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Nitrogen resorption in leaves of tree and shrub seedlings in response to increasing soil fertility

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In the present study an attempt was made to examine the relationship between availability of nitrogen in soil and the resorption of nitrogen before leaf fall. For this, common tree (*Quercus leucotrichophora*, *Pinus roxburghii*, *Cupressus torulosa*, *Alnus nepalensis* and *Populus ciliata*) and shrub species (*Desmodium elegans* and *Crataegus crenulata*) of Central Himalayan forests varying in leaf lifespan and other characters were selected. Seedlings of these species were raised from current year seed crop and grown at various levels of nitrogen availability. The species differed with regard to nitrogen level up to which their biomass increased with increasing nitrogen availability. In each species, the proportional resorption of nitrogen decreased continuously with increasing nutrient level. The nutrient use efficiency also decreased with increasing nutrient level in each species. These results suggest that as the availability of a limiting nutrient increases, the mechanisms used by plants to conserve that nutrient may become less efficient.

Keywords: Nitrogen resorption, soil fertility, nutrients, nitrogen availability.

THE resorption of nutrients prior to leaf fall is one of the key processes by which plants conserve them. This process reduces the likelihood of nutrient loss in litter dropped on the forest floor^{1,2} and subsequently, the withdrawn nutrients are redeployed in new tissues, such as leaves and reproductive structures or stored for later use³. The resorption accompanied by a reduction in nutrient restitution (through leaf litter) and requirements, affords the ecosystem a certain independence from the soil and the possibility of good management of the available elements⁴. Furthermore, nutrient resorption during leaf senescence greatly affects litter quality, litter decomposition and nutrient release. On average, plants withdraw about 50% of leaf N and P, but the proportion withdrawn⁵ varies widely across species, 5–80% of leaf N, and 0–95% of leaf P. Some studies suggest that with increasing availability of a limiting nutrient the mechanisms used by plants to conserve that nutrient, become less efficient^{6,7}. However, other studies have found that increased nutrients have little effect on the efficiency of internal nutrient-conservation strategies in plants^{8,9}. In infertile habitats, N and P in senesced leaves are reduced to lower levels than in fertile habitats³. Does it apply also to within-species trends in nutrient resorption?

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In the present study we examine the relationship between the availability of nitrogen in soil and its resorption before leaf senescence. Data used for the analyses are from three different experiments conducted during different time periods in a nursery condition at Kumaun University, Nainital. The main objectives were to see (i) the nutritional control on nitrogen resorption efficiency at species level, and (ii) how species differing in leaf lifespan and other characters respond in terms of adjusting resorption capacity along a gradient of nitrogen availability. The species varied in leaf characters and its phenology, and included evergreens with leaf lifespan about one year, shedding leaves annually with the commencement of new leaves (it included an oak and a pine), referred to as e-evergreen type, evergreen with several years of leaf lifespan referred to as ee- evergreen type (a cypress), deciduous (a poplar), and nitrogen fixers (an alder and *Desmodium* sp.). We considered species of different leaf characters to examine whether increase in soil fertility influences nutrient resorption from leaves in a particular pattern.

The seven species studied included trees as well as shrubs, nitrogen fixers as well as non-fixers, and all the three leaf life-span types. Tree species were *Quercus leucotrichophora* A. Camus, *Pinus roxburghii* Sarg., *Cupressus torulosa* D. Don., *Alnus nepalensis* D. Don, and *Populus ciliata* Wall. Shrub species were *Desmodium elegans* D. Don and *Crataegus crenulata* Roxb. Among these, *Q. leucotrichophora* is a dominant late successional forest-forming species of Central Himalayan region between 1800 and 2200 m elevation. *P. roxburghii* is the most extensively distributed species between 1500 and 2000 m elevation, and has ability to tolerate stress caused by deficiencies of water and nutrients. While the oak generally occurs on fertile sites, the pine is associated with dry infertile sites. *A. nepalensis* is nitrogen-fixing actinorhizal species (between 1000 and 2800 m altitude) and often forms monospecific stands on the steep slopes along the rivers and is a well-known colonizer of landslide-affected area. All these tree species have about one year leaf life longevity (e-evergreen). *C. torulosa* is an ee-evergreen and occupies infertile sites on steep slopes, often on limestones. It has most restricted distribution among the Himalayan species¹⁰. *P. ciliata* is a deciduous tree and occurs between 1800 and 3000 m elevation. It is an early colonizer of landslips in dry areas and often forms small gregarious patches on the banks of large watercourses. *C. crenulata* is an early successional evergreen shrub. It is common in chir pine and banj oak forests, especially along open streams.

To examine the relationship between nitrogen availability and resorption of nitrogen before leaf senescence, seedlings were raised in nursery condition. The three experiments were as follows: in the first experiment (A), nitrogen in soil ranged from 600 mg kg⁻¹ at the lowest level to 632 mg kg⁻¹ at the highest level, and this gradient was maintained by adding different dozes of urea fertilizer¹¹. Species used in this experiment were *A. nepalensis*, *P. ciliata*, *D. elegans* and *C. crenulata*. In the second experiment (B), the soil ni-

trogen ranged from 680 mg kg⁻¹ at the lowest level to 810 mg kg⁻¹ at the highest level, and this gradient was maintained by adding different dozes of 12:32:16 NPK fertilizer¹². Species used in this experiment were *Q. leucotrichophora* and *P. roxburghii*. In the third experiment (C), soil nitrogen ranged from 130 mg kg⁻¹ at the lowest level to 2080 mg kg⁻¹ at the highest level, and this gradient was maintained by mixing sieved oak forest soil and commercial sand in different proportions¹³. Species used in this experiment were *P. roxburghii*, *Q. leucotrichophora*, *A. nepalensis* and *C. torulosa*. Nitrogen present in the soil of the first experiment was similar to the range that occurred in oak forest of Nainital. In the second experiment it resembled the range typically found in oak, pine and deciduous forests, while in the third experiment the range exceeded that occurring across all kinds of sites (including landslips and fertile forest sites). In brief, the range of nitrogen in soil increased progressively, and the last one encompassed all the possible situations.

Seedlings of the tree and shrub species were raised from current year seed crops collected from healthy plants growing naturally in forests near Nainital town (29°22'N lat. and 79°25'E long.). After establishment, ten seedlings per species per treatment were maintained in each experiment in bags containing 1 kg soil and sand mixture. These experiments were carried out in a glasshouse at 2000 m asl, where the mean maximum temperature was 1–5°C higher than the air temperature. Bags were kept far apart from each other to minimize any shading and were watered regularly.

Leaf mass and nitrogen concentration of mature green leaves as well as senesced leaves were determined using the Kjeldhal technique¹⁴. Seedlings were harvested after two years, separated into different components, oven-dried at 80°C and weighed. Senesced leaves, those in which an abscission layer is formed in the base of petiole, were collected by a gentle flicking of the leaf or branch. They were easily separable from live leaves as they were of different colour. The direct collection from seedlings does not allow leaching loss of nitrogen from the leaves, which can happen when fallen leaves are collected from the ground. Several leaves were collected from each of the seedlings, and pooled for nitrogen analysis.

The proportional nitrogen resorption was calculated as¹⁵:

$$\text{Resorption (\%)} = \frac{\text{Nitrogen mass in mature leaves} - \text{Nitrogen mass in senesced leaves}}{\text{Nitrogen mass in mature leaves}} \times 100.$$

Nutrient use efficiency was calculated¹⁶ as:

$$\text{E-use} = \frac{\text{Plant dry mass (g)}}{\text{Plant nutrient mass (g)}}$$

Analysis of variance (ANOVA) was performed separately for each species in each experiment.

Table 1. Analysis of variance for each species for different parameters in three experiments

Experiment no.	Species	Parameter	DF	F-value
1	<i>P. ciliata</i>	Leaf N concentration	3	5.9
		N resorption	3	101.6
		Seedling biomass	3	38.4
	<i>C. crenulata</i>	Leaf N concentration	3	7.2
		N resorption	3	24.9
		Seedling biomass	3	613.1
	<i>A. nepalensis</i>	Leaf N concentration	3	1.2 ^{NS}
		N resorption	3	29.7
		Seedling biomass	3	25.5
	<i>D. elegans</i>	Leaf N concentration	3	7.4
		N resorption	3	287.8
		Seedling biomass	3	185.4
2	<i>Q. leucotrichophora</i>	Leaf N concentration	4	2.4 ^{NS}
		N resorption	4	124.7
		Seedling biomass	4	21.7
	<i>P. roxburghii</i>	Leaf N concentration	4	0.6 ^{NS}
		N resorption	4	223.7
		Seedling biomass	4	39.4
3	<i>Q. leucotrichophora</i>	Leaf N concentration	4	476.6
		N resorption	4	169.5
		Seedling biomass	4	314.0
	<i>P. roxburghii</i>	Leaf N concentration	4	316.2
		N resorption	4	169.5
		Seedling biomass	4	603.4
	<i>A. nepalensis</i>	Leaf N concentration	4	6.2
		N Resorption	4	65.4
		Seedling biomass	4	770.8
	<i>C. torulosa</i>	Leaf N concentration	4	199.1
		N resorption	4	261.7
		Seedling biomass	4	840.7

NS, Not significant.

Table 2. Regression parameters relating leaf nitrogen concentration to total soil nitrogen (mg/kg)

Species	Parameter	Experiment		
		1	2	3
<i>Q. leucotrichophora</i>	Intercept		-2.151	0.093
	Slope		0.006	0.0016
	Correlation coefficient	0.933**	0.994*	
<i>P. roxburghii</i>	Intercept		-3.193	0.164
	Slope		0.007	0.012
	Correlation coefficient		0.940**	0.998*
<i>A. nepalensis</i>	Intercept	-1.577		3.268
	Slope	0.009		0.0008
	Correlation coefficient	0.697 ^{NS}		0.810**
<i>C. torulosa</i>	Intercept			0.170
	Slope			0.0011
	Correlation coefficient			0.999*
<i>P. ciliata</i>	Intercept	-5.621		
	Slope	0.014		
	Correlation coefficient	0.965**		
<i>D. elegans</i>	Intercept	5.318		
	Slope	-0.003		
	Correlation coefficient	-0.691 ^{NS}		
<i>C. crenulata</i>	Intercept	8.672		
	Slope	-0.012		
	Correlation coefficient	-0.809 ^{NS}		

* $P < 0.01$; ** $P < 0.05$; NS, Not significant.

In each experiment, the nitrogen addition in soil showed significant effect on leaf nitrogen concentration, nitrogen resorption and dry mass production (Table 1). Leaf nitrogen concentrations generally increased with increasing soil nitrogen level in each experiment. However, in the two nitrogen-fixing species (*A. nepalensis* and *D. elegans*), leaf nitrogen concentration increased with an initial increase in soil nitrogen, and then decreased at higher soil nitrogen levels (Figure 1). Overall, the leaf nitrogen concentration showed significant positive correlation with soil nitrogen in most of the species (Table 2). In case of *A. nepalensis*, correlation was significant in experiment 3 and insignificant in experiment 1. This may be due to the wide range of soil nitrogen concentration in experiment 3 compared to experiment 1. Both in mature green leaf and abscessed leaf, N

concentration increased with increasing N availability, but it was far sharper in the latter.

With increasing nitrogen availability in each experiment, the dry mass of seedlings increased continuously in *P. roxburghii*, and *C. torulosa* only (Figure 2). In the rest of the species (*Q. leucotrichophora*, *A. nepalensis*, *P. ciliata*, *C. crenulata* and *D. elegans*), seedling dry mass decreased towards the higher side of the range in nitrogen concentration, possibly due to toxic effects of nitrogen¹⁷. In most of the species, the dry mass of seedling was significantly related to soil nitrogen availability (Table 3).

In all the species in the three experiments, the proportional nitrogen resorption of leaves declined with increasing soil nitrogen level, but species varied in the extent of decline (Figure 3). The decline in nitrogen resorption was sharper in non-nitrogen fixing (60–66%) species in comparison to nitrogen-fixing species (30%). The regression equations relating nitrogen resorption to soil nitrogen as well as leaf nitrogen showed significant negative correlations for most of the species examined (Tables 4 and 5).

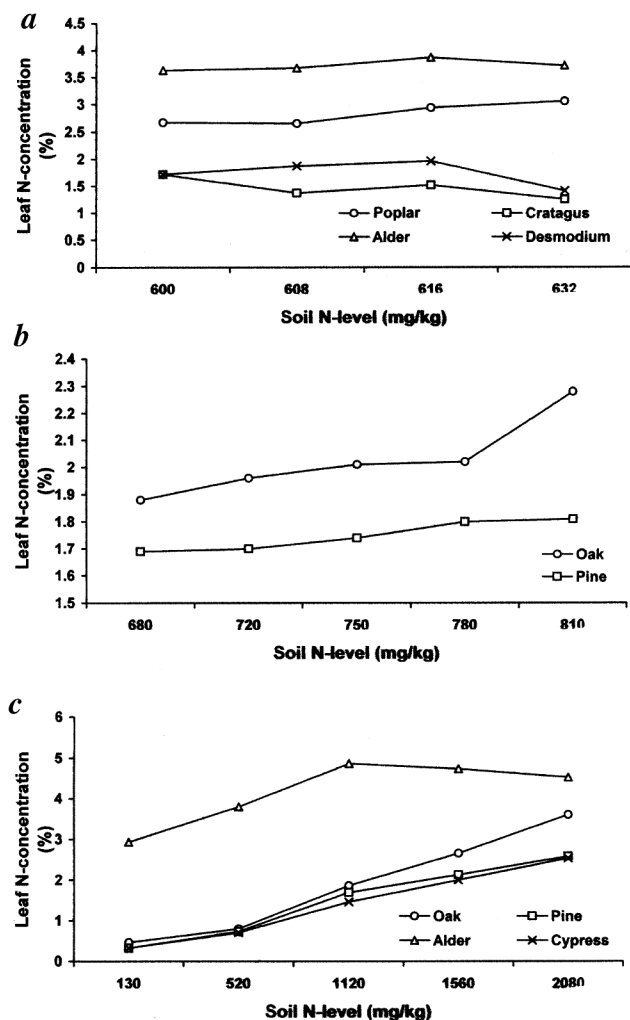


Figure 1. Leaf nitrogen concentration (%) in relation to soil nitrogen level (mg/kg) in first (a), second (b) and third (c) experiment. In the first experiment, N₁ = 600; N₂ = 608; N₃ = 616 and N₄ = 632 mg/kg nitrogen in soil. In the second experiment, N₁ = 680; N₂ = 720; N₃ = 750 N₄ = 780 and N₅ = 810 mg/kg nitrogen in soil. In the third experiment N₁ = 130; N₂ = 520; N₃ = 1120; N₄ = 1560 and N₅ = 2080 mg/kg nitrogen in soil.

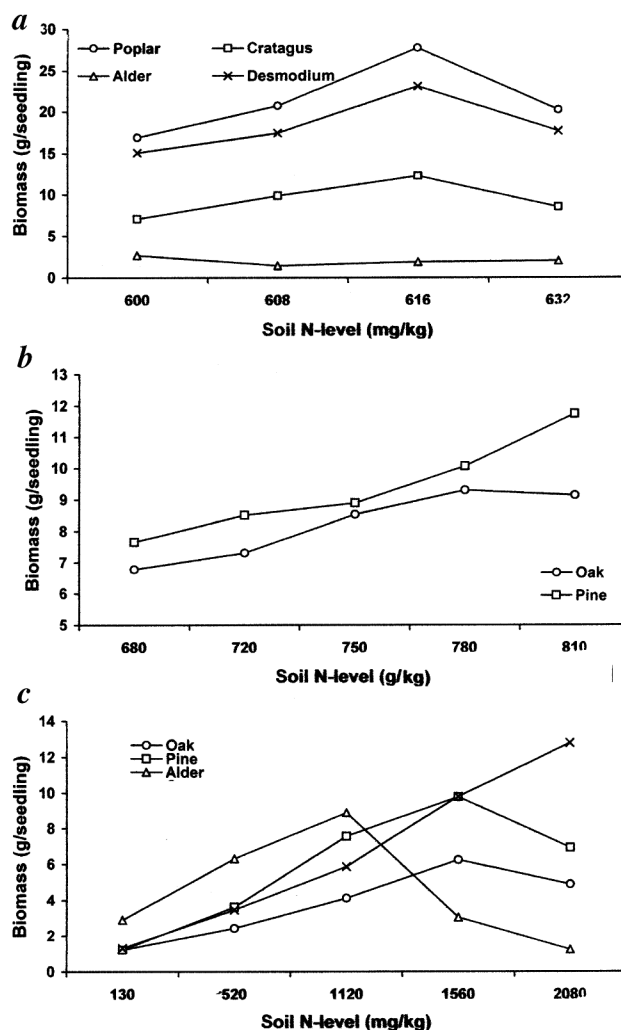


Figure 2. Seedling biomass (g seedling⁻¹) in relation to soil nitrogen level (mg/kg) in first (a), second (b) and third (c) experiment.

Table 3. Regression parameters relating total seedling biomass (g) to total soil nitrogen (mg/kg)

Species	Parameter	Experiment		
		1	2	3
<i>Q. leucotrichophora</i>	Intercept		-23.45	0.486
	Slope		0.044	0.002
	Correlation coefficient		0.936**	0.992*
<i>P. roxburghii</i>	Intercept		-31.72	0.431
	Slope		0.057	0.003
	Correlation coefficient		0.966*	0.998*
<i>A. nepalensis</i>	Intercept	0.54		3.061
	Slope	-0.011		0.0001
	Correlation coefficient	-0.308 ^{NS}		0.047 ^{NS}
<i>C. torulosa</i>	Intercept			0.414
	Slope			0.004
	Correlation coefficient			0.998*
<i>P. ciliata</i>	Intercept	-47.50		
	Slope	0.103		
	Correlation coefficient	0.309 ^{NS}		
<i>D. elegans</i>	Intercept	-39.88		
	Slope	0.084		
	Correlation coefficient	0.034 ^{NS}		
<i>C. crenulata</i>	Intercept	-13.26		
	Slope	0.034		
	Correlation coefficient	0.213 ^{NS}		

* $P < 0.01$; ** $P < 0.05$; NS, Not significant.

Table 4. Regression parameters relating proportional nitrogen resorption to total soil nitrogen (mg/kg)

Species	Parameter	Experiment		
		1	2	3
<i>Q. leucotrichophora</i>	Intercept		364.32	63.39
	Slope		-0.470	-0.023
	Correlation coefficient		-0.986*	-0.970*
<i>P. roxburghii</i>	Intercept		431.27	66.47
	Slope		-0.548	-0.020
	Correlation coefficient		0.892**	0.998*
<i>A. nepalensis</i>	Intercept	284.35		69.03
	Slope	-0.394		-0.011
	Correlation coefficient	-0.954**		-0.954**
<i>C. torulosa</i>	Intercept			66.82
	Slope			-0.022
	Correlation coefficient			-0.967*
<i>P. ciliata</i>	Intercept	473.70		
	Slope	-0.664		
	Correlation coefficient	-0.981**		
<i>D. elegans</i>	Intercept	663.8		
	Slope	-0.992		
	Correlation coefficient	-0.967**		
<i>C. crenulata</i>	Intercept	100.7		
	Slope	-0.222		
	Correlation coefficient	-0.757 ^{NS}		

* $P < 0.01$; ** $P < 0.05$; NS, Not significant.

Nutrient use efficiency (g g^{-1}) decreased significantly with increasing soil nitrogen level in each experiment (Figure 4).

The decline was sharper in non-nitrogen fixing species (e.g. from 244 g g^{-1} at N_1 to 38 g g^{-1} at N_5 nutrient level in *Q.*

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leucotrichophora) in comparison to nitrogen-fixing species (e.g. 45 gg^{-1} at N_1 to 33 gg^{-1} at N_5 nutrient level in *A. nepalensis*), particularly in experiment 3.

In our study, the nitrogen resorption decreased with increasing soil nitrogen availability in each species irrespective of leaf longevity, nitrogen concentration in leaf tissues and ability to fix nitrogen or lack of it. This plasticity in species performance is consistent with the fact that in nutrient-rich conditions, plants have better accessibility to soil nutrients and intra-cycling of nutrients becomes less important. Steyer¹⁸ reported that reabsorption efficiency in mangrove forests decreased with increasing fertility in natural condition. Similar results have also been obtained for several other ecosystems^{6,7,19}.

In contrast, Ares and Fownes²⁰ reported that *Fraxinus uhdei* stands with higher N status retranslocated a larger proportion of N, than did stands with less favourable N status. Several other studies have found little or no relationship between nutrient availability and reabsorption effi-

ciency^{8,9,21}. Our results supported the view that reabsorption can be controlled more by internal demand²² or nutritional sink²³ than by soil nutrient supply. In an analysis of published fertilization experiments covering 60 species²⁴, there was no response of N resorption in 63% of the experiments analysed, whereas in 32% of them there was a decrease in N resorption in response to increased nutrient availability.

Nutrients in new leaf tissues come either from soil or through resorption from senescing leaves, and both involve energy. The cost of nutrient uptake from the soil is likely to decrease with increase in soil nutrient availability. For resorption of nutrient to take place, energy is required to hydrolyse organic compounds for phloem loading of the resulting export molecules for osmotic adjustment and converting the withdrawn nutrients in forms in which they can be stored. Wright and Westboy³ observe that across the sites varying in soil nutrient availability, the balance of soil derived and resorption nutrients deployed in new leaf tissues

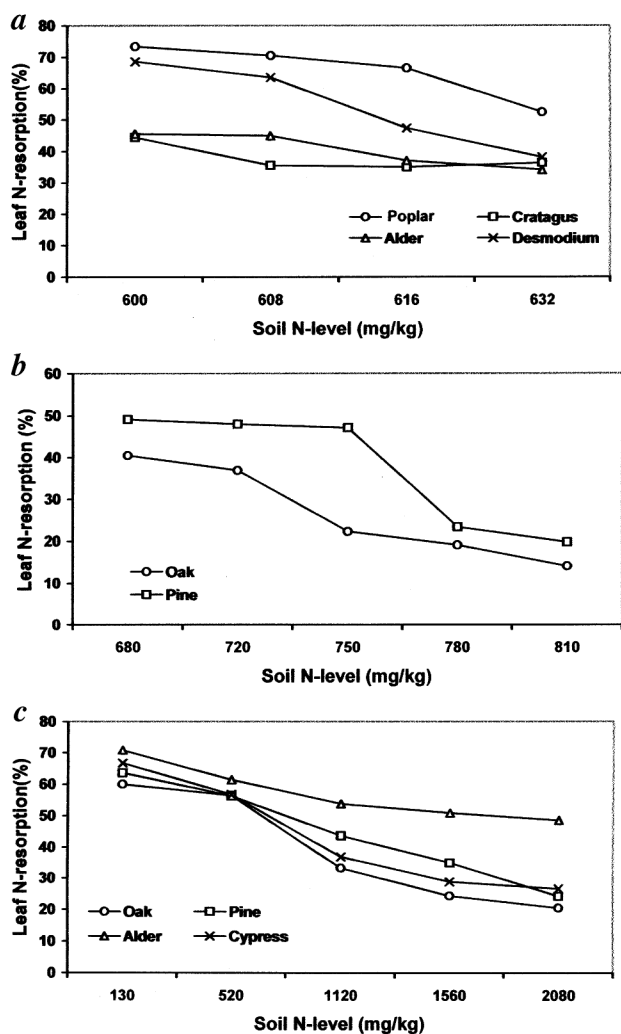


Figure 3. Nitrogen resorption (%) in relation to soil nitrogen level (mg/kg) in first (a), second (b) and third (c) experiment.

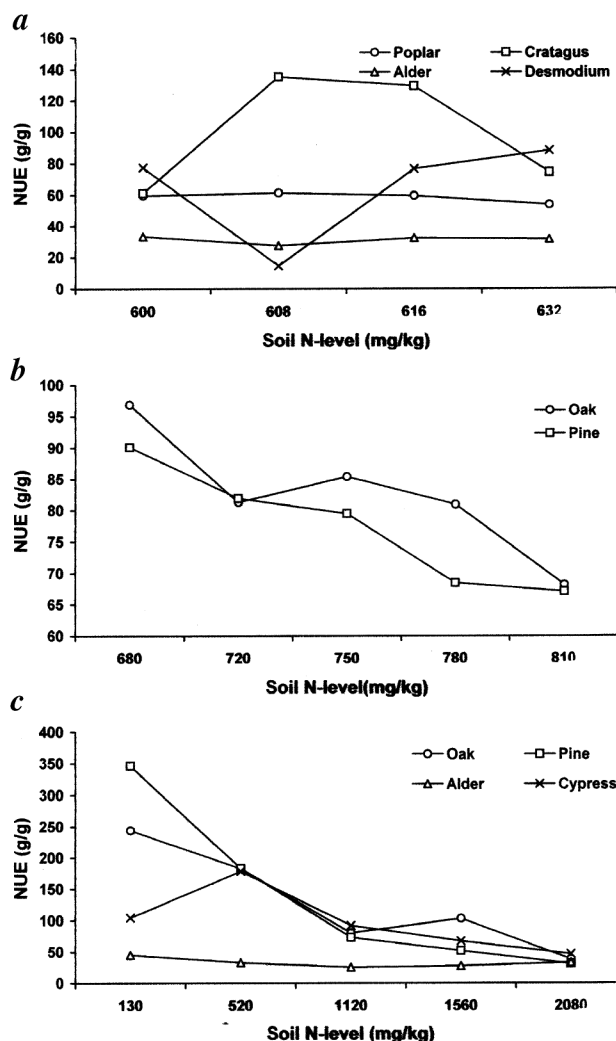


Figure 4. Nutrient use efficiency (NUE; gg^{-1}) in relation to soil nitrogen level (mg/kg) in first (a), second (b) and third (c) experiment.

Table 5. Regression parameters relating proportional nitrogen resorption to leaf nitrogen concentration (%)

Species	Parameter	Experiment		
		1	2	3
<i>Q. leucotrichophora</i>	Intercept		166.51	64.30
	Slope		-64.78	-13.69
	Correlation coefficient		0.878**	-0.961*
<i>P. roxburghii</i>	Intercept		181.21	69.12
	Slope		-78.31	-16.73
	Correlation coefficient		0.987*	-0.997*
<i>A. nepalensis</i>	Intercept	170.03		101.07
	Slope	-34.82		-10.54
	Correlation coefficient	-0.636 ^{NS}		-0.939**
<i>C. torulosa</i>	Intercept			70.18
	Slope			-19.12
	Correlation coefficient			-0.972*
<i>P. ciliata</i>	Intercept	70.68		
	Slope	-41.83		
	Correlation coefficient	0.895**		
<i>D. elegans</i>	Intercept	8.07		
	Slope	26.58		
	Correlation coefficient	0.456 ^{NS}		
<i>C. crenulata</i>	Intercept	13.39		
	Slope	16.66		
	Correlation coefficient	0.759 ^{NS}		

* $P < 0.01$; ** $P < 0.05$; NS, Not significant.

is set, where cost of soil nutrients becomes lower than that obtained from resorption. In all the species of the present study, proportion of soil nitrogen in plant tissues is likely to increase with increasing soil nutrient levels. This, in turn, might have resulted in a decline in the proportional nutrient resorption. The major consequences of the suppression of proportional withdrawn of nutrients with increasing soil fertility could be the rapid improvement in litter quality, hence in decomposition rate and nutrient cycling.

The nutrient use efficiency of species generally decreased with increase in nitrogen availability in the soil except for nitrogen-fixing species, which showed a fluctuating pattern. Schlesinger *et al.*⁶ and Escudero *et al.*⁷ noted that as the availability of a limiting nutrient increases, the mechanisms used by plants to conserve that nutrient may become less efficient. Many fertilization experiments have found that increased resource availability caused a decline in nutrient use efficiency²⁵⁻²⁷. These changes in internal nutrient-cycling processes in response to external enrichment, suggest that in nutrient-rich condition plant tissues have limited capacity as nutrient sinks.

Our experiments demonstrated that in nutrient-limited conditions, internal nutrient conservation via efficient nutrient resorption as well as use is advantageous and these processes are linked to the availability of this nutrient in soil. In a nutrient-rich condition, plants of a species have better accessibility to nutrients of soil and intra-nutrient cycling becomes less important.

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Estimation of groundwater recharge through neutron moisture probe in Hayatnagar micro-watershed, India

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This communication presents a simple technique to measure groundwater recharge through neutron depth moisture gauge under *in situ* conditions that are based on soil moisture content and groundwater-level data. The water-table fluctuation method may be the most widely used technique for estimating recharge, but needs knowledge of specific yield and changes in water-level over a time. The present technique is not dependent on the mechanism of water flow in the vadose zone.

Storativity values, otherwise called ‘coefficient of storage’ that is analogous to the ‘specific yield’ in the case of water-table aquifer condition, are estimated in Hayatnagar micro-watershed area using soil moisture content and rise in water-table of the region. Using average values of several such estimates for various depths of the saturated zone, the calibrated storativity value is obtained. This value is further used to translate the water-table rise during certain rainfall periods to quantify the groundwater recharge.

Keywords: Groundwater recharge, neutron moisture probe, storativity, vadose zone.

ESTIMATION of groundwater recharge in hard rock terrain is difficult in view of wide spatio-temporal variations in hydrological and hydrometeorological conditions. The groundwater-level fluctuation approach, when applied in isolation, requires values of specific yield. There are various other methods (including hydrogeological, hydrological, tracer, etc.) that are suitable to study spatial and temporal variations of recharge^{1–7}. For arid- and semi-arid regions, most of these methods provide long-term averages of recharge.

Estimation of recharge using injected tritium method, however, is comparatively easier. But, recharge measured by this technique over the years in the same area differs even when the quantum of total precipitation remains almost the same^{8–11}. This is because of the variation in rainfall pattern and its intensity.

Meyer¹² used neutron logs to determine the specific yield of unconfined aquifers measuring the log response against a falling water-table. Karanth¹³ also used neutron logs mainly for measurement of moisture content above the water-table and total porosity below the water-table. Estimation of recharge by studying movement of moisture in the vadose zone establishes the potential of neutron depth moisture

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