10. De, S. S., De, B. K., Sarkar, B. K., Bandyopadhyay, B., Haldar, D. K., Paul, S. and Barui, S., Analyses of Schumann resonance spectra from Kolkata and their possible interpretations. *Indian J. Radio Space Phys*., 2009, **38**, 208–214.
11. Price, C. and Melnikov, A., Diurnal, seasonal and interannual variations in the Schumann resonance parameters. *J. Atmos. Sol.-Terr. Phys.*, 2004, **66**, 1179–1185.
12. Roldugin, V. K. and Vasil'ev, A. N., Variations in the Schumann resonance polarization ellipse in the horizontal and vertical planes according to observations at the Barentsburg and Lovozero Observatories. *Geomag. Aeron.*, 2012, **52**, 68–76.
13. Schlegel, K. and Fullekrug, M., Diurnal harmonics in Schumann resonance parameters observed on both hemispheres. *Geophys. Res. Lett.*, 2000, **27**, 2805–2808.
14. Nickolaenko, A. P. and Hayakawa, M., *Resonances in the Earth–Ionosphere Cavity*, Kluwer Academic Publishers, Dordrecht, 2002, p. 380.
15. Balser, M. and Wagner, C. A., Diurnal power variations of the earth–ionosphere cavity modes and their relationship to worldwide thunderstorm activity. *J. Geophys. Res.*, 1962, **67**, 619–625.
16. Balser, M. and Wagner, C. A., On the frequency variations of the earth–ionosphere cavity modes. *J. Geophys. Res.*, 1962, **67**, 4081–4083.
17. Bliokh, P. V., Nikolaenko, A. P. and Filippov, Y. F., Diurnal variations of the natural frequencies of the earth–ionosphere resonator in relation to the eccentricity of the geomagnetic field (in Russian). *Geomagn. Aeron.*, 1968, **8**, 250–260.
18. Roldugin, V. C., Maltsev, Y. P., Vasiljev, A. N. and Vashenyuk, E. V., Changes of the first Schumann resonance frequency during relativistic solar proton precipitation in the 6 November 1997 event. *Ann. Geophys*., 1999, **17**, 1293–1297.
19. Roldugin, V. C., Maltsev, Y. P., Vasiljev, A. N., Schokotov, A. Y. and Belyajev, G. G., Schumann resonance frequency increase during solar X-ray bursts. *J. Geophys. Res*., 2004, **109**, A01216.
20. Chand, R., Israil, M. and Rai, J., Schumann resonance frequency variations observed in magnetotelluric data recorded from Garhwal Himalayan region India. *Ann. Geophys*., 2009, **27**, 3497–3507.
21. Sentman, D., Schumann resonances. In *Handbook of Atmospheric Electrodynamics*, *vol. 1* (ed. Volland, H.), CRC Press, Boca Raton, Fla, USA, 1995, pp. 267–295.

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Correlation patterns among floral traits in *Cleome viscosa* L., a sexually polymorphic species

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***Cleome viscosa* L., a multipurpose species, is reproductively versatile exhibiting variation in the sex of its flowers. Being predominantly andromonoecious, few plants occasionally exhibit functional monoecy. Andromonoecy is distinguished by the production of hermaphrodite and staminate flowers, while formation of pistillate, male and other intermediate flower types leads to functional monoecy. Size variation in these sexes is equally prevalent. Size dimorphy in all the flower types leads to significant differences in almost all the morphological features. Overall 12 different flower types thus distinguished were analysed for different morphological traits. The data generated were subjected to correlation analyses to determine the extent of relationship between them, and thereupon reflect on the mechanism of their selection in flowers of different sexes and sizes. Despite male fitness traits being at greater advantage in all flower types, female fitness is equally selected in hermaphrodites and exclusively in pistillate flowers. Others with staminodes show mixed fitness. A critical analysis of the morphological data and their correlations suggests that different pairs of traits in each flower type are evolved in ways unique to them and to maximize their functional potential. Natural selection is thus operating through differential correlation patterning and is probably driving the evolution of these flower types.**

Keywords: *Cleome viscosa*, correlation patterns, floral traits, hermaphrodite.

FLOWER is a specialized shoot apex in which different organs are functionally tailored to facilitate reproduction[1,2]. Structural and functional aspects of sex organs (male and female) and accessory (flower display unit) parts within a flower have mutually evolved and are strongly correlated to increase pollination efficiency which ultimately affects the reproductive potential of plants[1,2]. The correlation analyses on qualitative and quantitative floral traits carried out by various authors from time to time reveal that these are under continuous evolution and are stabilized by natural selection according to the needs of a plant. For example, pollinator-driven traits like corolla size, stamen length, pollen presentation and floral rewards are strongly correlated in xenogamous taxa where these traits facilitate out crossing. On the contrary, male and female traits are highly correlated structurally and functionally in selfers[3–9].

Interrelationships between various traits have been studied extensively in flowers of different sexes. In *Commelina communis*, an andromonoecious plant, the hermaphrodite flowers exhibit stronger stigma–anther correlation, while staminate ones show greater anther–petal correlation. Selection in hermaphrodites thus, favours successful pollen deposition and fertilization followed by seed set thereafter. However, in staminate flowers, presence of non-functional pistil excludes the possibility of self-pollination. Thus, male fitness is selected to enhance pollen donation and is accordingly expected to show correlation between such traits and insect visitation[8]. In insect-pollinated plants (like *Brassica*, *Raphanus*, etc.) stronger correlation between male fitness-related traits (stamen–corolla length) seems to have evolved due to

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pollinator-driven selection. The placement of anthers at the opening of the corolla tube facilitates effective pollen transport by pollinators in these species. Thus, floral correlations vary due to different selective pressures operating at different times in different flower types, leading to their evolution. However, not all are necessarily pollinator-driven; some can be imposed by ecological factors like physical gradients and still others by plant's developmental constraints[6].

Apart from the strategy of differential correlation, the flowers of various types borne by plants show tremendous variation in size and number of essential and accessory floral organs. These variations, in turn, have the potential to modify pollination success at individual flower and plant levels. By doing so, they provide the basic raw material on which natural selection operates and ultimately results in plant diversification[10,11]. Very few angiosperms are known to exhibit such variation[12–18]. Influenced as these are by various selective agents such as environment, resource patterning between male and female sexual functions, and pollinator behaviour, stabilization by natural selection is guaranteed owing to their functional significance[9].

No attempt seems to have been made to quantify the variation in floral traits and their correlation among different flower types borne on a single plant. The present study initiated with this objective in mind will prove helpful in our understanding of evolutionary pathways that have led to their differentiation. *Cleome viscosa* L. is versatile in that it exhibits variability in sex (hermaphrodite, staminate, pistillate and male**)** and size (large and small) of flowers borne by individual plants[19,20]. All flowers are initiated as hermaphrodites, but later sterility of either pistils or stamens in some leads to variation in sex expression. Further, each flower exhibits slight asymmetry and variation in stamen number and length. Polymorphy of this degree within a species makes it an excellent system for testing the evolution of such traits. The main objectives of the present study were as follows: (i) To analyse differences in male and female fitness traits. The former included data on flower length, stamen number and their length, and latter pistil length. (ii) Correlation patterning among the above-mentioned floral traits (male, female and mixed fitness) among flowers of different types, and also draw possible conclusion of the evolution of such traits.

C. viscosa L. (Cleomaceae) is an annual self-compatible herb propagating through seeds only. Plants grow luxuriantly in woodlands, fallow lands, roadsides, disturbed sites and agricultural lands on account of their quick blooming nature coupled with high fruit and seed sets[21]. By virtue of this property, it has assumed the status of a weed and is known to affect the yield of several important crops in agricultural fields[22–24]. Notwithstanding this, the species is known to be of immense medicinal, nutraceutical and agro-economical value and the literature is flooded with extensive studies carried out in these areas[25]. The species is currently finding its utility in nanotechnology and biodiesel production, thus showing the tendency to substitute the traditional sources of fuel[26,27].

Barring an initial but brief vegetative phase (30–44 days), the plants largely have simultaneous vegetative and reproductive phases culminating into a life cycle of about 5 months (May to October). Andromonoecy predominates as each plant profusely produces hermaphrodite and staminate flowers continuously from base to apical ends of the racemose raceme inflorescence. Hermaphrodites are bisexual, while staminate ones are functionally unisexual owing to sterilization of pistil in them. Ten to 36.6% of the plants also bear flowers, where androecium is characterized by a mixture of sterile and fertile stamens. One per cent flowers of a few plants were found to be pistillate and male. Pistillates are functionally unisexual due to sterility of stamens, while males are both structurally and functionally unisexual. Although andromonoecy is preponderant, other types are also differentiated, though rarely by some plants in a population. These together make the species polygamomonoecious. At the level of an individual plant, hermaphrodite flowers ($\bar{X}$ = 38.34) differentiate and bloom in higher numbers than the staminate ones ($\bar{X}$ = 22.6), making the sex ratio per plant biased towards hermaphroditism, i.e. 1.7 : 1. The size of all these flowers toward the terminal end decreases drastically and so do their floral parts forcing us to categorize the flowers into large and small. Large flowers of each sex expression significantly outnumber the small ones[28].

Henceforth, these flower types are abbreviated as H for hermaphrodite, S for staminate, M for male and P for pistillate, and those with varying number of staminodes are given a subscript 'st'. To indicate size dimorphism, L for large and S for small are appended with each type. For instance, LH_{st} and SH_{st} respectively, stand for large and small hermaphrodite flowers with staminodes.

The floral morphometry was conducted on mature and fully opened flowers of all types (sample size being n = 20 or 5 each depending upon the availability of flowers) collected randomly from each of 10 plants. These plants were carefully collected from naturally occurring populations along roadsides within the University of Jammu campus, and then transferred and raised thereof in experimental beds of the Botanical Garden, University of Jammu in 2011. The plants growing in natural populations do not differ from those established in the Botanical Garden and also exhibit a parallel pattern of sexual and size diversity. The individual floral parts were carefully and gently dissected under stereomicroscope and used for measurements. The length of pistil, long and short stamens, and staminodes was measured using scale or vernier callipers. The length of the flowers was measured as distance from base of petal to its tip. The total number of stamens, both long and short, and staminodes per

Table 1. Morphometric details of different flower types

Floral traits			Flower types[+]											
			LH	LS	LH_{st}	LS_{st}	LP	LM	SH	SS	SH_{st}	SS_{st}	SP	SM
Male fitness	Length	Flower	12.9 ± 0.5	12.1 ± 0.03	11.5 ± 0.48	11.3 ± 0.3	11.6 ± 0.9	10.8 ± 0.4	7.7 ± 0.31	7 ± 0.02	7.9 ± 0.12	7.4 ± 0.29	5.17 ± 0.4	6.8 ± 0.3
		Long stamen	10.2 ± 0.3	8.8 ± 1.1	9.1 ± 0.2	8.8 ± 0.3	–	7.8 ± 0.2	6.1 ± 0.3	4.8 ± 0.1	6.2 ± 0.7	5.8 ± 0.4	–	4.8 ± 0.1
		Short stamen	7.1 ± 0.2	6.1 ± 0.01	6.3 ± 0.4	6.6 ± 0.2	–	1 ± 0.6	4.5 ± 0.24	3.6 ± 0.1	3.4 ± 0.5	4.5 ± 0.3	–	–
		Staminode	–	–	4.01 ± 0.2	3.3 ± 0.2	3.5 ± 0.7	1.9 ± 0.3	–	–	2.9 ± 0.1	3 ± 0.3	1.6 ± 0.1	1.3 ± 0.13
	Number	Total stamen	18.9 ± 0.8	12.9 ± 0.9	18.7 ± 1.9	19.3 ± 1.7	16.3 ± 3.8	16.2 ± 1.9	8 ± 0.4	6.1 ± 0.3	14.1 ± 0.2	8.3 ± 0.6	5.7 ± 0.3	9.6 ± 0.6
		Long stamen	7.8 ± 0.7	5.6 ± 2.9	5.2 ± 1.2	6.5 ± 0.97	–	5.2 ± 0.9	4.2 ± 0.3	3.6 ± 1.2	4.8 ± 1.0	2.7 ± 0.3	–	3.2 ± 0.1
		Short stamen	11.1 ± 0.8	7.3 ± 2.9	7.8 ± 0.7	8.8 ± 1.2	–	0.4 ± 0.3	3.7 ± 0.3	2.6 ± 0.7	4.4 ± 0.2	2.7 ± 0.2	–	–
		Staminode	–	–	4.7 ± 1.1	4 ± 0.5	16.3 ± 3.8	10.6 ± 2.2	–	–	4.9 ± 0.98	2.9 ± 0.2	5.6 ± 0.3	6.4 ± 0.6
Female fitness		Pistil length	7.5 ± 0.4	3.3 ± 0.1	7.1 ± 0.1	2.6 ± 0.1	7 ± 0.4	–	4.8 ± 0.09	2.2 ± 0.5	5.3 ± 0.08	2.5 ± 0.1	4.2 ± 0.5	–

All values are in mm.

[+]LH, Large hermaphrodite; SH, Small hermaphrodite; LS, Large staminate; SS, Small staminate; LP, Large pistillate; SP, Small pistillate; LM, Large male; SM, Small male; LH_{st}, Large hermaphrodite with staminodes; SH_{st}, Small hermaphrodite with staminodes; LS_{st}, Large staminate with staminodes; SS_{st}, Small staminate with staminodes.

Table 2. *F*-value of different floral traits between flower types

Floral trait/flower types[+]			Between sizes						Between sexes					
			LH–SH	LS–SS	LH_{st}–SH_{st}	LS_{st}–SS_{st}	LP–SP	LM–SM	LH–LS	SH–SS	LH_{st}–LS_{st}	SH_{st}–SS_{st}	LP–LM	SP–SM
Male fitness	Length	Flower	91.62 *	193.4*	36.9*	48.03*	43.5*	33.3*	0.60**	6.087*	0.12**	0.95**	160.3*	49.9*
		Long stamen	50.5*	182.15*	25.3*	17.9*	0	39.6*	1.52**	11.14*	0.20**	0.29**	858.6*	108.1*
		Short stamen	48*	128.26*	10.8*	14.25*	0	0	0.39**	9.51*	0.64**	1.49**	0.75**	0
		Staminode	–	–	7.6*	0.26**	6.97**	1.09**	–	–	3.14**	0.008**	11.25*	12.03*
	Number	Total stamen	35.46*	50.57*	2.9**	28.8*	9.84*	7.5*	6.6*	15.22*	0.05**	9.09*	16.02*	27.04*
		Long stamen	17.8*	7.31*	0.07**	118.6*	0	3.12**	2.77**	3.65**	0.74**	3.2**	16.35*	192*
		Short stamen	27.96*	48.39*	3.2**	18.6*	0	1**	4.77*	12.89*	0.29**	1.33**	2.1**	0
		Staminode	–	–	0.01**	2.42**	9.84*	1.73**	–	–	0.49**	1.8**	8.1*	10.8*
Female fitness		Pistil length	61.08*	1.92**	18.3*	0.63**	19.06*	–	153.6*	104.68*	391.5*	49.57*	834.2*	122.4*

*$P < 0.05$, significant, **$P > 0.05$, Nonsignificant.

[+]LH, Large hermaphrodite; SH, Small hermaphrodite; LS, Large staminate; SS, Small staminate; LP, Large pistillate; SP, Small pistillate; LM, Large male; SM, Small male; LH_{st}, Large hermaphrodite with staminodes; SH_{st}, Small hermaphrodite with staminodes; LS_{st}, Large staminate with staminodes; SS_{st}, Small staminate with staminodes.

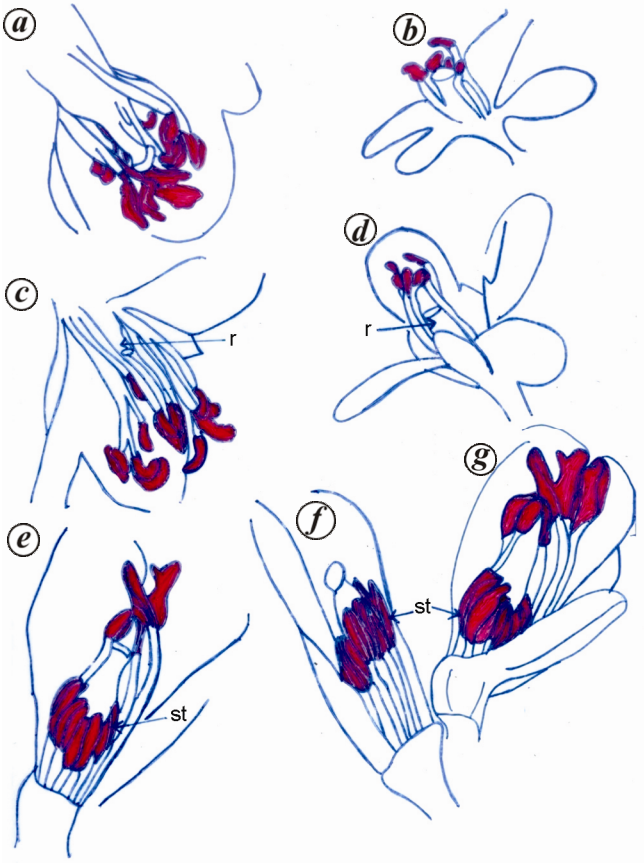

Figure 1 ***a–g.*** Diagrammatic representation of different flower types; hermaphrodite and staminate flowers; their respective large (***a–c***) and small (***b–d***) counterparts. Note the flowers with rudimentary pistil (***c*** and ***d***) and variable number of stamens (***a–e***). ***e–g***, A hermaphrodite flower with staminodes (***e***), pistillate (***f***) and male (***g***), flower. st, Staminode; *r*, Rudimentary pistil. Magnifications: ***a–g***: × 5.42, × 5.19, × 5.79, × 8.57, × 7.83, × 8.10 and × 8.70 mm respectively.

flower type was also counted and data compiled. Average values of size and number of different floral traits between sexes and sizes were compared by subjecting the data to one-way ANOVA.

Karl Pearson's coefficient of correlation was calculated to ascertain the linear relationship, if any, between all possible pairs of floral traits. The *r*-values so obtained were *t*-tested to determine their significance[29].

The variation in fitness of male and female functions among flower types, however, can be exactly depicted using functional fitness parameters of each type. Data on these have been discussed later in the text since details have been communicated elsewhere[28]. Male fitness covers pollen production by anthers of long and short stamens and staminodes and their respective viability. While ovule, fruit and seed production measures the female fitness.

Flowers of *C. viscosa*, irrespective of the type, are slightly asymmetric, hypogynous and tetramerous. The average flower length ranging from 11 to 12 mm is more or less uniform between sexes. But in LP–LM, SH–SS and SP–SM the average values differ significantly, which also tests within-size differences. Between sizes, the flower length differs considerably and obviously; the statistical results augment the same (Tables 1 and 2). Among larger counterparts, LH flowers are the longest and LM the shortest (Table 3).

Androecium consists of stamens in two lengths; long and short vis-a-vis pistil length (Figure 1 *a–g* and Table 1). While the former is always longer than the pistil in all flower types (Figure 1 *a–g*), the latter lies a little below the pistil in hermaphrodite flowers (Figure 1 *a* and *b*) and its types (Figure 1 *e* and *f*; LH, LH_{st}, SH and SH_{st}) and above the pistillode in staminate flowers (Figure 1 *c* and *d*) and its types. The placement of staminodes (Figure 1 *e–g*) is similar to that of short stamens. Stamen and pistil lengths in all types vary significantly among size groups, except staminode length in LS_{st} and SS_{st}, LP–SP and LM–SM; pistil length in LS–SS and LS_{st}–SS_{st}. Interestingly, significant differences in some traits also occur among sexual types (Table 2).

The stamen number is not constant but varies among flowers (Figure 1 *a–g*). It is maximum in LS_{st} ($\bar{X}$ = 19.3) followed by LH ($\bar{X}$ = 18.9) flowers and least in LS ($\bar{X}$ = 12.9). Among the small ones, the trend of SH_{st} > SM > SP is followed. It also varies significantly with the type and sex of the flower (Figure 1 *a–f*; Tables 1 and 2), with the exception of those with staminodes (LH_{st}–SH_{st} and LH_{st}–LS_{st}). In large counterparts of hermaphrodite (LH, LH_{st}) and staminate (LS, LS_{st}) flowers, short stamens significantly outnumber the long ones. A reverse trend is followed by their small-sized counterparts. In LP and SP, only staminodes are present, while in LM and SM, in addition to these long stamens do differentiate. The number of long stamens, thus, differs significantly between size groups, but not among those of different sexes (Tables 1 and 2).

The simple correlation coefficients computed between 15 pairs of floral traits indicated their mutual relationship, that is, an increase in one trait resulted in a corresponding increase in the other. The pairwise correlation analysis is as follows:

Length of flower and sex organs: The lengths of a flower and that of its sex organs (stamen and pistil) are positively correlated irrespective of the flower type. All *r* values are greater than 0.73. Correlation between flower and staminode lengths is either weak or negative in all, except SS_{st}, where it is strong and positive (r = 0.85). A similar relationship also exists between the lengths of flower and pistil in hermaphrodites. While these are least in staminate ones and negligible in males. The pistillates show lower staminode–flower but higher pistil–flower length correlations (r = 0.9 and 1 respectively, for LP and SP).

Male fitness traits: The male fitness associated traits (flower length with number of (i) total stamens, (ii) long stamens and (iii) short stamens) are also highly related.

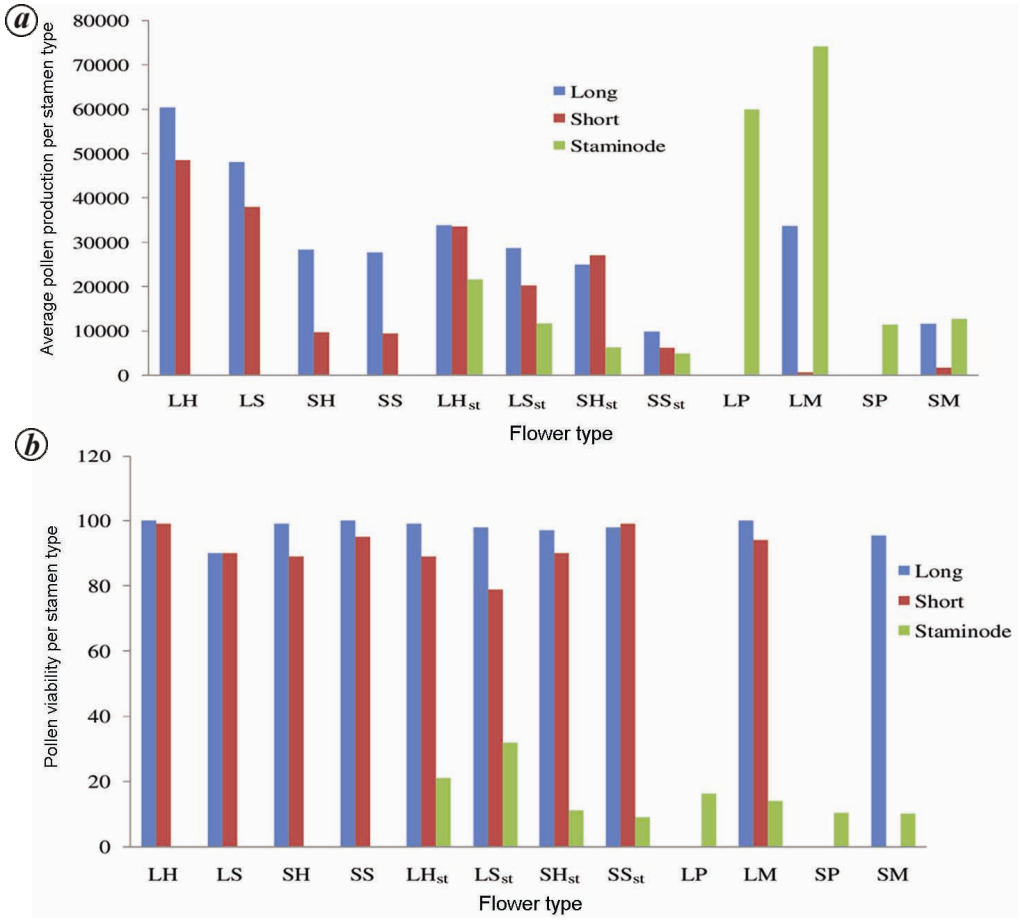

Figure 2. Comparative male fitness in terms of pollen production (***a***) and viability (***b***) among different flower types.

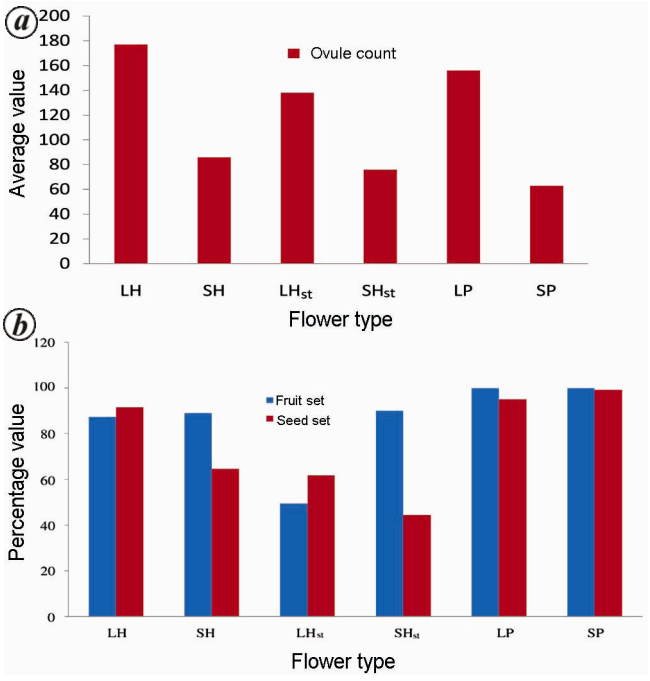

Figure 3. Comparative female fitness in terms of ovule number (***a***), and fruit and seed production (***b***) of different flower types.

The number of stamens in two groups and their respective lengths are also positively related in each flower type (Table 4).

Female fitness traits: The male and female sex organs lie in close proximity in hermaphrodites (Tables 1 and 2), which is further confirmed by their *r*-values (Table 4). Correlation between lengths of pistils and stamens is, however, more strong in LH ($r = 0.65$) and SH_{st} ($r = 0.84$). The sterile stamens are considerably shorter than the pistils, which correlate weakly and negatively. Positive correlations also exist between number of stamens and pistil length (Table 4).

The foregoing account points towards tremendous variation in the sex and size of flowers accompanied with differential correlation strategies of *C. viscosa*. Analyses of floral morphology reveal profound size and number dimorphism between flower types for both primary (androecium and gynoecium) and secondary (corolla) sexual characters. The lowest and highest value of each floral trait distributed among different flower types manifest the same (Table 3). Even though the statistical results reflect least among sex but significant among size differences (Tables 1 and 2), these counterbalancing strategies of

Table 3. Distribution of highest and lowest value of each floral trait among flowers of different types

Floral trait			Large type		Small type	
			Highest value	Lowest value	Highest value	Lowest value
Male fitness	Length	Flower	12.9 (LH)	10.8 (LM)	7.9 (SH_{st})	5.2 (SP)
		Long stamen	10.2 (LH)	7.8 (LM)	6.2 (SH_{st})	4.8 (SS, SM)
		Short stamen	7.1 (LH)	1 (LM), 6.1 (LS)	4.5 (SH)	3.4 (SH_{st})
		Staminode	4 (LH_{st})	1.9 (LM)	3 (SS_{st})	1.3 (SM)
	Number	Total stamen	19.3 (LS_{st})	12.85 (LS)	14.1 (SH_{st})	5.7 (SP)
		Long stamen	7.8 (LH)	5.2 (LM, LH_{st})	4.8 (SH_{st})	2.7 (SS_{st})
		Short stamen	11.1 (LH)	7.3 (LS), 0.4 (LM)	4.4 (SH_{st})	2.6 (SS)
		Staminode	16.33 (LP)	4 (LS_{st})	6.4 (SM)	2.9 (SS_{st})
Female fitness	Pistil length		7.5 (LH)	2.6 (LS_{st})	5.3 (SH_{st})	2.2 (SS)

sexual variation and size dimorphism are avenues evolved to negotiate reproductive costs imposed by overlapping and continuous vegetative and reproductive phases[20]. Sexual dimorphism is intrinsic in that it is neither affected temporally nor spatially. It may be recalled that plants produce hermaphrodite and staminate flowers continuously throughout the season and thereby remain/keep unaffected by time and space. On the contrary, size dimorphism is driven both by time and space, pronounced as it is at the terminal sites of primary and secondary racemes during the later resource-limited stages[28].

The pollen and ovule production (Figures 2 *a* and 3 *a*) by flowers of two sizes suggests that the plants invest least amount of resources on the development of small flowers. Large flowers produce less than twice the amount of pollen compared to their smaller counterparts. For instance, 60,455.6 pollen produced by the long stamens in LH is twice the amount (28,340.8) produced in SH. Similar pattern irrespective of stamen type is followed by others (Figure 2 *a*). Ovule production varies between flowers (Figure 3 *a*) and follows a ratio 1 : 2 among small and large, counterparts. Apart from these differences, formation of size dimorphic flowers is intriguing because both are reproductively productive (fruit set > 80% in each); with the smaller ones being less expensive (Tables 1 and 2). The exact reasons for this differential strategy are yet to be ascertained. However, notwithstanding the sex expression, correlation strategies of large flowers hold true for their smaller counterparts as well. This shows that differential correlation does not arise due to difference in size and that all are subjected to similar selective pressures.

In the light of evolutionary genetics, a preferential shift in the investment towards one sex (male or female) and not both, at a certain time in hermaphrodite flowers results in them evolving into different sexes[30]. According to developmental genetics, these variations occur due to alteration or mutation in male and female development genes as in *Arabidopsis thaliana* and *Antirrhinum majus*[31]. The correlation study conducted presently has been successful in answering how far sex-specific traits are selected in flower type. Strong correlation between flower length and sexual organs suggests that these traits are coevolving and in combination affect the pollination system. Among these correlations, the traits influencing male fitness are the strongest and least variable in all flower types, indicating that the selection on floral morphology acts strongly through male function. Correlations between stamen length and (i) the number of flowers and (ii) flower length (Table 4) suggest that these traits have coevolved to ensure pollen presentation, effective donation and pollinator accessibility[3–9]. A large number of pollinator fauna belonging to Diptera, Lepidoptera and Hymenoptera are frequent visitors to plants of *C. viscosa*, which further strengthens this hypothesis. Active feeding on pollen ensures transfer of these functional male units to the receptive stigmas during movement to other flowers (pers. obs.).

A feature peculiar to andromonoecious species like *Leptospermum*, *Solanum*, *Passiflora incarnata*, *Cneorum tricoccon*, *Isomeris arborea*, *Commelina benghalensis* and *Commelina caroliniana*[32–37], but not to *C. viscosa*, is the stability and/or constancy in stamen number. Variability in stamen number per flower and pollen production thereof along with flower size has different implications. Small types display less and have fewer rewards and accordingly tend to be less attractive. Staminate flowers are usually large and equipped with greater stamen number, which results in corresponding increase in pollen production. This enhances their fitness in terms of fulfilment of male function by pollen donation and requires more visits from pollinators than hermaphrodites[38]. On the contrary, hermaphrodites are generally greater or equal in size to staminate ones and are more rewarding in terms of the stamen number and pollen they produce in *C. viscosa* (Figure 2 *a* and *b*). Species of *Solanum*, *Leptospermum* and *Zigadens* also follow the same pattern[15,16,32]. The overall male fitness among flower types also varies in terms of stamen length, their corresponding number, quality of pollen produced and proportion actually viable (Table 1; Figures 2 *a* and *b*). More productive long stamen produces highest 60,455.6 (in LH) to lowest

Table 4. Correlation between different trait pairs in different flower types

Floral trait			Flower-type+											
			LH	LS	SH	SS	LH_{st}	LS_{st}	SH_{st}	SS_{st}	LP	LM	SP	SM
Male fitness	Length	Flower–long stamen	0.77	0.23	0.66	0.78	0.80	0.79	0.79	0.96	0	0.004	0	0.018
			5.13*	23.63*	3.73*	5.44*	3.77*	5.23*	3.76*	9.86*		0.007**		0.03**
		Flower–short stamen	0.733	0.319	0.74	0.76	–0.30	0.84	0.38	0.98	0	–0.034	0	0
			4.58*	1.43**	4.68*	7.58*	–0.90**	4.34*	1.15**	12.81*		–0.058**		
		Flower–staminode	0	0	0	0	–0.47	0.44	–0.27	0.85	–0.84	0.02	–0.54	–0.039
							–1.50**	1.37**	–0.78**	4.49*	–1.52**	0.035**	–1.83**	–0.067**
		Long–short stamen	0.7104	0.82	0.88	0.93	0.23	0.85	0.42	0.97	0	–0.045	0	0
			4.29*	6.08*	7.81*	10.5*	0.67**	4.62*	1.30**	16.83*		–0.08**		
		Long-stamen–staminode	0	0	0	0	–0.11	0.166	0.13	0.86	0	0.018	0	–0.002
							–0.32**	0.48**	0.38**	4.87*		0.032**		–0.003**
		Short-stamen–staminode	0	0	0	0	0.82	0.17	–0.096	0.87	0	–0.16	0	0
							4.10*	0.49**	0.27**	4.98*		–0.28**		
	Number–Length	Flower–total stamen	0.6199	–0.08	0.12	0.41	0.79	0.11	0.89	0.91	0.86	0.015	0.191	–0.019
			3.36*	0.35**	0.51**	0.56**	3.75*	0.31**	5.69*	6.07*	1.67**	0.026**	0.55**	–0.033**
		Flower–long stamen	0.4540	0.38	0.16	0.39	0.086	0.45	0.57	0.53	0	–0.009	0	0.021
			0.89**	0.92**	0.99**	0.92**	0.24**	1.43**	1.96**	1.79**		–0.016**		0.036**
		Flower–short stamen	0.5487	–0.46	0.11	0.41	0.81	–0.56	0.59	0.92	0	–0.034	0	0
			2.79*	2.22*	0.46**	1.9**	3.90*	–1.92**	2.1**	6.55*		–0.058**		
		Flower–staminode	0	0	0	0	0.30	0.83	0.14	0.26	0.86	0.028	0.191	–0.037
							0.90**	4.28*	0.41**	0.76**	1.67**	0.05**	0.55**	–0.065**
	Number	Long–short stamen	0.34	–0.09	0.17	–0.04	0.16	0.06	0.19	0.62	0	0.30	0	0
			1.52**	0.40**	0.74**	0.16**	0.45**	0.17**	0.54**	2.45*		0.55**		
		Long-stamen–staminode	0	0	0	0	–0.134	0.56	–0.41	0.39	0	–0.15	0	–0.022
							–0.38**	1.91**	–1.28**	1.21**		–0.26**		–0.038**
		Short-stamen–staminode	0	0	0	0	–0.17	–0.59	–0.44	0.85	0	–0.29	0	0
							–0.5**	–2.09**	–1.38**	4.62*		–0.53**		
		Total–long stamen	0.73	0.68	0.18	0.83	0.49	0.81	0.46	0.81	0	–0.035	0	–0.010
			4.25*	3.89*	0.79**	6.33*	1.6**	3.98**	1.47**	3.84*		–0.06**		–0.017**
		Total–short stamen	0.89	0.66	0.90	0.16	0.52	0.59	0.61	0.94	0	–0.06	0	
			8.29*	3.72*	8.88*	0.68**	1.7**	2.12**	2.15**	7.60*		–0.11**		
		Total–staminode	0	0	0	0	0.49	0.20	0.21	0.85	0	0.1	0.1	
							1.59**	0.59**	0.60**	4.55*		0.196**	0	
Female fitness	Length	Flower–pistil	0.69	0.0067	0.36	0.19	0.92	0.075	0.68	0.27	0.93	0	1.0	0
			4.05*	0.029**	1.65**	20.2*	6.5*	0.21**	2.66*	0.78**	4.2**		0	
		Pistil–long stamen	0.65	0.22	0.53	0.38	0.74	–0.10	0.84	0.22	0	0	0	0
			3.67*	0.94**	2.64*	1.73**	3.14*	–0.29**	4.32*	0.65**				
		Pistil–short stamen	0.68	0.41	0.61	0.38	–0.13	–2.00	0.59	0.19	0	0	0	0
			3.95*	2.11**	4.1*	1.73**	–0.37**	–0.57**	2.07**	0.55**				
		Pistil–staminode	0	0	0	0	–0.54	–0.028	–0.15	0.38	–0.69	0	–0.91	0
							–1.88**	–0.078**	–0.4**	1.16**	–0.95**		–6.6**	
	Number	Pistil–long stamen	0.42	0.34	0.46	0.12	0.14	–0.64	0.22	0.84	0	0	0	0
			1.97**	1.53**	2.20*	0.49**	0.41**	–2.4*	0.63**	4.41*				
		Pistil–short stamen	0.62	0.59	0.39	–0.98	0.84	–0.45	0.47	0.45	0	0	0	0
			3.59*	3.09*	1.8**	19.9*	4.43*	–1.44**	1.51**	1.42**				
		Pistil–staminode	0	0	0	0	0.26	0.20	–0.06	0.016	0.7	0	–0.31	0
							0.77**	0.58**	–0.16**	0.04**	0.99**		–0.92**	
		Pistil–total stamen	0.66	0.15	0.53	0.08	0.75	–0.65	0.49	0.53	0.7	0	–0.31	0
			3.71*	0.63**	2.63*	0.36**	3.25**	–2.44*	1.6**	1.75**	0.99**		–0.92**	

The *t* values are shown by asterisk. *$P < 0.05$, Significant and **$P > 0.05$, Non-significant. +Same as given in Table 1.

28,708.4 (in LS_{st}) pollen. The corresponding pollen figures are 48,489.7 (in LH) and 6074.8 (in LM) in short stamens. The viability by acetocarmine test of the pollen differentiated in these flowers, irrespective of the type, is quite high and ranges from 95.4 (SM) to 100% (LH, LM, SS) in long and 79 (LS_{st}) to 99% (LH, SS_{st}) in short stamens. The huge amount of pollen produced meets the needs of pollinator's food (transporting charge) and their delivery to receptive surfaces. In flowers with staminodes, low and non-viable pollen is compensated for/by its secondary attractant role, which is confirmed by fruit and seed production in pistillate flowers (Figure 3 *b*). This non-viable pollen is lowest in LS_{st} and highest in LM. The male fitness is at par as revealed at the structural and functional levels; further confirmed by their *r*-values. In fact, the mutual relationship of stamen numbers, their length and flower length indicates that these traits are strongly under the influence of similar selective forces, possibly pollinator-induced.

Structural proximity between sexual organs (Figure 1 *a–g*) coupled with synchronous events of anthesis, anther desiscence and stigma receptivity facilitate auto pollen deposition, which results in selection of higher pistil–stamen correlation in hermaphrodites[19]. These are suggestive of both self- and cross-pollination mechanisms adapted by hermaphrodites (LH, LH_{st} and their small counterparts) for efficient survival. Weaker female fitness correlation in staminate and male flowers interprets prime consideration of pollen donation in them, albeit some difference in the extent to which this is exerted[15,36,37,39]. Those with staminodes show an intermediate trend in male and female fitness depending upon the flower type and the number produced. While male fitness is exclusively selected in males and female fitness in pistillates.

Critical morphological and correlation analyses suggest that different pairs of traits in each flower are evolved in ways unique to them and to maximize their functional potential. The present study supports that natural selection is, thus, operating through differential correlation patterning and is probably driving the evolution of these flower types in *C. viscosa*.

1. Berg, R. L., A general evolutionary principle underlying the origin of developmental homeostasis. *Am. Nat*., 1959, **93**,103–105.
2. Berg, R. L., The ecological significance of correlation pleiades. *Evolution*, 1960, **43**, 1398–1416.
3. Conner, J. and Via, S., Patterns of phenotypic and genetic correlations among morphological and life-history traits in wild radish, *Raphanus raphanistrum*. *Evolution*, 1993, **47**, 704–711.
4. Stanton, M. and Young, H. J., Selecting for floral character in wild radish, *Raphanus sativus* L. *J. Evol. Biol.*, 1994, **7**, 271–285.
5. Conner, J. K., Genetic mechanisms of floral trait correlations in natural population. *Nature*, 2002, **420**, 407–410.
6. Conner, J. K. and Sterling, A., Testing hypotheses of functional relationships: a comparative survey of correlation patterns among floral traits in five insect-pollinated plants. *Am. J. Bot.*, 1995, **82**(11), 1399–1406.
7. Ushimaru, A. and Nakata, K., The evolution of flower allometry in selfing species. *Evol. Ecol. Res*., 2002, **4**, 1217–1227.
8. Ushimaru, A., Itagaki, T. and Ishii, H. S., Floral correlations in an andromonoecious species *Commelina communis* (Commelinaceae). *Plant Species Biol*., 2003, **18**, 103–106.
9. Strauss, S. Y. and Whittall, J. B., Non-pollinator agents of selection on floral traits. In *Ecology and Evolution of Flowers* (eds Lawrence, Hardet, L. D. and Barrett, S. C. H.), Oxford University Press, 2006, pp. 120–138.
10. Grant, V., Modes and origins of mechanical and ethological isolation in angiosperms. *Proc. Natl. Acad. Sci. USA*, 1994, **91**, 3–10.
11. Levin, D. A., *The Origin, Expansion, and Demise of Plant Species*, Oxford University Press, Oxford, 2002.
12. Primack, R. B. and Lloyd, D. G., Andromonoecy in New Zealand montane shrub manuka, *Leptospermum scoparium* (Myrtaceae). *Am. J. Bot.*, 1980, **67**, 361–368.
13. Solomon, B. P., Environmentally influenced changes in sex expression in an andrmonoecious plant. *Ecology*, 1985, **66**, 1321–1332.
14. Solomon, B. P., Sexual allocation and andromonoecy: resource investment in male and hermaphrodite flowers of *Solanum carolinense* (Solanaceae). *Am. J. Bot*., 1986, **73**, 1215–1221.
15. Emms, S. K., Andromonoecy in *Zigadenus paniculatus* (Liliaceae): spatial and temporal patterns of sex allocation. *Am. J. Bot.*, 1993, **80**, 914–923.
16. Emms, S. K., Temporal patterns of seed set and decelerating fitness returns on female allocation in *Zigadenus paniculatus* (Liliaceae): an andromonoecious lily. *Am. J. Bot.*, 1996, **83**, 304–315.
17. Diggle, P. K., Development plasticity, genetic variation, and the evolution of andromonoecy in *Solanum hirstum* (Solonaceae). *Am. J. Bot.*, 1993, **80**, 967–973.
18. Narbona, E., Ortiz, P. L. and Arista, M., Functional andromonoecy in *Euphorbia* (Euphorbiaceae). *Ann. Bot.*, 2002, **89**, 571–577.
19. Saroop, S. and Kaul, V., Phenological events of *Cleome viscosa* L. growing in Jammu district. *Int. J. Plant Reprod. Biol.*, 2011, **3**(2), 161–164.
20. Saroop, S., A preliminary analysis on seed to seed cycle of *Cleome viscosa* L. M Phil dissertation, University of Jammu, Jammu, 2011.
21. Anon., *The Wealth of India (Raw Materials)*, 1950, vol. 2c, p. 427.
22. Singh, G., Ram, I. C. and Singh, D., Crop–weed competition studies in green gram and black gram. *Trop. Pest Manage.*, 1991, **37**, 144–148.
23. Reddy, M. M., Vilatha, A. M. and Rao, L. J., Integrated weed management in pigeon (*Cajanus cajan*) and soybean (*Glycine max*) intercropping system on vertisol under rainfed conditions. *Indian J. Agric. Sci.*, 2007, **77**(3), 177–178.
24. Olorunmaiye, P. M. and Olorumaiye, K. S., Weed flora of a maize/cassava intercrop under integrated weed management in an ecological zone of southern Guinea Savanna of Nigeria. *Ethnobot. Leaflets*, 2008, **12**, 784–800.
25. Chatterjee, A. and Pakrashi, S. C., *The Treatise on Indian Medicinal Plants*, Publication and Information Directorate, CSIR, New Delhi, 1991, vol. 1, p. 215.
26. Sudhalakshmi, Y. G., Banu, F., Ezhilarasan, Arumugam, Sahadaven, Green synthesis of silver nanoparticles from *Cleome viscosa*: synthesis and antimicrobial activity. In International Conference on Bioscience, Biochemistry and Bioinformatics, IPCBEE, IACSIT Press, Singapore, 2011, vol. 5.
27. Kumari, R., Tyagi, A., Sharma, V., Jain, V. K. and Kumar, S., Variability in the accessions from Aravali range assessed for domestication of the Cleomaceae biodiesel plant Linn. *Indian J. Nat. Prod. Resour.*, 2012, **3**(2), 246–255.
28. Saroop, S. and Kaul, V., Intra-plant floral variation in *Cleome viscosa* L. and its possible significance in breeding system. *Indian J. Exp. Biol.*, 2015, **53**, 468–475.
29. Sokal, R. R. and Rohlf, J. F., *Introduction to Biostatistics*, W.H. Freeman and Company, San Francisco, 2001.

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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