Patterns of water potential among forest types of the central Himalaya

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Water potential (ψ) of soil and trees was measured in 16 forests from 450 to 2310 m elevation in the Kumaun Himalaya, during a two-year period. Predawn ψ, averaged across all species at a site was high (i.e. not stressful) at low elevations and variable at higher elevations. The incidence of low ψ at high elevations was opposite the usual pattern elsewhere. Midday ψ varied similarly. Patterns of plant and soil ψ differed. ψ values, especially in summer and winter, were severe enough to affect tree growth adversely.

A major factor controlling vegetation development and species distribution is water availability[1]. Central Himalayan forests grow in a strongly seasonal climate with several dry months. Indirect evidence and initial measurements indicate that this long dry period does limit tree species distribution and forest development[2]. Himalayan forests extend from the lowest mountain slopes with nearly tropical temperatures to timberline[3]. The low elevations appear likely to be drier than above; although precipitation varies inconsistently with elevation[4], lower temperatures and greater cloudiness at higher elevations should increase the effectiveness of precipitation. The status of water availability is assessed using 'water potential'[1], for which the highest value normal is zero; a high water potential (near zero) means that water is easily available to plants and a low value means that it is not easily available, inducing water stress. This report addresses one hypothesis of Zobel and Singh[2] that water potentials become low enough to determine the distribution of Himalayan trees and vary among forest types, with lowest potentials during winter at high elevations and during the pre-monsoon heat at low elevations. This is a description of landscape-level patterns of tree moisture status in monsoon climate forests of Asia and in forests dominated by evergreen trees with leaf longevity of one year. It helps to test further our contention that Himalayan forests differ significantly from those in other regions[5].

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Sixteen stands at nine locations from 450 to 2310 m elevation were selected to represent major forest types near Nainital, Kumaun region. Rainfall in Kumaun varies substantially; the Nainital basin is particularly wet. Weather during the years of the study included a very warm, dry pre-monsoon season in 1995 and a wet one in 1996; winters also differed in precipitation. Soils at the sites varied, including 60 to 75% sand, 6–29% silt and 8–24% clay. Coarse fragments were high within pine and cypress forests, and sand was highest beneath forests of cypress and sal. pH varied from 6.4 to 7.1. Stands were classified subjectively into five forest types based on the estimated potential late seral dominant tree species. Types were named by the shortest appropriate common name of the dominant tree: sal, *Shorea robusta*; pine, *Pinus roxburghii*; oak *Quercus leucotrichophora* (banj), *Q. floribunda* (tilonj) or both; cypress, *Cupressus torulosa*; and mixed, which included at least 2 oaks and at least 2 deciduous species per stand. The number of stands and the species sampled for each type was: sal (3), sal and pine; pine (2), pine; oak (6), banj, tilonj, *Rhododendron arboreum*; and pine; cypress (2), cypress, banj, tilonj and *Cornus macrophylla*; and mixed (3), banj, tilonj, *Q. lanuginosa, R. arboreum, Carpinus viminea, Machilus duthiei, Fraxinus micrantha* and *C. macrophylla*. For 13 sites in and near the Nainital basin, sites were grouped to determine whether physiographic location (basin, lower ridges, higher ridges) produced any consistent patterns in water potential.

At each stand, 3–5 trees of each major species were selected within 1 ha or less. Sample trees were 2–19 m tall; heights were usually similar among species at a given site.

Water relation attributes were sampled during six seasons per year for two years (October 1994–December 1996): fall – after monsoon rains with high soil moisture, but clear, dry and cooling weather; winter – after the dry fall months, with effects of extended freezing weather at higher elevations; spring – with warming temperatures, but before most new leaf production begins; early summer – with warm weather, supporting most production of new leaves; summer – the hottest season at the end of the dry months before the monsoon rains begin, while some leaves are continuing to expand; and, rainy season – hot, but wet, with generally very high soil moisture (sampled only in 1995). Water potential (ψ) was measured as described by Zobel and Singh[2], before dawn when tree ψ should be maximal and at equilibrium with soil moisture, and at midday, when ψ should be minimal. Measurements of plant ψ were made on twigs with leaves, using a pressure chamber (Model 1000, PMS Instrument Co, Corvallis, OR, USA); during winter and spring, leafless twigs of deciduous species were measured. Soil ψ was measured once per sample date at 60-cm depth for

Table 1. Soil water potential at 60-cm depth (MPa) for five forest types for six seasons. Values are averages of two years and are measured at 2–6 sites per forest type using a thermocouple psychrometer. Within the 'All types' row, seasonal means with the same letter are not significantly different ($P = 0.05$, Tukey's multiple range test)

Type	Season					
	Fall	Winter	Spring	Early summer	Summer	Rainy
Sal	−0.44	−1.19	−0.58	−1.42	−1.81	−0.06
Pine	−0.83	−1.20	−0.55	−1.61	−3.36	−0.76
Oak	−0.81	−1.06	−0.55	−1.43	−3.51	−0.66
Mixed	−0.43	−0.97	−1.05	−1.37	−2.00	−0.34
Cypress	−1.22	−1.26	−0.84	−2.46	−1.79	−0.50
All types	−0.71[ab]	−1.12[bc]	−0.68[ab]	−1.57[c]	−2.60[d]	−0.48[a]
P for each season	0.1121	0.9629	0.1783	0.2512	0.1139	0.4491

three representative locations per stand using a thermo-couple psychrometer (SC-10A, Decagon Devices, Pullman, WA, USA, with a NT3 microvoltmeter). For statistical analysis, variables were tested for normality using the Kolmogorov statistics. Those significantly departing from normality were transformed to produce a normal distribution.

Overall the sites mean soil water potential (ψ) at 60-cm depth varied from −0.48 MPa during the rainy season to −2.60 MPa during summer (Table 1), with an extreme low for the oak type of −3.51 MPa in summer. Such soils are dry enough to reduce growth and meta-bolic processes for mesophytes[1].

Soil ψ did not change significantly with elevation, both overall and in individual seasons. Physiographic position, after considering the effects of elevation, did not significantly affect soil ψ overall ($P = 0.312$), but influenced it significantly during the dry summer of 1995 ($P = 0.020$) and the dry winter of 1995–1996 ($P = 0.033$); the Nainital basin had higher soil ψ than the adjacent ridges, by at least 2.6 MPa in summer and by 0.7 MPa in winter. Despite substantial differences among means for individual forest types, there was much variability in soil ψ within types and the differ-ences among them were not significant overall or in any season (Table 1). The two study years differed signifi-cantly ($P < 0.0001$) in soil moisture during both summer (1995, −3.43 MPa, 1996, −1.27 MPa, $P = 0.0001$) and winter (1994–1995, −0.36 MPa, 1995–1996, −1.59 MPa, $P < 0.0001$), considering only sites sampled during both years. This allowed us to contrast plant ψ between a wet and a dry year for summer and winter.

Predawn plant ψ varied significantly among sites at all sampling times except early summer 1995. Predawn ψ was significantly and negatively related to elevation overall and in all individual seasons, with low eleva-tions having high ψ, and high elevations having a wide range of ψ (Figure 1). The correlation of predawn ψ with elevation was strongest in fall and winter ($r^2 = 0.521$ and 0.489, respectively) and weakest in spring and the rainy season ($r^2 = 0.158$ for both). Predawn ψ

varied with physiographic position differently than did soil ψ, being significant only in the drier winter when the lower elevation ridge sites had predawn ψ 0.4 MPa higher than the Nainital basin and the higher ridge ($P = 0.002$).

Forest types, based on dominant late-seral tree spe-cies, differed significantly ($P < 0.0001$), and the relative values of types changed with season (Table 2). Within individual seasons, types varied in all seasons, except the rainy season (Table 2). The sal type was most con-sistently high and the mixed type, most consistently low. All other seasons were significantly drier than the rainy season; summer was driest and summer, winter and early summer were all drier than fall. The contrast between dry and wet summers seen in soil ψ was re-flected also in predawn plant ψ, but the difference was much less (1995, −1.22 MPa; 1996, −0.70 MPa; $P < 0.0001$). In winter, however, despite a strong differ-ential in soil ψ, predawn plant ψ values were similar between years (1994–1995, −0.75 MPa; 1995–1996, −0.82 MPa; $P = 0.433$).

Water potential during midday declined significantly as elevation increased ($r^2 = 0.147$, $P < 0.0001$), consid-ering data from all seasons. Variation with elevation was significant during all individual seasons, except the rainy season and strongest in winter and fall ($r^2 = 0.502$ and 0.402, respectively). Physiographic position was significantly related to midday plant ψ only during the dry winter 1995–1996, when sites on lower ridges were 0.5 MPa lower than those in the basin and higher ridges. Midday ψ varied significantly among seasons ($P < 0.0001$) and among forest types ($P < 0.0001$). Av-eraged across types, values were highest during the rainy season, lower and similar from fall through spring, and lowest in early summer and summer (Table 3). Values varied significantly among forest types in most seasons, most strongly in fall and winter. The sal types had the highest midday ψ in all seasons; cypress and mixed types were each lowest in two seasons. The contrast between the dry and wet summers seen in soil and predawn ψ also occurred in midday (1995,
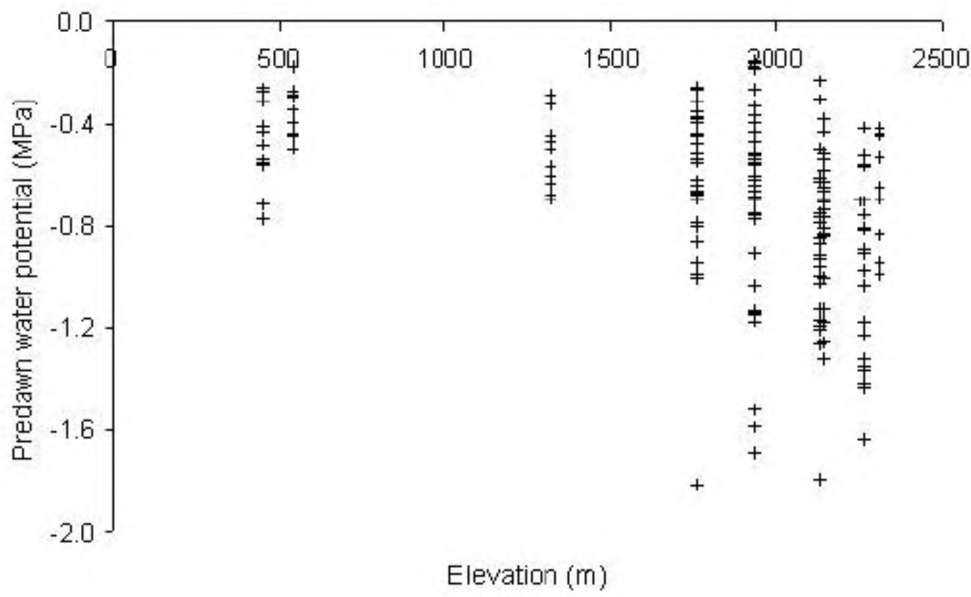
Figure 1. Relationship between mean values for predawn plant ψ and elevation each value is the mean for all species at one site for one sampling date.

Table 2. Predawn water potential (MPa) for five forest types for six seasons. Values are the average for two years, measured on leafy twigs using a pressure chamber. Within a season, types with the same letter are not significantly different ($P = 0.05$, Tukey's multiple range test). Within the 'All types' row, seasons with the same letter are not significantly different

Type	Season					
	Fall	Winter	Spring	Early summer	Summer	Rainy
Sal	-0.31^a	-0.41^a	-0.56^a	-0.57^a	-0.57^a	-0.25
Pine	-0.55^{ab}	-0.67^{ab}	-0.65^{ab}	-0.99^{ab}	-1.21^{ab}	-0.28
Oak	-0.47^a	-0.69^{ab}	-0.55^a	-0.74^{ab}	-1.09^{ab}	-0.40
Mixed	-0.69^b	-1.06^c	-0.97^b	-0.92^b	-1.21^b	-0.39
Cypress	-0.79^b	-0.89^{bc}	-0.64^{ab}	-0.88^{ab}	-0.98^{ab}	-0.41
All types	-0.60^x	-0.85^y	-0.75^{xy}	-0.83^{yz}	-1.06^z	-0.37^w
P for each season	<0.0001	<0.0001	0.0002	0.0197	0.0243	0.5655

-2.07 MPa; 1996, -1.29 MPa; $P < 0.0001$). In winter, however, the dry and wet years were similar (1994–1995, -1.05 MPa; 1995–1996, -1.13 MPa) as they were for predawn ψ. Extreme values of midday ψ were most frequent in summer, with 62% of site × species means below -1.5 MPa, in contrast to none during the rainy season and 14% during fall (Table 4); however, means of midday $\psi < -2$ MPa occurred in all seasons, except the rainy season.

Plant ψ was less severe than that of the soil, but was low enough to limit growth and physiological processes of forest trees[6,7]. Almost half the species × site means of predawn ψ measured in summer were below -1 MPa, with a secondary concentration of low values in winter; winter predawn ψ below -1 MPa occurred at all sites above 2000 m elevation. Reduction in osmotic potential associated with cold-hardiness, may contribute to low winter ψ; likewise, cold-induced xylem cavitation may

also reduce winter ψ values[7]. ψ values lower than ours have been measured for these species[8] (and also S. P. Singh and A. Tewari, unpublished data). For only two species, however, and then rarely, were our ψ values below the turgor loss point, determined using pressure–volume analysis (S. P. Singh and S. C. Garkoti, unpublished data).

Extreme predawn ψ values for each site (the average for all species at the time of measurement with the lowest average) were compared with three studies in the summer-dry climate of western Oregon, USA (Figure 2). Two studies[9,10] used data from a single year, and third one[11] used the minimal value for each site from 2 to 4 years of sampling. At higher elevations, Himalayan tree ψ values were within the range of those from the forests in Oregon, but below 1600 m they were higher than most ψ values from Oregon. Oregon forests were sampled by measuring conifer saplings 1–2 m tall,

Table 3. Midday plant water potential (MPa) for five forest types for six seasons. Values are means for two years. Within a season, types with the same letter are not significantly different (P = 0.05, Tukey's multiple range test). Within the 'All types' row, seasons with the same letter are not significantly different

	Season					
Type	Fall	Winter	Spring	Early summer	Summer	Rainy
Sal	−0.69[a]	−0.74[a]	−1.05	−1.18[a]	−1.26	−0.31
Pine	−1.24[bc]	−1.15[ab]	−1.18	−1.68[ab]	−1.91	−0.66
Oak	−1.17[b]	−1.09[a]	−1.14*	−1.57[ab]	−1.81	−0.64
Mixed	−1.04[b]	−1.54[b]	−1.52*	−1.50[ab]	−1.90	−0.54
Cypress	−1.49[c]	−1.45[b]	−1.33	−1.81[b]	−1.66	−0.41
All types	−1.10[y]	−1.31[y]	−1.32[y]	−1.53[z]	−1.75[z]	−0.53[x]
P for each season	< 0.0001	< 0.0001	0.0095	0.0250	0.1934	0.3576

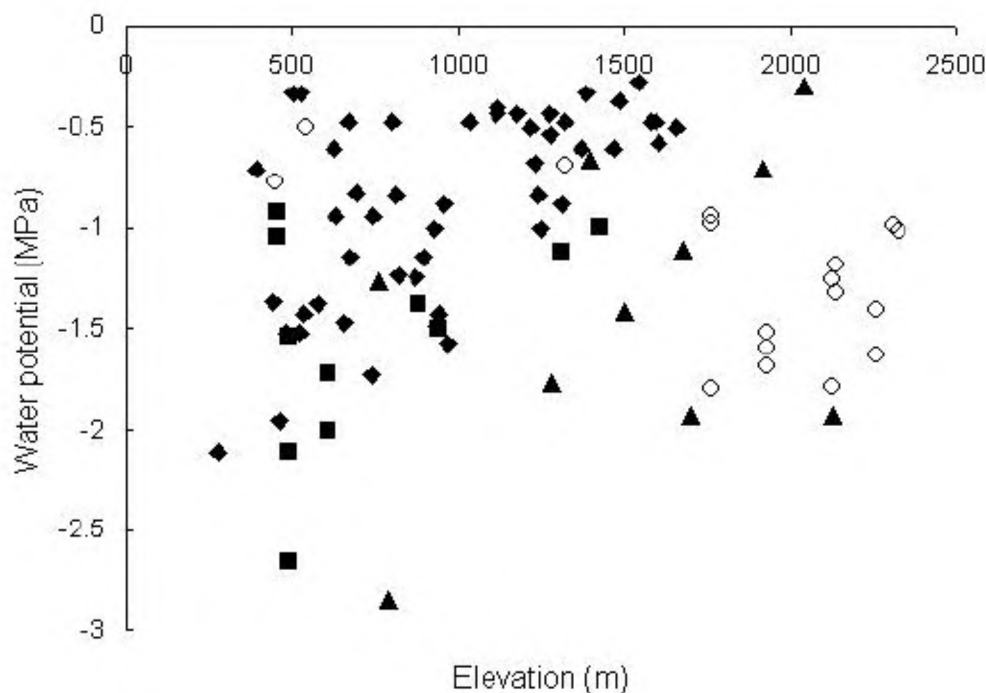*In spring, the only significant difference between types is that mixed < oak.

Figure 2. Relationship between extreme low predawn plant ψ and elevation for data from this study and for measurements made at three locations[9-11] in western Oregon, USA (O), Data from this study, (▲) from Waring and Cleary[9], from Minore[10] (◆), and (■) from Zobel et al.[11]

whereas Himalayan trees were all larger. In both regions, ψ during drought becomes more extreme as tree size declines[9,12]. The fall predawn ψ in the Himalaya would be 0.4–1.3 MPa lower if 1–2 m tall trees had been used, based on samples of two oaks at one site[12]. Thus, at higher elevations, drought appears to affect our sampled trees to an equivalent or greater degree as in the summer-dry situation in conifer forests of western Oregon. At lower elevations, however, the Oregon forests would have had more severe ψ even if 1–2 m tall trees had been sampled in our study.

Low elevation forests of sal and pine with sal at or below 1320 m, did not suffer low plant ψ (Figure 1), despite several circumstances that might have caused

them: a longer and more severe dry season at low elevations[3], midday temperatures of 40–42°C during summer sampling, and occasional dry soil. At high elevations, ψ in some sites was as high as for the sal type, but in some situations all the higher elevation types reached lower potentials than forests including sal. The gradient of decreasing ψ with increasing elevation in the Himalaya is opposite that described for other forest gradients. In those areas, the lower elevational limit of forest appears to be set by drought[13]. In the western coastal United States, for example, where drought coincides with the warm season, the lowest elevation forests exhibit the lowest ψ (Figure 2). Higher elevation forest types are differentiated by temperature, but not by their

Table 4. Frequency by season for midday plant ψ for different ranges of values (MPa). Each value is the mean for one species at one site on one sampling date

Species	> – 1.5	–1.5–2	–2–2.5	–2.5–3	< –3
Fall	72	11	1	0	0
Winter	56	29	4	1	0
Spring	56	15	5	2	0
Early summer	41	23	14	0	0
Summer	23	18	12	8	2
Rainy	39	0	0	0	0

growing season ψ and even small trees in higher elevation communities may show little evidence of moisture stress. Three studies[9–11] in western Oregon, USA illustrate this difference (Figure 2): extreme predawn ψ is positively and significantly correlated with elevation for the combined Oregon data set ($r^2 = 0.128$, $n = 70$, $P = 0.0014$), whereas our extreme Himalayan predawn ψ values are negatively and significantly correlated with elevation ($r^2 = 0.437$, $n = 16$, $P = 0.0053$). Similar to our situation, ψ in evergreen Mediterranean oak forest declined from 400 to 1145 m elevation, although the decline exceeded 0.7 MPa only in winter[14]. The reversed gradient in the Himalaya may result from several factors: (1) The sal forests we measured are still far up a rainfall gradient from any climatically-determined ecotone to non-forest vegetation[15]. (2) There is ample subsurface water movement down the lower slopes of the study area, which outcrops in the terai marshlands south of our study area, paralleling the base of the Himalaya[15]. (3) Sal trees are deeply rooted[15] (S. P. Singh and D. B. Zobel, unpublished data). (4) Other forest types, not yet studied by ecologists, may occupy the drier sites of the lower slopes in the study area. These forests, distributed amongst the sal types we measured on the mountain slopes, include drought-deciduous, tropically-derived taxa among the dominant trees.

The difference between predawn and midday plant ψ(Δψ) varied significantly among forest types, considering all seasons and in fall and early summer. Δψ was high in cypress and oak types, and low in sal and mixed types. It was least in the rainy season (0.16 MPa), and greatest in early summer and summer (0.70 MPa in both). Δψ did not vary significantly with elevation in any season or overall. Similarly to predawn and midday ψ values, Δψ differed significantly between summers with dry and wet soil, but not between the contrasting winter seasons.

Predawn plant ψ was positively and significantly correlated with soil ψ. Correlation was strongest during the rainy season ($r^2 = 0.55$) and significant in all other seasons, except spring. Despite this correlation, plant ψ varied in patterns different from those of soil ψ. Contrasts in soil ψ between wet and dry summers and winters were large and significant. Although predawn plant

ψ differed similarly between summers (albeit less) as did soil, predawn plant ψ did not differ between winters, despite a difference in mean soil ψ of > 1.2 MPa. In contrast, midday plant ψ differed between years only in winter. The decline in plant ψ with elevation occurred despite no significant gradient in soil moisture. Plant predawn ψ was higher (i.e. moister) than that of soil over all seasons for both years and in all individual seasons except fall of both years (plant was ψ no different from soil) and in winter and spring of 1994–1995 (plants drier than soil). Among 96 site × season combinations, 43 showed predawn plant ψ moister than soil; 11 combinations had plants drier than soil; and the remaining 42 showed no significant difference between plant and soil. Of the 11 situations in which plant predawn ψ was drier than soil, six were during the rainy season. Tree species that we measured produce 58–99 % of their fine roots in the top 60 cm of soil (S. P. Singh and G. C. Pathak, unpublished data), but apparently come into ψ equilibrium with moister soil layers than we measured on most sites, especially during the drier seasons.

These results represent the collective behaviour of the most important tree species in the most important forest communities along a 1900 m gradient, from tropical to cool-temperate forests. The patterns of ψ that we report suggest that water availability exerts substantial control over Himalayan forest distribution and composition. Rikhari et al.[16] reported a similar conclusion based on measurements of soil moisture in oak forests in the same area.

Even in its broad scope, as presented here, some aspects of water availability in the central Himalaya occur in patterns contrary to those reported from other forest regions. As for other characteristics of central Himalayan trees and forest ecosystems[4,5], these forests are distinctive in important aspects of their water relations. They cannot be accurately represented or understood only by reference to forests studied elsewhere.

To summarize, our data confirm the hypotheses of Zobel and Singh[2] that Himalayan trees suffer significant water stress and that forest types differ in their degree of water stress; the pattern of plant ψ among types, however, differed from that proposed. Low elevation sal and pine forests retained high water potentials the year round, whereas trees in some high elevation types became significantly dry in both summer and winter. Also, soil ψ at 60-cm depth could not be used to predict patterns of plant ψ.

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A highly mosquitocidal *Bacillus thuringiensis* var. *thompsoni*

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A strain of *Bacillus thuringiensis* isolated from a soil sample in Pondicherry was examined for its flagellar antigenicity, mosquito larvicidal activity and protein composition. This strain was found to agglutinate with the antisera belonging to *B. t. thompsoni* and exhibit high toxicity towards the larvae of the species of *Culex quinquefasciatus*, *C. tritaeniorhynchus*, *C. sitiens*, *Anopheles stephensi* and *Aedes aegypti*, respectively. The 28 kDa protein which has been reported to be predominantly present in the mosquitocidal strains of *B. thuringiensis* was found to be present in a higher amount in this strain. Also, the mosquito larvicidal activity and electrophoretic profile were comparable to that of a strain of *B. t.* var. *israelensis* which is known to be highly toxic to mosquitoes.

THE use of bacterial agents for mosquito control, especially *Bacillus thuringiensis* var. *israelensis* (*Bti*) is gaining widespread importance[1–4]. Among various species of *B. thuringiensis*, serotypes *B. t. israelensis*[5], *B. t. darmstadensis*[6], *B. t. kyushuensis*[7], *B. t. morrisoni*[8], *B. t. fukuokaensis*[9], *B. t. medellin*[10], *B. t. canadensis*, *B. t. shandongiensis*[11], *B. t. amagiensis*[12], *B. t. jegathesan*[13] and *B. t. higo*[14] are reported to be toxic to mosquitoes. However, among all these varieties, *Bti* holds its place as the highly toxic mosquitocidal serotype. At the Vector Control Research Centre, Pondicherry a survey for the isolation of mosquito larvicidal bacterial agents was undertaken and during this

programme several strains of *B. thuringiensis* were isolated from various sources, i.e. soil, water, larvae and roots of aquatic weeds representing diverse habitats. Among these, one strain of *B. thuringiensis* belonging to the serotype *B. t. thompsoni* (H-12) was found to be highly toxic to different species of mosquitoes.

This strain (VCRC Accession No. B175) was isolated from a soil sample collected near Pondicherry[15]. Water dispersible powder (WDP) was prepared from spore-crystal complex (SCC) of this strain and mosquito larvicidal activity determined as described by Manonmani *et al.*[15]. For comparison, a strain of *Bti* (VCRC Accession No. B17) was included in all the studies. The *B. t. thompsoni* strain was found to be toxic to 5 species of mosquitoes tested, namely *Culex quinquefasciatus*, *C. tritaeniorhynchus*, *C. sitiens*, *Anopheles stephensi* and *Aedes aegypti* and the LC_{50} values of this strain for these mosquito species were 250, 220, 300, 790 and 600 ng/ml, respectively. The corresponding values for *Bti* strain were almost similar to those of *B. t. thompsoni*. As per this, the relative susceptibility of the different mosquito species to the two *B. thuringiensis* strains, can be arranged as *C. tritaeniorhynchus* < *C. quinquefasciatus* < *C. sitiens* < *A. aegypti* < *A. stephensi*. Thus, the LC_{50} values were lower for culicines than for anophelines (Table 1). This is in agreement with the findings of several other workers[16–19].

The protein profiles of the SCC of the two subspecies of *B. thuringiensis* were compared. Proteins were extracted as per the procedure of Yamamoto *et al.*[20] and SDS electrophoresed on 10% polyacrylamide gel[21]. The proteins of both strains were found to resolve into 9 bands (Figure 1). However, 6 were present in major amounts in *Bti* (MW: 12, 24, 28, 40, 53 and 65 kDa), whereas only 4 were seen in *B. t. thompsoni* (MW: 12, 24, 28 and 40 kDa).

Although solubilization of the crystalline parasporal inclusions from final whole culture of the 2 strains gave a complex profile of proteins, a 28 kDa protein reported

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