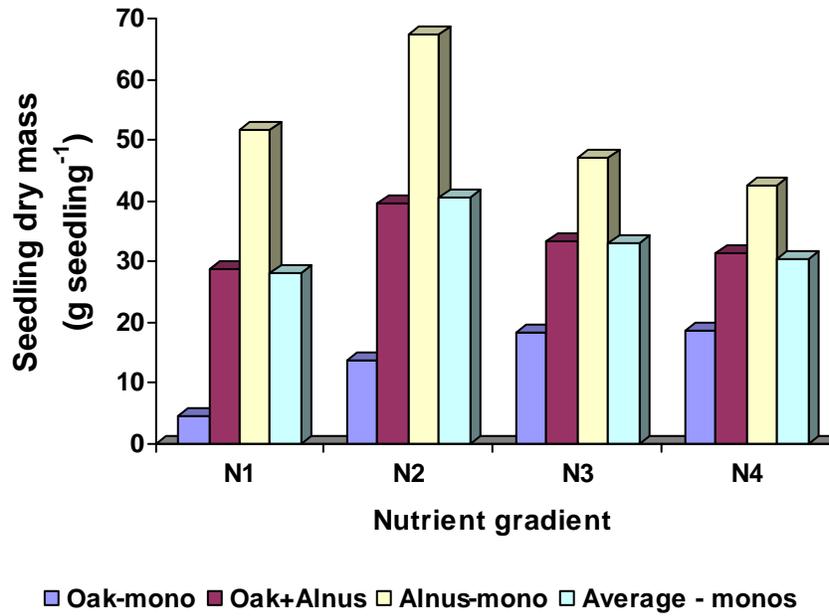
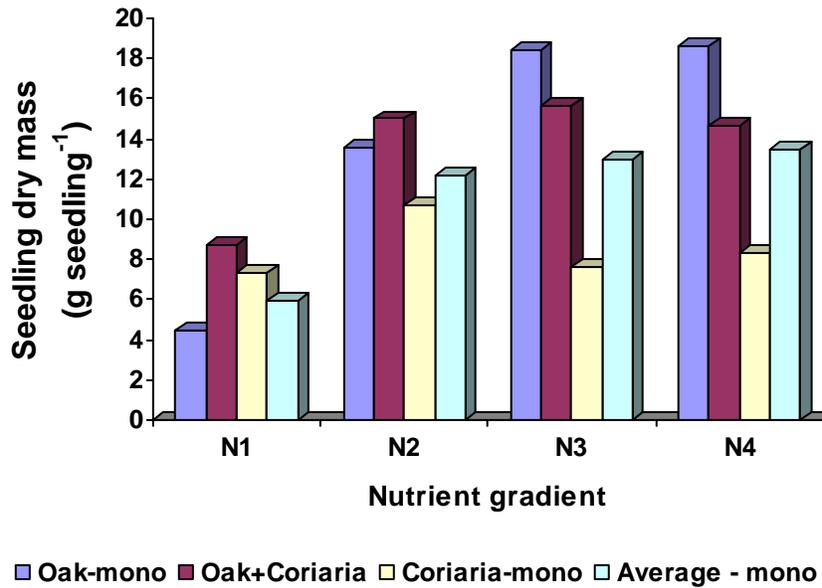


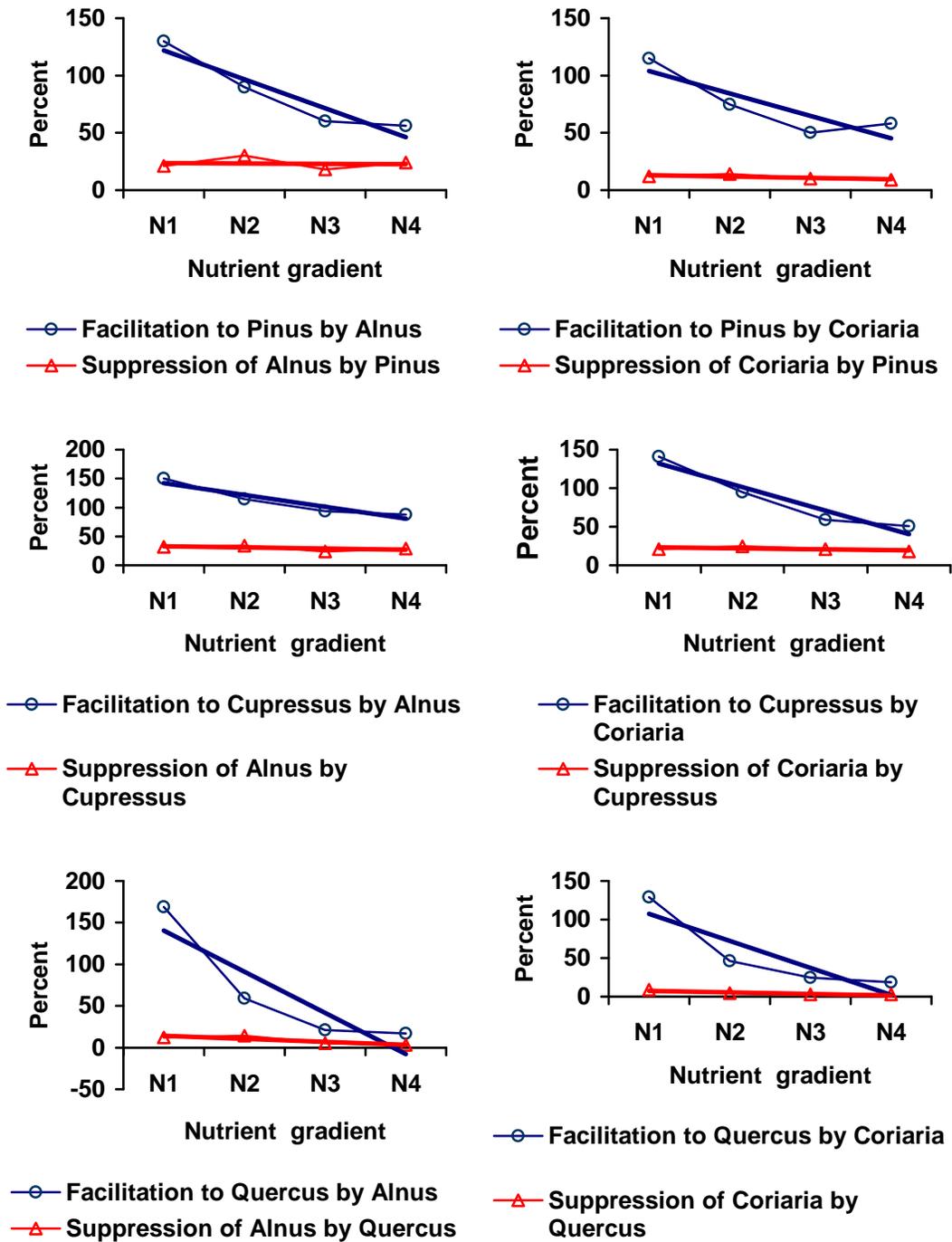
Fig. D: The sum of dry mass in mono and mixtures of cypress and *Coriaria* (g seedling<sup>-1</sup>) along the nutrient gradients.



**Fig. E:** The sum of dry mass in mono and mixtures of oak and *Alnus* ( $\text{g seedling}^{-1}$ ) along the nutrient gradients.



**Fig. F:** The sum of dry mass in mono and mixtures of oak and *Coriaria* ( $\text{g seedling}^{-1}$ ) along the nutrient gradients.



**Fig. M:** Values of facilitation and suppression of seedlings along a nutrient gradient (N1-N4). Facilitation was calculated as percent increase in growth of a seedling in a mixture over its growth in monoculture. Suppression is percent decrease in seedling growth in mixture over than in monoculture. In all combinations facilitation exceeded suppression, consequently the combined mass of seedlings of any two species was greater in mixture than the combined mass in monocultures.

## References

- Austin M.P. and Austin B.O. 1980. Behavior of experimental plant communities along a nutrient gradient. **J. Ecol.** **68**: 891-918.
- Bertness M.D. and Callaway, R.M. 1994. Positive interactions in communities. **Trends in Ecology and Evolution.** **9**:191-193.
- Chapin F.S. III. 1980. The mineral nutrition of wild plants. **Ann. Rev. Ecol. Syst.** **11**: 233-260.
- Chaturvedi O.P. 1983. **Biomass structure, productivity and nutrient cycling in *Pinus roxburghii* forest.** Ph. D. Thesis, Kumaun University, Nainital. 347 pp.
- Gauthier D., Diem H.G. and Dommergues Y. 1983. In: **Casuarina: Ecology, Management and Utilization** (S.J. Midgeley, J.W. Turnbull and R.D. Johnston, eds.), pp. 211-217. CSIRO. Melbourne.
- Goldberg D.E. 1982. The distribution of evergreen and deciduous trees relative to soil type: A example from the Sierra Madre, Mexico and a general Model. **Ecology.** **63(4)**: 942-951.
- Grime J.P. 1979. Plant strategies and vegetation processes. Wiley, New York. 222 pp.
- Grime J.P. and Curtis A.V. 1976. The interaction of drought and mineral nutrient stress in calcareous grassland. **J. Ecol.** **64**:976-998.
- Hocking D. 1972. Current rearing knowledge proceedings of a workshop on container planting in Canada. **Information Report DPC-X-2** Ontario 48-66.
- Luxmoore R.L. and Millington R.J. 1971. Growth of perennial grass (*Lolium perenne* L.) in relation to water, N and light intensity. **Plant and Soil.** **34**:269-281.
- Mahmood, A. and Grime, J.P. 1976. An analysis of competitive ability in three perennial grasses. **New Phytol.** **77**:431-435.
- Nye P.H. and Timber P.B. 1977. **Solute movement in the soil root system.** Berkeley, Calif. Univ. California Press. 342 pp.
- Parrish J.A.D. and Bazzaz F.A. 1982a. Responses of plants from three successional communities on a nutrient gradient. **J. Ecol.** **70**:233-248.
- Parrish J.A.D. and Bazzaz F.A. 1982b. Niche responses of early and late successional tree seedlings on three resource gradients. **Bull. Torrey. Bot. Club.** **109**:451-456.
- Rawat Y.S. 1983. **Plant Biomass, net primary production and nutrient cycling in oak forests.** Ph. D. Thesis, Kumaun University, Nainital. 355 pp.
- Reddy R., Khan M.A. and Dabryiol. 1976. Effect of compost and mineral fertilization on development of mycorrhiza in chir pine (*Pinus roxburghii* Sarg.) and petula pine (*P. patula* Schlecht. & Cham). **Ind. For.** **102**:463-471.
- Sharma E. and Ambasht R.S. 1988. Nitrogen accretion and its energetics in the Himalayan alder. **Functional Ecology.** **2**:229-235.

- Singh J.S. and Singh S.P. 1987. Forest vegetation of the Himalaya. **Bot. Rev.** **53**:80-192.
- Singh J.S. and Singh S.P. 1992. **Forests of Himalaya - structure, functioning and impact of man.** Gyanodaya Prakashan, Nainital, India.
- Singh S.P., Rawat Y.S. and Chaturvedi O.P. 1984. Replacement of oak forest with pine in the Himalaya: effects on the nitrogen cycle. **Nature.** **311**:54-56.
- Snedecor G.W. and Cochran W.G. 1969. **Statistical Methods.** Sixth edition. Oxford and IBH Publishing Co., India. 593 pp.
- Tilman D. 1982. **Resource competition and community structure.** Princeton University Press. Princeton. New Jersey. USA.
- Troup R.S. 1921. **The silviculture of Indian trees Vol. I-III.** Oxford at the Clarendon Press, Oxford.
- White L.M. 1973. Carbohydrate reserves of grasses. **Review Journal of Range Management.** **26**: 13-18.
- Zangerl A.R. and Bazzaz F. A. 1983. Responses of an early and a late successional species of *polygonum* to variation in resource availability. **Oecologia.** **56**:397-404.

**Acknowledgements:** Financial support from C.S.I.R., New Delhi is gratefully acknowledged. We also thank Prof. S. P. Singh (FNA), Department of Botany, Kumaun University, Nainital for valuable co-operation.

**Corresponding address:**

Dr. Deepti Goel, D/o Shri S.R. Prasad, LIG-71, Awas- Vikas, Haldwani, Nainital-263139 (Uttarakhand)

2/28/2009