Phenology of a temperate fern *Dryopteris wallichiana* (Spreng.) Hyl. (Dryopteridaceae) in Uttarakhand, India

N. Punetha[1,*], J. N. Pant[2], R. Punetha[1] and K. Bhakuni[1]

[1]Department of Botany, Government Post Graduate College, Pithoragarh 262 502, India
[2]Department of Botany, Government Post Graduate College, Berinag (Pithoragarh) 262 531, India

Initiation and proliferation of leaf primordia, leaf expansion and maturation of a basket fern *Dryopteris wallichiana* are described based on two years of observation. The phenology of these events is strictly seasonal beginning with the onset of spring in the temperate Himalayan climate. Leaf primordia initiated during late summer often remain dormant but expand in the next growing season. Maturation of most of the leaves of a growing season is completed before the start of winter, but these withstand the winter cold. Leaves of the previous growing season remain erect on the rhizome for about 20 months after which they collapse. Significance of the presence of green and dry collapsed leaves on the rhizome is discussed.

Keywords: Dormancy of leaf primordia, *Dryopteris wallichiana*, Indo-Himalaya, phenology, temperate forest.

THE mixed (oak-conifer) temperate forests of the west and central Himalayas are as rich as the forests of the lower elevations, but the constituents of these forests include understorey herbaceous vegetation which contains a large number of temperate ferns. The importance of the fern understorey plants as constituents of the biodiversity of these forests cannot be neglected though they may have less economic importance than plants of other groups. Some ferns are evergreen, i.e. they produce leaves round the year thus contributing to the winter vegetation of forests. The role of ferns in general in the ecosystem dynamics of any particular area is little studied[1–3] and information on temperate ferns is very sparse[4–6]. Overwintering of one-year old *Dryopteris crassirhizoma* Nakai leaves in Japan is reported to contribute to overall carbon gain but serves very little as nutrient storage[7]. Studies on some temperate fern life cycles reveal that the leaf length and production rates vary during different periods of the year[8–12]. Annual variation in leaf production has also been observed in other temperate ferns such as *Polystichum braunii* (Spenn.) Fée, *P. tripteron* (Kunze) C. Presl, *Dryopteris crassirhizoma* Nakai[13], *D. intermedia* (Muhl. ex Willd.) A. Gray and *P. acrostichoides* (Michx.) Schott[6].

*For correspondence. (e-mail: punethan_bot@yahoo.co.uk)

Among higher altitude species of *Dryopteris*, *D. wallichiana* (Spreng.) Hyl. is confined to upper-mid to higher altitude zones, from c. 2000–3000 m altitude west Himalayan forests and has a wide range of distribution from the eastern part of the west to the east Himalayas within the Indo-Himalayas[14–16], which is an obvious indication of it being a successful forest floor fern. The populations of *D. wallichiana* we studied probably belong to subsp. *nepalensis* Fraser-Jenk., which is already known from Pithoragarh. Our goal was to increase understanding of its life cycle by observing seasonal and annual changes in leaf production rate, size and longevity in some living populations of this fern in Kumaon (west Indo-Himalayas).

Phenological events were studied on the live populations at Dhaj forest (29°40′N, 80°14′E), c. 22 km north of Pithoragarh (Uttarakhand State, India). The locality contains a temperate flora, lying at 2400–2600 m altitude. We studied the population of *D. wallichiana* mainly on the north-facing side. In addition to several deciduous ferns, many evergreen species, particularly *Dryopteris* and *Polystichum* species, occupy humus-rich shady floors of north-facing slopes of the forests where the climate is strikingly seasonal with moderate summers and cold winters. The range of humidity varies from 18.4% during winter months to 95.97% during the summer rainy season. Rainfall levels are high in this area: the amount of precipitation varies from 5.05 mm in December to 382 mm in July and winter precipitation is often in the form of snow. Fluctuations in the annual range of temperature are also striking: while the mean minimum and maximum temperature recorded in February was 1°C and 5°C respectively, the fluctuation in July was between 12°C and 19°C.

Chemical analysis of the humus-rich dark soil reveals that it is rich in N, K, Na and organic carbon and is generally acidic (pH 5.68) in nature.

We made monthly observations on the emergence of leaf-primordia from the rhizome apex, formation of croziers, maturation of the leaf and dessication and death of older leaves. We grouped the plants into two size-classes based on leaf count: category I = 1–5 leaves; category II = 6–10 leaves. This is mainly because in younger plants the basket comprises only up to five expanded leaves, whereas in relatively older plants up to 10 leaves are present. Sixteen plants in each category were selected in a limited area of the forest. Each selected plant was tagged to differentiate it from the others. The study was spread over a two-year period from May 1999 to April 2001 and the results given below are the averages from the two years.

D. wallichiana is a rosette fern with an erect compact, perennial rhizome which in a full grown plant may attain a height of about 10 cm. The leaves arise in a spiral and are 75 to 80 cm long and 30 cm wide and form a basket on the rhizome. The number of leaves on a rhizome may vary from 1 to 10 depending on the age of the plant. A full grown leaf bears 30 to 35 pair of lateral pinnae. Whereas many leaves on selected plants were green and semi-erect, some were at the primordial stage and some others (particularly those of outer spiral of leaves that had matured the previous year) were flat on the ground but still attached to the plant. Some dormant leaf primordia of the previous year were present on the rhizome apex and the new leaf primordia usually emerge from April onwards and are dome shaped and covered with thick scales. The average number of leaf primordia including those of the previous year and those newly appeared during April in category I was 2 in May, 2.5 in June, 3.5 in July and 5 in August, but in category II the average number of leaf primordia on the rhizome apex was relatively higher: 3 in May to 6.5 in August.

Emergence of primordia and increase in length of leaf in both categories is strikingly variable: the average height of dormant primordia formed late in the previous growing season was 3 cm at the beginning of the growing season in May in category I. These grew to about 67 cm in June (the maximum length attained was 70.5 cm in July). Other primordia initiated during the previous growing season that remained dormant measured about 2.5 cm and started growth in June. These grew to 40.5 cm in July and reached 63.5 cm in August (the maximum length attained was 64.5 cm in September). About 30% of the primordia that emerged in the current growing season started growth in July and 17% in August; these grew faster for approximately the next one month. Primordia which started growth in July were longer (up to 50 cm) than those which started growth in August (up to 35 cm) (Figure 1). Some primordia of variable height persisted on the rhizome apex and remained dormant throughout the winter.

Dormant primordia initiated in the previous growing season on the rhizome apex in category II were relatively longer (3.0 to 3.5 cm) than those of category I. These were released from dormancy in May and 50% of them became active and started growth; on expansion they grew to about 79.5 cm in August. The remaining 50% started growth in June and grew to about 70 m in September (Figure 2). Of some additional primordia initiated in the current growing season, 50% started growth by August, but the expanded leaves developed from these primordia were smaller than leaves that expanded early in the growing season (Figure 2). The remaining 50% of primordia initiated in the current growing season became dormant and become the leaves of the next growing season.

In category I, only 22.8% of leaves formed in early summer (May, June) were fertile but a total of 85.4% of the leaves present at the end of the growing season were vegetative, i.e. 36.3% formed late in the summer remained vegetative. More precisely, all leaves in plants bearing up to three leaves were vegetative, whereas in plants with 4–5 leaves only one leaf in each plant was fertile. In category II, all leaves produced and expanded in early summer (May, June) were fertile (100% fertile) but leaves formed later (July, August) remained vegetative. At the end of the growing season only 20% of leaves were fertile whereas the remaining 80% were non-soriferous.

Only those leaves which were formed during early summer were fertile, i.e. producing sporangia on the under-surface of the pinnae. Sori are usually absent in the lower third of the leaf and are formed along with the growth of the mid and upper pinnae. Leaves formed late in summer or during autumn often remain vegetative. There is no striking difference in the growth-period and rate of elongation of vegetative and fertile leaves.

Lateral pinnae in fern leaves are produced in acropetal succession and simultaneously with the apical growth of the leaf. A fully curled up crozier is not formed in *D. wallichiana* but the growing leaf apex always remains free and downwardly directed until 10 to 15 pairs of lateral pinnae are formed when it straightens out in line

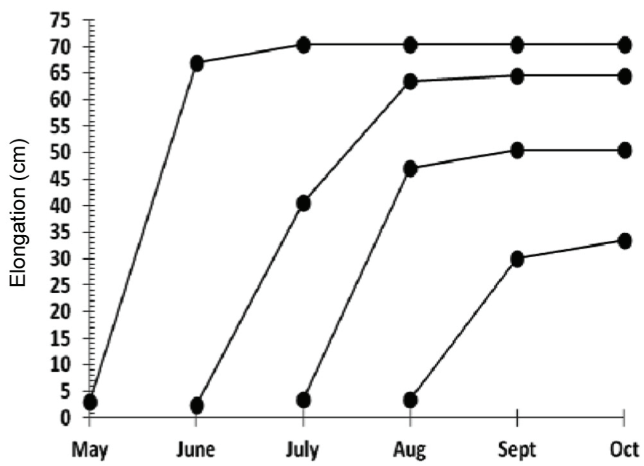

Figure 1. Average monthly elongation of leaf (size-class I).

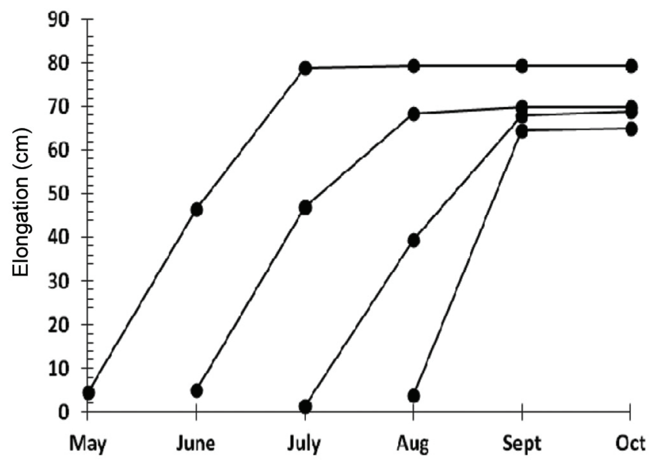

Figure 2. Average monthly elongation of leaf (size-class II).

with the rest of the leaf. At the primordial stage, lateral pinnae are not discernible. The first pair of pinnae appeared when the leaf grew to about 5 cm in length in both the categories. The number of pairs of lateral pinnae depends on the length of the growing leaf in both categories (Figures 3 and 4). Similarly the expansion of lateral pinnae also depends on the growth and length of the leaf. However the leaves which arise late in the growing season (July–August) were smaller than those which were formed in earlier months and the number of pairs of lateral pinnae in leaves formed later was also lower than in those which were formed earlier (Figures 3 and 4).

The average number of lateral pairs of pinnae in leaves which began to grow in May in category I was 0.5 as against 1.0 in leaves which started growth in August. As many as 27 pairs of lateral pinnae were formed by July in the former case whereas the highest number of lateral pair of pinnae in the later case was 17 in October (Figure 3). The average number of lateral pairs of pinnae per leaf was 1.0 in May in category II but the average number of pinnae for leaves which started growth in August was only 0.8. In the leaves of this category, which matured by August, an average of 31.7 pairs of lateral pinnae were formed in the former case (category I) but only 28.5 pairs of lateral pinnae were present in category II (Figure 4). There is no further increase in length of leaf and obviously no more lateral pairs of pinnae are added after October in either case.

The life-span of leaves from when the leaf begins to expand, which is generally in May, through to August in this fern, until they collapse and become dry was noted. As expected, the dormant primordia of last growing season start expanding first (in May) and grow faster during next two months in both categories until the final length is attained. Other primordial start growth successively until August and grow to full length in following months. The maximum number of fully expanded green leaves was present between September and November (Figure 5), but then the older green leaves (which were formed during the previous growing season more than a year earlier) collapse (Figure 6). This process continues until April the next year. The green collapsed leaves become dry but still remain attached to the rhizome. Thus the average life-span of leaves in this fern is about 20 months.

Species diversity has a significant role in the ecosystem dynamics of the subtropical and temperate Himalayas, and to understand the plant ecology of the region, it is important to know the longevity of the floristic

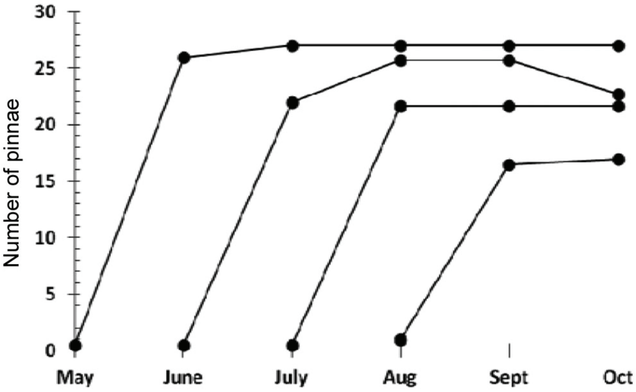

Figure 3. Average number of pinnae per leaf per plant (size-class I).

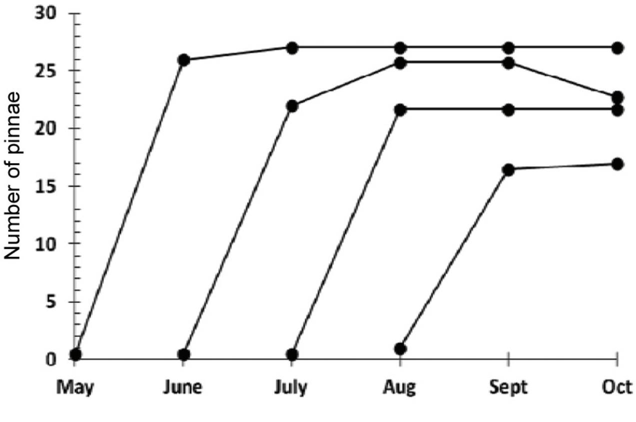

Figure 4. Average number of pinnae per leaf per plant (size-class II).

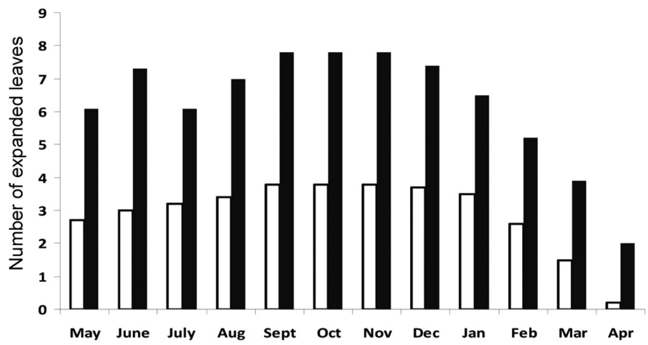

Figure 5. Average number of expanded leaves in two size-classes (blank, short bars represent category I; dark long bars represent category II).

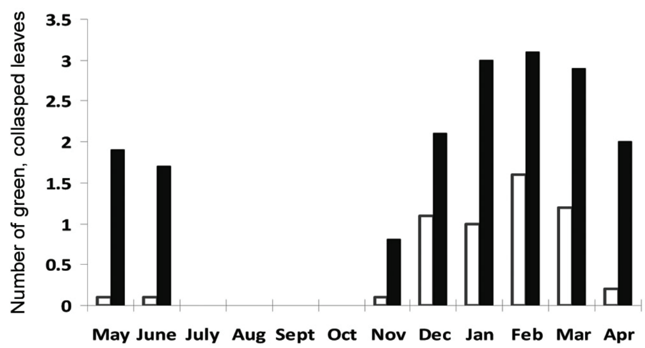

Figure 6. Average number of green collapsed leaves in two size-classes (blank, short bars represent category I; dark long bars represent category II).

components and their rate of replacement. Though rare in occurrence, *Cyathea spinulosa* Wall. ex Hook., a tree fern, has been studied as an interesting example of a woody component of the forest ecosystem of the eastern part of the west Himalayas[17], but the role of herbaceous ferns has not been so well studied. Quite a large number of ferns found in the herbaceous vegetation of the temperate forests of the Indo-Himalayas are deciduous. In deciduous ferns, the mature leaves wither or abscise at the onset of winter, and their role becomes limited to formation of litter and humus. On the other hand, a good number of leaves remain attached to the rhizome during winter in other ferns including *D. wallichiana*; these species are categorized as winter-green ferns[18] in contrast to evergreen ferns in which the leaves are produced round the year[9]. Ferns of these two categories can withstand the extreme temperatures of winters and continue to take an active role in winter metabolism and ecosystem function through photosynthesis. The one-year old, but still green leaves of *D. intermedia* subsp. *intermedia* in North America are known to contribute 29% of overall carbon gain in deciduous forest, but substantially more, 63%, in boreal forest[19].

The emergence and expansion of leaves in *D. wallichiana* are highly seasonal: new leaf-buds are initiated only during a certain period of the year in both size-classes. Sigmoid leaf growth is known in ferns such as *Osmunda cinnamomea* L.[20] in North America and *Lygodium japonicum* (Thunb.) Sw.[21] in the Indo-Himalayas and is also observed in the present species, in which the leaf-apex grows acropetally and the lateral pinnae are initiated. This is in contrast to the growth of compound leaves of some seed-plants in which the leaves often arise basipetally[22,23]. The present study reveals that initiation, proliferation of leaf primordia and expansion of the leaf is influenced by seasonal climate; leaves initiated in early summer grow at a faster rate and are relatively larger in size than those which are initiated in later months. The number of lateral pairs of pinnae is also higher in leaves formed first in the growing season. Leaf primordia formed in later months may remain dormant until the next growing season. Dormancy of various parts of fern sporophytes has been considered an important part of phenology[24].

Members of Polypodiaceae and Davalliaceae, which are common epiphytes in the temperate forests of central Himalayas nearly all have a short leaf life-span as the leaves abscise in late autumn, being impossible to maintain on dry tree-trunks. But in *D. wallichiana*, inhabiting damp forest-soils, the leaf life-span is spread over 20 months suggesting the ability of this fern to withstand the winter cold. Winter-hardening of leaves in low temperature has been reported in the New Zealand populations of the introduced European species, *Dryopteris filix-mas*[25]. Retention of leaves during winter, either as green collapsed or as dry collapsed leaves, is of great advantage for ferns. All the sporangia present on the under-side of the leaves do not dehisce at one time, but those present on the distal pinnae remain intact and dehisce on further drying of the dry collapsed lamina. Prolonged and gradual dispersal of spores provides additional opportunity for spore-germination and spread of populations. Retention of spores within sporangia of the leaves of previous year throughout winter in ferns of central Iowa, USA, has been reported by Farrar[26]; release of some spores from these sporangia during winter is also indicated. Although not investigated in the present study, the senescent, dry collapsed leaves of *D. wallichiana* are marcescent later, still bearing intact sporangia on their under side[27]. In addition to this advantage, these leaves add to the forest litter and humus. The role of marcescent leaves of *Dicranopteris linearis* (Burm.f.) Underw. in Hawai'i: in soil dynamics has been studied in detail by Russell and Vitousek[28].

1. Tanner, E. V. J., Leaf demography and growth of the tree fern *Cyathea pubescens* Mett. ex Kuhn in Jamaica. *Bot. J. Linn. Soc.*, 1983, **87**, 213–227.
2. Von Aderkas, P. and Green, P. E. J., Leaf development of the ostrich fern *Matteuccia struthiopteris* (L.) Todaro. *Bot. J. Linn. Soc.* 1986, **93**, 307–312.
3. Willmot, A., The phenology of leaf life span in woodland populations of the ferns *Dryopteris filix-mas* (L.) Schott and *D. dilatata* (Hoffm.) A. Gray in Derbyshire. *Bot. J. Linn. Soc.*, 1989, **99**, 387–395.
4. Minoletti, M. L. and Boerner, R. E., Seasonal photosynthesis, nitrogen and phosphorus dynamics, and resorption in the winter-green fern *Polystichum acrostichoides* (Michx.) Schott. *Bull. Torrey Bot. Club.*, 1993, **120**, 397–404.
5. Nooden, L. D. and Wagner Jr, W. H., Photosynthetic capacity and leaf reorientation in two wintergreen ferns, *Polystichum acrostichoides* and *Dryopteris intermedia*. *Am. Fern J.*, 1997, **87**, 143–149.
6. Sharpe, J. M., Annual variation in leaf production of reproductively mature sporophytes of *Dryopteris intermedia* and *Polystichum acrostichoides* (Dryopteridaceae: Pteridophyta) two common ferns of temperate north-eastern USA. *Indian Fern J.*, 2012, **29**, 240–253.
7. Tani, T. and Kudo, G., Overwintering leaves of a forest fern, *Dryopteris crassirhizoma* (Dryopteridaceae): a small contribution to the resource storage and photosynthetic carbon gain, *Ann. Bot.*, 2005, **95**, 263–270.
8. Cousens, M. I., *Blechnum spicant*: habitat and vigor of optimal, marginal and disjunct populations, and field observations of gametophytes. *Bot. Gaz.*, 1981, **142**, 251–258.
9. Punetha, N., Leaf growth and productivity in two western Himalayan thelypteroid ferns. *Indian Fern. J.*, 1989, **6**, 68–72.
10. Bartsch, I. and Lawrence, J., Leaf size and biomass allocation in *Thelypteris dentata*, *Woodwardia virginica* and *Osmunda regalis* in central Florida. *Am. Fern J.*, 1997, **87**, 71–76.
11. Greer, G. K. and McCarthy, B. C., Patterns of growth and reproduction in a natural population of the fern *Polystichum acrostichoides*. *Am. Fern J.*, 2000, **90**, 60–76.
12. Tessier, J. T., Leaf habit, phenology and longevity of 11 forest understory plant species in Algonquin state forest, northwest Connecticut, USA. *Botany*, 2008, **86**, 457–465.
13. Sato, T., Estimation of chronological age for sporophyte maturation in three semi-evergreen ferns in Hokkaido. *Ecol. Res.*, 1990, **5**, 55–62.

14. Khullar, S. P., *An Illustrated Fern Flora of the West Himalaya* vol II. International Book Distributors, Dehra Dun, 2000, pp. 342–344.
15. Fraser-Jenkins, C. R., A monograph of Dryopteris (Pteridophyta: Dryopteridaceae) in the Indian subcontinent. *Bull. Brit. Mus. Nat. Hist. Bot.*, 1989. **18**(5), 354–359.
16. Fraser-Jenkins, C. R., *New Species Syndrome in Indian Pteridology and the Ferns of Nepal*, International Book Distributors, Dehra Dun, 1997, pp. 124–138.
17. Punetha, N. and Pant, J. N., Leaf demographic studies on central Himalayan *Cyathea spinulosa* Wall. ex Hook. In *Advances in Pteridology* (ed. Trivedi, P. C.), Pointer Publishers, Jaipur, 2002, pp. 104–109.
18. Chabbot, B. F. and Hicks, D. J., The ecology of leaf life spans. *Annu. Rev. Ecol. Syst*., 1982, **13**, 229–259.
19. Goldblum, D. and Kwit, M. C., The relative photosynthetic contribution of old and new fronds of the wintergreen fern *Dryopteris carthusiana*, Ontario, Canada. *J. Torrey Bot. Soc.*, 2010, **139**, 270–282.
20. Briggs, W. R. and Steeves, T. A., Morphogenetic studies on *Osmunda cinnamomea* L. The expansion and maturation of vegetative fronds. *Phytomorphology*, 1958, **8**, 234–238.
21. Punetha, N., Phenology of the climbing leaf of *Lygodium japonicum* (Thunb.) Sw. (Schizeaceae). *Phytomorphology*, 2000, **50**, 75–85.
22. Bower, F. O., On the comparative morphology of the leaf in the vascular cryptogams and gymnosperms. *Philos*. *Trans*. *R*. *Soc. London*, 1884, **175**, 565–615.
23. Foster, A. F., Leaf differentiation in Angiosperms. *Bot. Rev.*, 1936, **2**, 349–372.
24. Sharpe, J. M. and Mehltreter, K., Ecological insights from fern population dynamics. In *Fern Ecology* (eds Mehltreter, K., Walker, L. R. and Sharpe, J. M.), Cambridge University Press, Cambridge, New York, 2010, pp. 61–110.
25. Bannister, P., The seasonal course of forest resistance in some New Zealand Pteridophytes. *New Zealand J. Bot.*, 1984, **22**, 557–563.
26. Farrar, D. R., Spore retention and release from overwintering fern fronds. *Am. Fern J*., 1976, **66**, 49–52.
27. Punetha, N., Bhakuni, K. and Pant, A. K., Marcescent habit in Himalayan ferns (Abstract). In International Symposium on Perspectives in Pteridophytes, National Botanical Research Institute, Lucknow, India, 2008, pp. 88–89.
28. Russell, A. N. and Vitousek, P. M., Decomposition and potential nitrogen fixation in *Dicranopteris linearis* litter on Mauna Loa, Hawai'i. *J. Trop. Ecol.*, 1997, **13**, 579–594.

ACKNOWLEDGEMENTS. We thank Joanne M. Sharpe, Maine, USA, for going through the script critically, for helpful suggestions and for making available some literature related to this subject and to Chris Fraser-Jenkins, Kathmandu, for correcting the typescript in detail.

Received 2 September 2017; revised accepted 15 June 2018

doi: 10.18520/cs/v115/i9/1805-1809