30. Meagher, T. R. and Costich, D. E., Impacts of floral gender and whole-plant gender on floral evolution in *Ecballium elaterium* (Cucurbitaceae). *Biol. J. Linn. Soc.*, 2001, **74**, 475–487.
31. Meagher, T. R., Linking the evolution of gender variation to floral development. *Ann. Bot.*, 2007, **100**, 165–176.
32. Andersen, A. N., Andromonoecy in four Australian species of *Leptospermum*. *Aust. J. Bot.*, 1990, **38**, 511–516.
33. Miller, J. S. and Diggle, P. K., Diversification of andromonoecy in *Solanum* section *Lasiocarpa* (Solanaceae): the roles of phenotypic plasticity and architecture. *Am. J. Bot.*, 2003, **90**(5), 707–715.
34. May, P. G. and Spears, E. E., Andromonoecy and variation in phenotypic gender of *Passiflora incarnata* (Passifloraceae). *Am. J. Bot.*, 1988, **75**, 1830–1841.
35. Traveset, A., Reproductive ecology of *Cneorum tricoccon* L. (Cneoraceae) in the Balearic Islands. *Bot. J. Linn. Soc.*, 1995, **117**, 221–232.
36. Kaul, V. and Koul, A. K., Floral phenology in relation to pollination and reproductive output in *Commelina caroliniana* (Commelinaceae). *Aust. J. Bot.*, 2008, **56**, 59–66.
37. Kaul, V. and Koul, A. K., Sex expression and breeding strategy in *Commelina benghalensis* L. *J. Biosci.*, 2009, **34**(6), 977–990.
38. Bell, R. L., On the function of flowers. *Proc. R. Soc. Landon, Ser. B*, 1985, **14**, 223–265.
39. Lovett Doust, J. and Harper, J. L., The resource costs of gender and material support in anandromonoecious umbellifer *Smyrnium olusatrum* L. *New Phytol.*, 1980, **85**, 251–264.

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Physico-chemical properties along soil profiles of two dominant forest types in Western Himalaya

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Physico-chemical properties of soil of two dominant forest types in Western Himalaya, viz. oak (*Quercus leucotrichophora*) and pine (*Pinus roxburghii*) across three soil depths, and winter and rainy seasons were analysed. In general, all the soil parameters, viz. soil moisture, water-holding capacity, organic carbon and total nitrogen decreased significantly with increasing soil depth in both the forests. However, pH did not show any trend with soil depth. All the soil physico-chemical parameters were found significantly higher for oak forests compared to pine forests. The topsoil layer (0–30 cm depth) of both the forests had high concentration of soil organic carbon (SOC) and total N. Shallower distribution of the most limiting nutrients for plants such as N was in agreement with earlier reports. A declining nutrient concentration with increasing soil depth may explain that the zone of accumulation of nutrients is not well established in the forest soils of this mountainous region due to strong leaching effect. With regard to nutrient extraction from deeper soil layers, the deep-rooted oak forest has competitive advantage over the shallow-rooted pine forest. Considering that SOC stored in the surface layer is more vulnerable and less stable than that in the deeper layers, the topsoil of these forests should be protected to minimize the risk of large carbon release. The oak forests should be given priority over the pine forests in afforestation and conservation programmes to sequester and stock high amounts of carbon in the soil pool and contribute towards mitigation of climate change impacts.

Keywords: Nutrient concentration, oak and pine forests, soil depth, soil physico-chemical properties.

THE influence of tree species on forest soil properties has been studied by ecologists for a long time[1,2]. Vertical patterns of soil organic carbon (SOC), total nitrogen (N) and C : N stoichiometry are crucial for understanding biogeochemical cycles in ecosystems, but remain poorly understood[3]. The vertical distribution of soil nutrients yields insights into nutrient inputs, outputs, and cycling processes[4]. Leaching moves nutrients downward and may increase nutrient concentration with depth. In contrast, biological cycling generally moves nutrients upwards through absorption by roots and then returning to soil surface by litter fall and throughfall[5,6]. Plant cycling should therefore produce nutrient distributions that are shallower or decreasing with depth[7]. Therefore, hitherto poorly explored nutrient availability in deep soil layers (>1 m depth) in the Western Himalayan forests may play an important role in ecosystem functioning[8–10].

In the Western Himalayan region (Uttarakhand, India), oak (*Quercus leucotrichophora*) and pine (*Pinus roxburghii*) are the two major forest types spread over a large part of the forested landscape. Oak is a deep-rooted and moderate-sized evergreen tree that occurs in the moist and cool aspects in the lower Western Himalayan temperate forests between altitudes 1000 and 2300 m amsl (ref. 11). Pine is a shallow-rooted and large evergreen conifer and a principal species of the Himalayan subtropical forests, which occurs between 800 and 1700 m amsl (ref. 12). Oak forests mostly occupy deep, moist and fertile soils, whereas pine forests thrive better on shallow and

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nutrient-poor soil and dry habitats[13]. In this region most studies on the physico-chemical characteristics of forest soils have dealt with the topsoil layer (0–30 cm depth)[14–21], and the distribution and seasonal variations of soil nutrients across the deeper layers remain poorly understood. This study was therefore aimed to investigate soil physico-chemical properties up to 1 m depth across two seasons in these two dominant forest types that may have nutrient cycling and forest management implications, particularly for C sequestration and mitigation of climate change impacts.

The oak and pine forests selected for this study were located in Chamoli (site-I) and Champawat (site-II) districts of Uttarakhand (between 28°43′N and 31°27′N lat. and 77°34′E and 81°02′E long. respectively), at an elevation range 1000–2000 m amsl. Management history of the selected forest sites is not available as these forests are not managed by the Forest Department. Both the oak and pine forests across site-I and site-II had old growth trees with regenerating stands of various ages. The pine forests encountered frequent forest fires every summer, which was not the case with the oak forests. In general, biotic disturbance such as lopping for fuelwood and fodder and foraging by livestock was common among both the forests. In the oak forests at site-I and site-II respectively, tree density (1130 and 1160 trees/ha), relative density (62.4 and 46.9) and importance value index (IVI) of trees (152 and 134) were recorded. Similarly, in the pine forests at site-I and site-II, tree density (875 and 1090 trees/ha), relative density (90.9 and 95.4) and IVI of trees (288 and 274) were recorded[22].

In each of these two study sites, three representative stands of oak and pine forests were selected to collect soil samples periodically. Soil samples from three different depths (0–30, 30–60, 60–90 cm) were collected using a soil auger from selected stands of these forests during rainy season (September 2008) and late winter (February 2008), and brought to the laboratory for analyses of different physico-chemical properties. Soil moisture was determined gravimetrically by taking 5 g fresh soil and oven-drying at 105°C for about 24 h, weighed again after drying. Water holding capacity (WHC) of the soil was determined using preweighed perforated brass cups[23]. Soil pH was measured (soil to distilled water ratio, 1 : 10) with the help of digital pH meter. SOC was determined by Walkley and Black method[24]. Total N was determined following TSBF method[25]. Data were also analysed statistically[26].

Physico-chemical properties of the soil of both forest types varied significantly across soil depth and seasons (Tables 1 and 2). In the oak forests soil moisture and SOC decreased significantly (ANOVA significant at $P < 0.05$) with increasing soil depth across both the sites during winter season (Table 1). WHC and total N were found to decrease significantly ($P < 0.05$) with soil depth only at site-I (Table 1). At site-II, this difference was insignificant. Similarly, during the rainy season in the oak forests all the above-mentioned soil physico-chemical parameters decreased with increasing soil depth (Table 2). However, this difference was significant ($P < 0.05$) only for SOC and total N at both the sites. At site-I only WHC decreased significantly ($P < 0.05$) with increasing soil depth. pH was variable and did not show any trend across soil depth.

In the pine forests also all the soil physico-chemical parameters decreased with increasing soil depth across both the sites during winter season (Table 1). ANOVA indicated that only SOC decreased significantly with increasing soil depth ($P < 0.05$) at both the sites. Total N decreased significantly only at site-I. During the rainy season also, all these soil parameters decreased with increasing soil depth across both the sites (Table 2). However, this difference was significant ($P < 0.05$) for total N only at site-II. A comparison of the two seasons for the measured soil physico-chemical parameters across both the forests revealed that soil moisture and SOC showed strong seasonality. Soil moisture and SOC during rainy season were found about twice compared to winter season; however, WHC for both the seasons was almost equal. pH and total N were found almost the same for both the seasons. However, pine forests recorded higher total N during rainy season.

Physico-chemical properties of forest soils vary in space and time because of variation in topography, climate, weathering process, vegetation cover and microbial activities[27], and several other biotic and abiotic factors. Oak forests having closed canopy[28] are found conducive for soil water storage compared to pine forests[29]. This observation was supported by significantly greater ($P < 0.001$) soil moisture recorded in oak forests (range 15.0–33.0%) compared to pine forests (range 7.0–17.0%) during both winter and rainy seasons (Table 3). It has been pointed out that deep soil rich in organic matter and detritus layer in the oak forests might have resulted into higher water retention capacity[30], despite almost equal litter fall in the oak (5.8 t/ha/yr) and pine forests (6.5 t/ha/yr)[13]. In this investigation because of lack of studies on soil structure and litter layer, the site-specific differences in soil moisture and WHC could not be explained and require further research.

Forest soil organic matter is an important component of the global carbon cycle, and the changes of its accumulation and decomposition directly affect terrestrial ecosystem carbon storage and global carbon balance. SOC (range 0.85–3.28%) recorded in the oak forests in the present study is comparable to that reported in this region (range 0.8–2.93%)[19,31]. In the pine forests, SOC (range 0.46–1.64% during both seasons) was significantly low compared to the oak forests. SOC recorded in the present study was comparable (range 0.62–2.89%) with that reported by other studies on pine forests of this region (1.66–2.89%)[21,31,32]. Mean value of SOC for oak forests

Table 1. Soil physico-chemical properties of oak and pine forests during winter season

	Oak forest		Pine forest	
Soil physico-chemical characteristics	Site-I	Site-II	Site-I	Site-II
Moisture content (%)				
0–30 cm	17.8 ± 0.82	16.49 ± 0.68	6.73 ± 0.55	8.39 ± 1.05
30–60 cm	15.0 ± 1.44	15.51 ± 0.31	5.73 ± 0.94	7.85 ± 0.63
60–90 cm	11.8 ± 1.14	13.09 ± 0.80	5.33 ± 0.41	6.73 ± 1.30
Mean	14.87 ± 1.04	15.03 ± 0.60	5.93 ± 0.39	7.66 ± 0.57
LSD	4.02 (S)	2.19 (S)	2.32 (NS)	3.57 (NS)
Water holding capacity (%)				
0–30 cm	72.08 ± 1.50	68.21 ± 6.25	55.80 ± 2.90	48.07 ± 4.30
30–60 cm	69.33 ± 2.49	65.63 ± 2.19	52.29 ± 4.05	44.01 ± 2.57
60–90 cm	52.37 ± 3.83	62.86 ± 4.44	49.08 ± 2.05	43.02 ± 3.19
Mean	64.60 ± 3.38	65.56 ± 2.43	52.39 ± 1.83	45.03 ± 1.88
LSD	9.60 (S)	15.93 (NS)	10.76 (NS)	11.87 (NS)
pH				
0–30 cm	4.01 ± 0.003	6.74 ± 0.11	4.38 ± 0.10	6.37 ± 0.39
30–60 cm	4.54 ± 0.26	5.81 ± 0.30	4.39 ± 0.06	6.37 ± 0.29
60–90 cm	4.18 ± 0.04	6.30 ± 0.43	4.29 ± 0.08	6.24 ± 0.32
Mean	4.24 ± 0.11	6.28 ± 0.21	4.35 ± 0.04	6.33 ± 0.17
LSD	0.53 (NS)	1.07 (NS)	0.280 (NS)	1.16 (NS)
Organic carbon (%)				
0–30 cm	2.94 ± 0.20	3.08 ± 0.21	1.51 ± 0.23	1.52 ± 0.16
30–60 cm	1.64 ± 0.36	1.19 ± 0.16	0.91 ± 0.08	0.75 ± 0.05
60–90 cm	1.29 ± 0.20	0.85 ± 0.08	0.46 ± 0.16	0.50 ± 0.03
Mean	1.95 ± 0.28	1.71 ± 0.36	0.96 ± 0.17	0.92 ± 0.16
LSD	0.55 (S)	0.55 (S)	0.57 (S)	0.34 (S)
Nitrogen (%)				
0–30 cm	0.47 ± 0.01	0.45 ± 0.06	0.17 ± 0.02	0.16 ± 0.06
30–60 cm	0.32 ± 0.02	0.37 ± 0.05	0.10 ± 0.02	0.12 ± 0.02
60–90 cm	0.18 ± 0.04	0.31 ± 0.02	0.07 ± 0.02	0.08 ± 0.02
Mean	0.32 ± 0.05	0.38 ± 0.03	0.11 ± 0.02	0.12 ± 0.02
LSD	0.10 (S)	0.16 (NS)	0.067 (S)	0.16 (NS)

was significantly high ($P < 0.05$) compared to pine forests both during winter and rainy seasons (Table 3).

Total soil N reported for oak forests in this study (range 0.07–0.57% across the two seasons) was found comparable to that reported for oak forests of this region (range 0.25–0.70%)[17,31]. However, very poor soil N in oak forests (0.040–0.045%) compared to the present study has also been reported[21]. Similarly, in the pine forests total N recorded in the present study (range 0.07–0.28%) was comparable to that reported by Jina *et al.*[31] (0.19%), and much higher than that reported by Singh *et al.*[21] (0.031–0.037%). Pine forest soil had significantly lower N both during winter ($P < 0.01$) and rainy seasons ($P < 0.05$) compared to oak forest (Table 3). It is probably due to humus added to the soil by decomposition of nutrient-rich leaf litter of oak forests[33]. Oak leaf litter is rich in nitrogen ($N = 1.56\%$) compared to pine needles ($N = 1.02\%$) that maintains fertility of soil in oak forests[34]. Also the oak leaf litter decomposes faster and improves the soil fertility compared to slow-decomposing resin containing pine leaf litter[35]. Poor soil N has been attributed to degradation of forests in this region[31].

The topsoil layer (0–30 cm depth) in both the forests studied here had high concentration of SOC and total N, and concentration of these nutrients decreased significantly with increasing soil depth. A decreasing trend of total N across three soil depths (0–30 cm) in oak and pine forests has also been reported in this region[36]. In Kashmir Himalaya, pH, moisture and SOC were found significantly higher in surface soil (0–5 cm depth) than at 5–10 cm depth[37]. It has been pointed out that at the interface between the atmosphere, biosphere and lithosphere, the soil undergoes an intense vertical exchange of materials resulting in steep chemical and physical gradients from surface to bedrock[7]. Shallower distribution of the most limiting nutrients for plants (those required by them in high amounts relative to soil supply) such as N was in agreement with earlier reports[7]. A declining nutrient concentration with increasing soil depth recorded in the present study may explain that the zone of accumulation of nutrients is not well established in the forest soils of this region due to strong leaching effect[38,39]. In this regard two opposing strategies for plants to obtain scarce nutrients have been suggested[7]. The first is to develop a dense root system in the topsoil (apogeotropic roots), exploring the zone of maximum accumulation and intercepting nutrients as they move downward by leaching[40]. In our study region the shallow-rooted pine trees show such a

Table 2. Soil physico-chemical properties of oak and pine forests during rainy season

	Oak forest		Pine forest	
Soil physico-chemical characteristics	Site-I	Site-II	Site-I	Site-II
Moisture content (%)				
0–30 cm	40.2 ± 2.78	31 ± 0.67	22.20 ± 2.16	15 ± 0.64
30–60 cm	37.8 ± 3.12	29 ± 1.53	19.73 ± 3.29	13 ± 1.11
60–90 cm	35.6 ± 0.76	26 ± 1.91	20.53 ± 3.56	12 ± 1.22
Mean	37.87 ± 1.39	28.62 ± 0.98	20.82 ± 1.57	13.49 ± 0.63
LSD	8.49 (NS)	3.83(NS)	5.06(NS)	3.53(NS)
Water holding capacity (%)				
0–30 cm	70.0 ± 1.15	71 ± 1.25	52.67 ± 1.45	50 ± 1.26
30–60 cm	61.0 ± 2.08	68 ± 1.10	50.72 ± 2.91	44 ± 4.92
60–90 cm	59.0 ± 1.53	66 ± 1.77	48.33 ± 1.97	40 ± 3.02
Mean	63.33 ± 1.88	68.28 ± 1.05	50.57 ± 1.26	44.72 ± 2.26
LSD	5.65(S)	4.86(NS)	7.59(NS)	11.82(NS)
pH				
0–30 cm	5.25 ± 0.06	5.40 ± 0.07	5.10 ± 0.50	5.57 ± 0.35
30–60 cm	5.46 ± 0.06	5.33 ± 0.16	5.65 ± 0.03	5.46 ± 0.25
60–90 cm	5.36 ± 0.03	5.41 ± 0.32	5.06 ± 0.37	5.81 ± 0.02
Mean	5.36 ± 0.04	5.38 ± 0.11	5.27 ± 0.20	5.61 ± 0.13
LSD	0.18(NS)	0.72(NS)	1.25(NS)	0.86(NS)
Organic carbon (%)				
0–30 cm	3.28 ± 0.26	2.16 ± 0.03	1.64 ± 0.22	1.56 ± 0.07
30–60 cm	2.72 ± 0.31	1.68 ± 0.18	1.28 ± 0.14	1.30 ± 0.05
60–90 cm	1.56 ± 0.35	1.28 ± 0.11	1.00 ± 0.11	1.08 ± 0.14
Mean	2.52 ± 0.30	1.71 ± 0.14	1.31 ± 0.12	1.31 ± 0.08
LSD	1.07(S)	0.43(S)	0.57(NS)	0.33(S)
Nitrogen (%)				
0–30 cm	0.50 ± 0.03	0.57 ± 0.02	0.21 ± 0.06	0.28 ± 0.02
30–60 cm	0.38 ± 0.01	0.37 ± 0.05	0.19 ± 0.05	0.19 ± 0.04
60–90 cm	0.25 ± 0.02	0.07 ± 0.02	0.08 ± 0.04	0.13 ± 0.03
Mean	0.38 ± 0.04	0.34 ± 0.08	0.16 ± 0.03	0.20 ± 0.03
LSD	0.08 (S)	0.12 (S)	0.17 (NS)	0.11 (S)

Table 3. Mean values of physico-chemical properties of soil of oak and pine forests for two different seasons (N = 18 for all the parameters)

	Winter season		Rainy season	
Soil parameters	Oak forest	Pine forest	Oak forest	Pine forest
Moisture content (%)	15.0 ± 0.90	7.0 ± 0.48	33.0 ± 2.25	17.0 ± 1.76
	t = 11.14, P < 0.001 (S)		t = 24.65, P < 0.001 (S)	
Water holding capacity (%)	65.0 ± 2.9	49.0 ± 2.0	66.0 ± 2.0	48.0 ± 1.94
	t = 5.97, P < 0.01 (S)		t = 6.68, P < 0.01 (S)	
pH	5.26 ± 0.48	5.34 ± 0.44	5.37 ± 0.03	5.44 ± 0.12
	t = 5.32 (NS)		t = 0.70 (NS)	
Organic carbon (%)	1.83 ± 0.39	0.94 ± 0.19	2.11 ± 0.31	1.31 ± 0.10
	t = 4.33, P < 0.01 (S)		t = 3.32, P < 0.05 (S)	
Total nitrogen (%)	0.35 ± 0.04	0.12 ± 0.02	0.36 ± 0.07	0.18 ± 0.03
	t = 8.36, P < 0.001 (S)		t = 3.38, P < 0.05 (S)	
C : N ratio	5.2	7.8	5.86	7.28

S, Significantly different; NS, Non-significant.

strategy. In the other strategy, plants that are able to grow roots below the zone of high depletion may obtain a source of nutrients with relatively little competition[41], which holds good for the deep-rooted oak forests in our study region.

In conclusion, the oak forests were characterized by a significantly high SOC and total N concentration in the soil profile compared to the pine forests. More fertile top-soil layer of oak forests can be attributed to nutrient-rich litter and its deep-rooted system absorbing nutrients from deeper soil layers and accumulating them in the surface layer through litter fall, which eventually improves the physical, chemical and biological properties of the soil[42]. Pine being a shallow-rooted species and prone to forest fire and nutrient leaching is left with low SOC and total N in the soil. Considering that SOC stored in the surface layer is more vulnerable and less stable than that in deeper layers[43], the topsoil of these forests should be protected to minimize the risk of large C release. It has been reported that high clay content in soil promotes sorption of dissolved OC in deeper soil layers, which may account for 25–98% of the measured SOC stock in the soil[44]. Therefore, a soil texture study is important, which could not be carried out in the present investigation. The high proportion of clay content in oak forests compared to pine forests (22% versus 17.8%) reported in this region[45] signifies the importance of the former to sequester C in soil pool. Thus oak forests should be given priority over pine forests in afforestation programmes in order to contribute towards mitigation of climate change impacts in this region.

1. Zinke, P. J., The pattern of influence of individual forest trees on soil properties. *Ecology*, 1962, **43**, 130–133.
2. Vesterdal, L., Schmidt, I. K., Callesen, I., Nilsson, L. O. and Gundersen, P., Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *For. Ecol. Manage*., 2008, **255**, 35–48.
3. Yang, Y. H., Fang, J. Y., Guo, D. L., Ji, C. J. and Ma, W. H., Vertical patterns of soil carbon, nitrogen and carbon: nitrogen stoichiometry in Tibetan grasslands. *Biogeosci. Discuss*., 2010, **7**, 1–24.
4. Kirby, M. J., A basis for soil profile modeling in a geomorphic context. *J. Soil Sci*., 1985, **36**, 97–121.
5. Trudgill, S. T., *Soil and Vegetation System*, Oxford University Press, New York, USA, 1988.
6. Stark, J. M., Causes of soil nutrient heterogeneity at different scales. In *Exploitation of Environmental Heterogeneity by Plants* (eds Caldwell, M. M. and Pearcy, R. W.), Academic Press, San Diego, 1994.
7. Jobbagy, E. G. and Jackson, R. B., The distribution of soil nutrients with depth: global patterns and the imprint of plants. *Biogeochemistry*, 2001, **53**, 51–77.
8. Richter, D. D. and Markewitz, D., How deep is soil? *BioScience*, 1995, **45**, 600–609.
9. Jackson, R. B., Mooney, H. A. and Schulze, E. D., A global budget for fine root biomass, surface area, and nutrient contents. *Proc. Natl. Acad. Sci. USA*, 1997, **94**, 7362–7366.
10. Lal, R., Forest soils and carbon sequestration. *For. Ecol. Manage*., 2005, **220**, 242–258.
11. Singh, J. S. and Singh, S. P., Forest vegetation of the Himalaya. *Bot. Rev*., 1987, **52**, 80–192.
12. Champion, H. G. and Seth, S. K., *A Revised Survey of the Forest Types of India*, Government of India Publ., New Delhi, 1968.
13. Singh, J. S. and Singh, S. P., *Forests of Himalaya: Structure, Function and Impact of Man*, Gyanodaya Prakashan, Nainital, 1992.
14. Upreti, N., A study on phytosociology and state of regeneration of oak forests in Nainital, Ph D thesis, Kumaun University, Nainital, 1982.
15. Sharma, C. M. and Kumar, A., Community structure of some natural forest stands in Lansdowne forest range of Garhwal Himalaya. *J. Trop. For. Sci*., 1992, **5**(1), 8–12.
16. Singh, R. D. and Bhatnagar, V. K., Differences in soil and leaf litter nutrient status under *Pinus, Cedrus* and *Quercus*. *Indian J. For*., 1979, **20**(2), 147–149.
17. Bhandari, B. S., Mehta, J. P. and Tiwari, S. C., Dominance and diversity relation of woody vegetation structure along an altitudinal gradient in a montane forest of Garhwal Himalaya. *J. Trop. For. Sci*., 2000, **12**(1), 49–61.
18. Dhanai, C. S., Panwar, V. P. and Sharma, C. M., Effect of aspect and soil on the structure of *Quercus leucotrichophora* natural stands in western Himalaya. *Indian J. For*., 2000, **23**(3), 349–356.
19. Khera, N., Kumar, A., Ram, J. and Tewari, A., Plant biodiversity assessment in relation to disturbances in mid-elevational forest of Central Himalaya, India. *Trop. Ecol*., 2000, **42**(1), 83–95.
20. Kumar, M., Sharma, C. M. and Rajwar, G. S., Physico-chemical properties of forest soil along altitudinal gradient in Garhwal Himalaya. *J. Hill Res*., 2004, **17**(2), 60–64.
21. Singh, H., Kumar, M. and Sheikh, M. A., Distribution pattern of Oak and Pine along altitudinal gradients in Garhwal Himalaya. *Nat. Sci*., 2009, **7**(11), 81–85.
22. Joshi, Gunjan, Quantification and valuation of some selected forest ecosystem services in the Western Himalayan region, Ph D thesis, Kumaun University, Nainital, 2012.
23. Piper, C. S., *Soil and Plant Analysis*, Interscience Publications Inc, New York, 1944.
24. Walkley, A., A critical examination of a rapid method for determining organic carbon in soils – effects of variations in digestion conditions and inorganic soil constituents. *Soil Sci*., 1947, **63**, 251–264.
25. Okalebo, J. R., Gathua, K. W. and Woomer, P. L., *Laboratory Methods of Soil and Plant Analysis – A Working Manual*, The Tropical Soil Biology and Fertility Programme, UNESCO, Nairobi, Kenya, 1993.
26. Snedecor, G. W. and Cochran, W. G., *Statistical Methods*, Oxford University Press, New Delhi, 1967.
27. Paudel, S. and Sah, J. P., Physico-chemical characters of soil in tropical sal (*Shorea robusta* Gaertn.) forests in eastern Nepal. *Himalayan J. Sci*., 2003, **1**(2), 107–110.
28. Saxena, A. K., Ecology of vegetation complex of north western catchments of river Gola, Ph D thesis, Kumaun University, Nainital, 1979.
29. Tyagi, J. V., Qazi, N., Rai, S. P. and Singh, M. P., Analysis of soil moisture variation by forest cover structure in lower western Himalaya. *J. For. Res*., 2013, **24**(2), 317–324.
30. Sheikh, M. A. and Kumar, M., Nutrient status and economic analysis of soils in oak and pine forests in Garhwal Himalaya. *J. Am. Sci*., 2010, **6**(2), 117.
31. Jina, B. S., Bohra, C. S., Lodhiyal, L. S. and Sah, P., Soil characteristics in oak and pine forests of Indian Central Himalaya. *Int. Sci. Res. J*., 2011, **3**(1), 19–22.
32. Chaturvedi, O. P., Biomass structure, productivity and nutrient cycling in *Pinus roxburghii* forests, Ph D thesis, Kumaun University, Nainital, 1983.
33. Upadhyay, V. P., Singh, J. S. and Meentemeyer, V., Dynamics and weight loss of leaf litter in Central Himalayan forests: abiotic versus litter quality influences. *J. Ecol*., 1989, **77**, 147–161.
34. Negi, G. C. S. and Singh, S. P., Leaf nitrogen dynamics with particular reference to retranslocation in evergreen and deciduous tree species of Kumaun Himalaya. *Can. J. For. Res*., 1993, **23**, 349–357.
35. Kandpal, K. D. and Negi, G. C. S., Studies on leaf litter decomposition rate for rain-fed crop soil fertility management in the western Himalayas. *J. Hill Res*., 2003, **16**(1), 35–38.
36. Semwal, D. P., Uniyal, P. L., Bahuguna, Y. M. and Bhatt, A. B., Soil nutrient storage under different forest types in a part of Central Himalaya, India. *Ann. For*., 2009, **17**(1), 43–52.
37. Jahangir, M. M. R. *et al*., Denitrification potential in subsoils: a mechanism to reduce nitrate leaching to groundwater. *Agric. Ecosyst. Environ*., 2012, **147**, 13–23.
38. Pandey, A. N., Pathak, P. C. and Singh, J. S., Water, sediment and nutrient movement in forested and non-forested catchments in Kumaun Himalaya. *For. Ecol. Manage*., 1983, **7**, 19–29.

39. Mehra, M. S., Pathak, P. C. and Singh, J. S., Nutrient movement in litter fall and precipitation components for Central Himalayan forest. *Ann. Bot.*, 1985, **55**, 153–170.
40. Sanford, R. L., Apogeotropic roots in Amazon rain forest. *Science*, 1987, **235**, 1062–1064.
41. Lipps, R. C. and Fox, R. L., Subirrigation and plant nutrition. II. The utilization of phosphorus by alfalfa from the surface to the water table. *Soil Sci. Soc. Am.*, 1956, **20**, 28–32.
42. Sharma, J. C. and Sharma, Y., Effect of forest ecosystems on soil properties – a review. *Agric. Rev.*, 2004, **25**(1), 16–28.
43. Fontaine, S., Barot, S., Barre, P., Bdioui, N., Mary, B. and Rumpel, C., Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, 2007, **450**, 277–280.
44. Basile-Doelsch, I., Amundson, R., Stone, W. E. E., Borschneck, D. and Bottero, J. Y., Mineral control of carbon pools in a volcanic soil horizon. *Geoderma*, 2007, **137**, 477–489.
45. Raina, A. K. and Gupta, M. K., Soil and vegetation studies in relation to parent material of Garhwal Himalayas, Uttarakhand (India). *Ann. For.*, 2009, **17**(1), 71–82.

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Patterns of dominance relationships among the females of a captive female-only group of lion-tailed macaques (*Macaca silenus*) during the course of the introduction of a new adult male

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Lion-tailed macaques are generally considered to have more despotic than egalitarian dominance relationships; however, research lacks any conclusive evidence. In the present study, we examined dominance relationships among the females (of which the genealogical relationships were known) of a captive female-only group of lion-tailed macaques (*Macaca silenus*) during the course of introduction of a new adult male to the group at the Wels Zoo, Wels, Austria. We determined the structure of dominance hierarchy and the corresponding changes in dominance relationships, possibly mediated by an increase in sexual competition among the females. When the females were housed together without any adult male for over four months following the death of the former breeding male, the dominance hierarchy almost followed the principle of youngest ascendency. When a new male was housed for 26 days in an enclosure adjacent to that of the females (such that the females and the new male could interact with each other through a wire mesh between their enclosures), changes in dominance hierarchy were observed. During this phase, there was a temporary change in the dominance hierarchy, leading to a higher degree of aggression of the nursing female and an increase in its dominance rank. This is corroborated by the fact that when the new male was housed together with the females in the same enclosure, it resulted in infanticide and subsequently, the nursing mother lost the higher rank. We consider the implications of the present study in the captive management and breeding of long-tailed macaque.

Keywords: Captive management, dominance, hierarchy, lion-tailed macaque, rank instability.

THE asymmetrical outcome of intragroup agonistic interactions, that is, dominance hierarchy, is a defining characteristic of macaque societies[1]. According to some studies[2–4], such asymmetrical outcomes owe to limited resources among females. de Waal[5] found that these can vary with the degree of social bonding, tolerance and reconciliation after aggressive conflicts. While comparing the strength of dominance hierarchies between the females of different species of macaques, Flack and de Waal[6] defined four distinct categories: despotic, tolerant, relaxed and egalitarian, the degree of asymmetry in agonistic interactions increasing from egalitarian to despotic. Similarly, on the basis of certain aspects of their social behaviour (particularly the frequency of inter-individual agonistic and socio-positive interactions), Thierry[7] attempted to classify 22 species in *Macaca* genus along the egalitarian–despotic continuum. According to Kutsukake[8], when females of a group acquire dominance ranks relative to one another, creating a linear distribution of social dominance, the hierarchy is termed as 'linear'; whereas when a daughter's dominance rank is determined by her mother's, the former never outranks the latter, and sisters rank inversely in the order of their age, the dominance hierarchy is termed as 'reverse' or following the 'principle of youngest ascendency'. Reverse dominance hierarchies are commonly observed in female-bonded species, typically comprising genetically related individuals

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