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Photosynthetic Pigments on Plant Bearing Surfaces in the Himalayas*

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Abstract

The concentration of chlorophyll ($a + b$) and total carotenoids and their amount on unit area basis were assessed for different plant groups and plant-bearing surfaces in the Himalayas within an altitudinal range of 1500—2050 m during the wet season of the year. The concentration of pigments increased in the order: gymnospermic trees < angiospermic trees < shrubs < lower plants < herbs. The concentration in different strata of the forests was inversely related with relative illuminance. Such special habitats as rocks with deep soil in crevices, tree-trunks with epiphytic vegetation, and grasslands, could develop as much chlorophyll (chl) per unit area as did the croplands. There was a considerable amount of variation in the vertical distribution pattern of chl among the different forest types investigated. The overall percent contribution by epiphytic flora to chl amount in several forest types was greater than or equal to the combined contribution of herb and shrub layers. The role of these special plant covers in the overall carbon cycle is unknown. One has only to imagine the vastness of the surface area covered by epiphytic flora in the Himalayas in order to appreciate their significance.

The Himalayan chain of mountains is characterized by a thoroughly dissected topography involving high ridges and deep valleys, with an immense yet unestimated, exposed surface area. A large proportion of this surface harbours perennial plant cover, while rather extensive areas are represented by barrenlooking exposed rocks. During the rainy season, each year from the middle of June to September, all these surfaces acquire an intense green colour because of rapid development of ephemeral plant cover. Such an extensive plant-bearing surface will undoubtedly have tremendous effect on the continental carbon cycle due to photosynthetic assimilation of CO_2. The pigment content of the biological communities has often been used as an index of potential dry matter production (Bray 1960, 1962, Brougham 1960, Lieth 1961, 1962, 1965, Whittaker and Garfine 1962, Aruga and Monsi 1963, Medina and Lieth 1963, 1964, Lieth *et al.* 1965, Šesták 1966, Newbould 1967, Ovington and Lawrence 1967, Sanger 1971).

In the present study an attempt has been made to assess the pigment (total chlorophylls and total carotenoids) concentration and amount in different plant groups and landscape units (such as forest, grassland, cropland, exposed rocks and walls, and tree-trunk surfaces) during the wet season between the altitudes of 1500—2050 m in Western Himalaya. In addition, the areal plant biomass of different landscape units was also estimated.

MATERIAL AND METHODS

The study has been carried out at Naini Tal (29° 24′ N lat. and 79° 28′ E long.) and environs, involving the following vegetation types: a *Quercus leucotrichophora* (= *Q. incana*) forest, a *Quercus floribunda* (= *Q. dilatata*) forest, a *Cupressus torulosa* forest, a *Pinus roxburghii* forest,

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Abbreviations: car — total carotenoids; chl — chlorophyll ($a + b$).

a mixed forest, grassland, cropland, and herbaceous cover on exposed rocks, walls and tree-trunks. The climate is warm temperate being influenced by monsoon conditions and the year is divisible into three distinct seasons, *viz.*, rainy (middle of June-September), winter (October-February) and summer (March-middle of June).

The soil is residual, originating from krol limestone (dolomite lime, bluish in colour, bedded and wall-jointed). On gentle slopes the soil is fairly deep.

For the determination of chlorophyll $(a + b)$ and carotenoids, fully expanded leaves were sampled from different heights of the tree and shrub canopies, by species, whereas for herbs and lower plants composite samples were taken to represent the photosynthetic part of the communities. Each sample (in the case of trees and shrubs from at least 4—5 individuals of each species and at three different heights, *i.e.* lowest, middle and top parts of canopies, and in the case of herbaceous and lower plant communities at least from 4—5 locations), was chopped into small pieces and thoroughly mixed. From each of these samples, six replicates (100 mg each) were drawn; three for the determination of % dry matter by drying the preweighed material to a constant value in an oven at 80 °C and the others for pigment determination. Measurements of absorbance were made on a *Spectronic-20* photometer. Chlorophyll $(a + b)$ concentration (chl) was estimated following Arnon (1949) and the total carotenoids (car) concentration following Duxbury and Yentsch (1956).

Since the pigment estimations through a *Spectronic-20* are not considered to be as precise as those through a high grade spectrophotometer, the data obtained were calibrated by using a *Beckman DK-2* spectrophotometer. For this purpose the absorbance of acetone extracts for six species was read in both the spectrophotometers. Separate calculations for total chlorophyll $(a + b)$ and total carotenoids were then made. The chl content obtained through *Spectronic-20* was positively related ($r = 0.998$, $p = <0.001$) with that obtained through the *Beckman DK-2* spectrophotometer according to the following regression:

$$Y = 0.415 + 0.863\,X$$

where Y = chl [g kg^{-1}] obtained by the *Beckman DK-2* spectrophotometer, and X = chl [g kg^{-1}] obtained through the *Spectronic-20*.

The car content measured through the *Spectronic-20* was also positively related ($r = 0.862$, $p = <0.005$) to that obtained through the *Beckman DK-2* spectrophotometer according to the regression:

$$Y = 0.781 + 0.880\,X$$

where Y = car content [g kg^{-1}] obtained through the *Beckman DK-2* spectrophotometer and X = car content [g kg^{-1}] obtained through the *Spectronic-20*. The above regression equations were used to convert the *Spectronic-20* values to *Beckman DK-2* spectrophotometer values in all cases.

The total amount of chl per unit land area was computed by multiplying the chl content per unit dry matter of a component with its total dry matter. The biomass for shrubs, herbs and lower plants was estimated by the harvest method using quadrats of different sizes: 10 × 10 cm for trunk surfaces, 50 × 50 cm for walls, rocks, grassland and cropland, 2 × 2 m for shrubs. At least five quadrats were used for each sampling location. The tree biomass and the foliage biomass were estimated by allometry (Whittaker and Woodwell 1968) using the generalised regression equations developed by Sharma (1977) and Negi (1979). Relative illuminance was measured by a *Metrax* luxmeter.

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RESULTS AND DISCUSSION

The chl $(a + b)$ and total car concentrations have been averaged for each life-form (Table 1).

The lower plants occurred on tree trunks, walls, rocks, forest floor and grassland, and consisted of ferns, liverworts and mosses, and *Selaginella*. The concentrations of chl and car were greater in ferns compared to liverworts and mosses. *Selaginella* had exceptionally high values for chl and car.

The chl concentration in herbs was in the range 5.77—6.02 g kg^{-1} (dry matt.) in *Quercus leucotrichophora*, *Quercus floribunda*, *Cupressus torulosa*, and mixed forests. These values approach the chl concentration of 6.21 g kg^{-1} in herbs occurring on shady walls. The herb layer in the *Pinus roxburghii* forest contained 4.40 g kg^{-1} total chl, and the grassland vegetation 4.14 g kg^{-1}. Herbs on exposed rocks with deep and shallow soils had chl concentration of 3.75 g kg^{-1} and 2.82 g kg^{-1}, respectively. These values match the chl concentration of 3.53 g kg^{-1} for herbs on exposed walls (Table 2). Based on the above data, the herb layer can be categorised into: (*a*) herbs growing in shady places such as under dense forest canopies and on shady walls, with highest chl concentration, 5.77—6.21 g kg^{-1}, (*b*) herbs growing on partially shady surfaces such as under the *P. roxburghii* forest with an intermediate concentration, 4.40 g kg^{-1}, and (*c*) herbs exposed to sunlight as in grassland and on exposed rocks exhibiting the minimum values, 2.82 to 4.14 g kg^{-1}.

The herbs had car concentration in the range 1.61—2.88 g kg^{-1} with an overall average of 1.94 g kg^{-1}. The concentration of chl and car in different parts of the crop plants, and in composite samples are listed in Table 3. The composite values for crops and weeds were higher compared to the foliage values for shrubs and trees and were in the range of 5.62 to 7.15 g kg^{-1}. The high chl concentration in crop plants may be related with their enhanced capacity of growth due to rapid photosynthesis (Loomis and Gerakis 1975). The average value for car in the crops was 2.10 g kg^{-1} which was also higher compared to other plant types.

Table 1
Average pigment concentration [g kg^{-1} (dry matt.)] in different plant groups.

Life forms	Chlorophyll $(a + b)$	Variability* [%]	Total carotenoids	Variability* [%]
Lower plants				
Mosses	3.42	22.95	1.75	107.4
Ferns	4.70	80.52	1.88	132.88
Selaginella	9.92	—	2.94	—
Average	6.00	51.74	2.19	120.14
Higher plants				
Herbs	4.82	140.50	1.94	153.19
Crops	6.02	19.57	1.96	4.44
Weeds	7.10	1.56	2.37	9.25
Average	5.98	50.54	2.09	55.63
Shrubs	4.07	15.20	1.78	11.86
Angiospermic trees	3.68	67.53	1.63	29.73
Gymnospermic trees	3.15	39.05	1.39	77.50
Average for all trees	3.46	53.29	1.56	53.62

* Difference between the lowest and highest values of pigment concentration as % of the lowest value calculated for each species separately and then averaged for the group.

Table 2

Pigment concentration in herbs occurring in habitats with differential irradiance.

Herbs in different habitats	Chlorophyll $(a + b)$	Total carotenoids
	[g kg^{-1}(dry matt.) ± 1 SE]	
Exposed herbs		
Rocks		
Deep soil in crevices	3.75 ± 0.09	1.89 ± 0.10
Shallow soil	2.82 ± 0.07	1.62 ± 0.05
Walls	3.53 ± 0.03	1.70 ± 0.03
Grassland	4.14 ± 0.12	1.61 ± 0.18
Partially exposed herbs		
P. roxburghii forest	4.40 ± 0.09	1.68 ± 0.10
Herbs under shade		
Q. leucotrichophora forest	6.02 ± 0.08	1.89 ± 0.07
Q. floribunda forest	5.83 ± 0.03	1.78 ± 0.04
C. torulosa forest	5.77 ± 0.10	2.54 ± 0.06
Mixed forest	5.71 ± 0.04	1.85 ± 0.09
Herbs on shady and moist walls	6.21 ± 0.27	2.88 ± 0.07

Table 3

Pigment concentration in different components of crop fields.

Crop and weeds	Total chlorophyll $(a + b)$	Total carotenoids
	[g kg^{-1}(dry matt.) ± 1 SE]	
Raphanus sativa field		
Raphanus sativa (composite)	6.64 ± 0.12	1.97 ± 0.07
Weeds (composite)	7.05 ± 0.06	2.30 ± 0.01
Phaseolus mungo field		
Leaf	6.27 ± 0.18	1.98 ± 0.09
Stem	1.95 ± 0.10	1.05 ± 0.04
Composite	5.77 ± 0.07	1.91 ± 0.06
Zea maize field		
Leaf	5.64 ± 0.19	1.94 ± 0.08
Stem	0.78 ± 0.05	0.89 ± 0.03
Fruit coat	1.21 ± 0.03	1.00 ± 0.07
Composite	5.62 ± 0.05	2.02 ± 0.09
Weeds (composite)	7.16 ± 0.28	2.44 ± 0.09

The ferns growing on exposed rocks, and on tree-trunks and branches, exhibited slightly lower pigment concentration compared to herbs growing on the forest floor. On an average, however, the chl concentration of ephemeral vegetation (including herbs, ferns, liverworts, *etc.*) developed on exposed rocks, walls and tree-trunks was comparable with the overall average for herbs (Table 1). Grassland vegetation which was exposed to the sun had lower pigment concentration compared to herbs which grew under shade.

A total of 18 shrub species occurred in various vegetation types. The data revealed a 4-fold difference between the highest and the lowest values of chl concentration in the shrub foliage. Several of the shrubs were common to more than one habitat, among these the highest concentration values were: for *Indigofera gerardiana* 6.23 g kg^{-1} in the mixed forest, for *Boenninghausenia albiflora* 4.96 g kg^{-1} in the *C. torulosa* forest, for *Sarcococca pruniformis* 4.05 g kg^{-1} in the grassland, and the lowest values were: for *Pyrenacantha crenulata* 1.84 g kg^{-1} in the *C. torulosa* forest, for *Leptodermis lanceolata* 3.14 g kg^{-1} in the *P. roxburghii* forest, for *Berberis asiatica* 3.21 g kg^{-1} in the mixed forest, and for *Wikstromia canescens* 3.36 g kg^{-1} in the *Q. floribunda* forest. The average chl concentration for all the shrubs across all habitats was 4.07 g kg^{-1}. The car concentration for shrub species was higher compared to trees and ranged from 1.41 (*Strobilanthes dalhousianus*) to 2.64 g kg^{-1} (*Viburnum cotinifolium*) with an average of 1.92 g kg^{-1}.

Total number of angiospermic tree species investigated was 14 and that of gymnospermic trees was 10. Among the angiospermic species the highest chl concentration was about four times more than the lowest value, whereas gymnospermic species showed a 3-fold difference between the highest and the lowest values. Among the angiospermic tree species which grew in more than one forest type, the highest chl concentrations were: *Cornus oblonga* 5.55 g kg^{-1} in the *Q. leucotrichophora* forest, *Ilex odorata* 5.28 g kg^{-1} in mixed forests, *Quercus floribunda* 2.92 g kg^{-1} in the *C. torulosa* forest, *Rhododendron arboreum* 2.54 g kg^{-1} in the *P. roxburghii* forest, and the lowest values were: *Acer oblongum* 1.68 mg g^{-1} in *Quercus leucotrichophora* forest, *Q. floribunda* 2.64 mg g^{-1} in *Q. floribunda* forest, and *Lyonia ovalifolia* 2.47 mg g^{-1} in mixed forest. Among the gymnospermic trees which occurred in more than one forest type, the highest values for chlorophyll concentration were: *Picea smithiana* 5.19 mg g^{-1} in mixed forest, *Cedrus deodora* 3.13 mg g^{-1} in *Cupressus torulosa* forest, *Pinus roxburghii* 1.93 mg g^{-1} in *Q. leucotrichophora* forest, and the lowest values occurred in: *Pinus roxburghii* 1.89 mg g^{-1} in mixed forest, and *Cupressus torulosa* 2.41 mg g^{-1} in *Q. floribunda* forest. The average total chlorophyll content for all the angiospermic and gymnospermic tree species was 3.68 and 3.15 mg g^{-1}, respectively, and the average for all the tree species was 3.46 mg g^{-1}.

The total carotenoid concentration in angiospermic and gymnospermic trees ranged from 1.26 (*Ilex dipyrena*) to 2.07 (*Cornus oblonga*) and from 1.14 (*Pinus roxburghii*) to 1.81 mg g^{-1} (*Picea smithiana*), respectively. Thus, the angiospermic trees and higher carotenoid content as compared to gymnospermic trees. The average values for carotenoid in angiospermic and gymnospermic trees were 1.63 and 1.39 mg g^{-1}, respectively, and the overall average for all the trees was 1.56 mg g^{-1}.

Thus, the concentration of chlorophyll and carotenoid increased in the order: gymnospermic trees < angiospermic trees < shrubs < lower plants < herbs. The pigment concentration was greatest in crop plants and agricultural weeds. Florov (1977) reported more Chl in *Aegopodium podagraria* occurring in deep shade under forest-steppe oakwood compared to the plants growing in moderately shaded habitat or in clearings. Similar observations were reported by Masarovičová and Eliáš (1980). Eliáš and Masarovičová (1980) found lower Chl content in sun leaves of tall trees which formed a canopy surface in an oak-hornbeam forest compared to the leaves of shrub-sized individuals or those from middle or lower crown region.

In the present study, the concentration of total chlorophyll in herbs was in the range 2.82 to 7.16 mg g^{-1}. This compares with the range 1.17 to 10.33 mg g^{-1} reported by Billore and Mall (1976) for grassland species near Ratlam, India, 3.80 mg g^{-1} reported by Singh and Billore (1975) for *Andropogon* community in Ujjain, India, and 2.56 mg g^{-1} for herbs in the open prairie, 2.92 mg g^{-1} for herbs in partial shady savanna, 5.53 mg g^{-1} for herbs under dense oak canopies as reported by Ovington and Lawrence (1967). The chlorophyll concentration of 8.50 mg g^{-1} reported by Ovington and Lawrence (1967) for maize crop was higher as compared to the present value of 5.62 mg g^{-1} for the same crop. The chlorophyll concentration for different tree species studied was in the range 1.83 to 5.55 mg g^{-1}. This range compares favourably with the range of chlorophyll concentration in foliage of other temperate and tropical forest ecosystems (Table 4).

The difference in lowest and highest pigment concentration as percent of lowest value for different plant groups is given in Table 1. Among the lower plants, the maximum variability for total chlorophyll and carotenoid was observed in ferns. In higher plants the variability in pigment concentration followed the order: herbs > angiospermic trees > gymnospermic trees > crop plants > shrubs > weeds. The greatest variability in the herbaceous plant cover is perhaps on account of differential shade levels.

The pigment concentrations in different layers of plant cover in various forests together with relative illumination are compared in Table 5. The pigment concentration in various strata was inversely related with light intensity. This finding is in accordance with the studies of Rabinowitch (1945), Odum *et al.* (1959), Whittaker and Garfine (1962) and Ovington and Lawrence (1967). An analysis of vertical distribution of Chl concentration in an oak-hornbeam forest revealed the following sequence: herbaceous layer, shrub layer and tree layer (Masarovičová and Eliáš 1981). Evidently, the shaded plants increase their pigment concentration to compensate for reduced illuminance.

Special habitats such as rocks with deep soil in crevices, tree-trunks with epiphytic vegetation, and grasslands, develop as much chl per unit area as the croplands (Table 6). Even the walls constructed as toe support for roads on hill sides develop a significant amount of pigments in their plant cover. The role of these plant covers in the overall productivity or CO_2 cycle has not yet been assessed. Ferns emerge as a very important component of the vegetation on tree-trunks and on the floors of *Q. leucotrichophora* and mixed forests in terms of chl content. Similarly, the contribution of the herb layer to the total photosynthetic pigments of the forest is remarkably high.

Table 4

Comparison of foliar chlorophyll content in trees from different regions.

Region	Total chlorophyll [g kg^{-1}(dry matt.)]	Author(s)
Temperate		
Central Minnesota, U.S.A.	1.70—8.70	Bray (1960)
Tennessee/North Carolina, U.S.A.	1.80—5.00	Whittaker and Garfine ((1962)
Minnesota, U.S.A.	4.60—9.80	Sanger (1971)
Naini Tal, India	1.83—5.24	Present study
Tropical		
El-Verde, Puerto Rico	1.40—2.80	Odum *et al.* (1970)
Varanasi, India	1.20—4.30	Gopal and Bandhu (1972)
Ujjain, India	0.77—5.12	Billore *et al.* (1976)
Varanasi, India	1.10—8.40	Singh and Singh (1977)

Table 5

Chlorophyll ($a + b$) concentrations and relative illuminance in different layers in various forests.

Life-forms	*Q. leucotrichophora* forest		*Q. floribunda* forest		Mixed forest		*P. roxburghii* forest		*C. torulosa* forest	
	Illuminance [% of sun light]	Chl [g kg^{-1}]	Illuminance [% of sun light]	Chl [g kg^{-1}]	Illuminance [% of sun light]	Chl [g kg^{-1}]	Illuminance [% of sun light]	Chl [g kg^{-1}]	Illuminance [% of sun light]	Chl [g kg^{-1}]
Ferns	7.39	5.04	7.38	6.31	7.28	6.36	—	—	2.57	6.27
Herbs	7.39	6.02	7.38	5.83	7.28	5.71	13.47	4.40	2.57	5.77
Shrubs	7.95	4.36	7.65	4.60	7.50	4.38	22.90	3.70	3.52	4.05
Angiospermic trees	55.68*	3.11	54.81*	3.51	55.87*	3.75	62.90*	2.41	52.38*	2.91
Gymnospermic trees	55.68*	1.93	54.81*	2.73	55.87*	3.31	62.90*	1.87	52.38*	2.73

* Average of upper and lower parts of canopies.

Table 6

Total above-ground plant biomass and standing crop of chlorophyll (chl) in different vegetation types.

Vegetation type	Lower plants: Mosses Biomass [g m^{-2}]	Mosses Chl [mg m^{-2}]	Ferns Biomass [g m^{-2}]	Ferns Chl [mg m^{-2}]	*Selaginella* Biomass [g m^{-2}]	*Selaginella* Chl [mg m^{-2}]	Higher plants: Herbs Biomass [g m^{-2}]	Herbs Chl [mg m^{-2}]	Shrubs Biomass [g m^{-2}]	Shrubs Chl [mg m^{-2}]	Trees Biomass [g m^{-2}]	Trees Chl [mg m^{-2}]	Total Biomass [g m^{-2}]	Total Chl [mg m^{-2}]
Rocks with deep soil in crevices	3.0	9.91	7.0	31.48			540.0	1829.98					550.0	1870.54
Walls	14.0	42.70	13.0	32.35	7.0	103.11	16.0	112.61					50.0	289.52
Tree trunks	88.0	224.32	137.0	630.41									265.0	854.79
Grassland	10.0	34.07	9.0	30.62			262.0	958.35	245.0	169.13			526.0	1167.62
Croplands														
R. sativa field													67.0	443.13
P. mungo field													90.0	397.40
Z. maize field													528.0	847.02
Forest type														
Q. leucotrichophora forest			88.0	406.03			93.0	490.33	75.3	67.12	100226.6	8052.21	100482.3	9042.32
Q. floribunda forest			12.0	71.18			44.0	223.43	71.2	66.00	86873.4	10071.63	87000.6	10440.99
Mixed forest			79.0	470.15			160.0	837.53	76.8	72.30	61183.8	10201.08	61499.6	11579.80
C. torulosa forest			8.0	47.29			212.0	1113.69	171.3	131.94	41980.9	4824.59	42372.3	6116.25
P. roxburghii forest							172.0	664.93	62.4	62.64	46985.9	4073.78	47220.3	4800.51

In the mixed forest the herb layer contributes 1/8 as much as the tree foliage, about 1/6 as much as tree foliage in the *P. roxburghii* forest and about 1/4 as much as tree foliage in the *C. torulosa* forest. Notwithstanding the amount of pigments, the biomass of herbs and ferns is almost negligible compared to that of the tree layer in these forests.

The standing crop of chl for the herbs was in the range 112.61 to 1829.98 mg m^{-2} on various plant-bearing surfaces. This compares with the range of 300 to 1000 mg m^{-2} reported by Bray (1960) for plant communities in Central Minnesota, USA, and of 400 to 1000 mg m^{-2} reported by Bliss (1966) for seven alpine communities. The chl contents reported for maize crop field by Ovington and Lawrence (1967) (1075.7 mg m^{-2}), and by Mall *et al.* (1974) (1950 mg m^{-2}) were higher than the present value for the same crop in the Himalayas.

The shrub layer in different forests and in the grassland accounted for 62.64 to 169.13 mg m^{-2} chl. In terms of chl, *Indigofera gerardiana* emerged as the dominant shrub in the mixed forest (23.03 mg m^{-2}), the *P. roxburghii* forest (41.58 mg m^{-2}) and the *Q. floribunda* forest (27.86 mg . m^{-2}) (Fig. 1). Likewise, *Aechmanthera tomentosa* was the dominant shrub in the grassland (70.15 mg m^{-2}), *Daphne cannabina* (19.49 mg m^{-2}) and *Leptodermis lanceolata* (20.26 mg m^{-2}) in the *Q. leucotrichophora* forest, and *Boenninghausenia albiflora* (60.31 mg m^{-2}) in the *C. torulosa* forest.

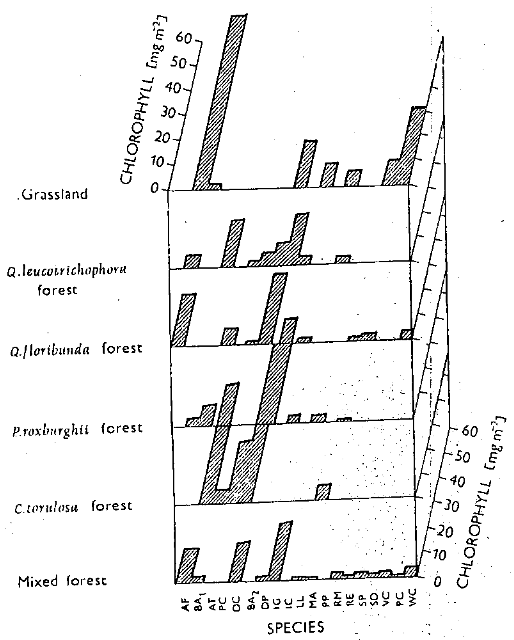

Fig. 1. Amounts of chlorophyll in different shrubs growing in various forests and grassland. Abbreviations: AF = *Arundinaria falcata* Nees, BA_1 = *Berberis asiatica* Roxb., AT = *Aechmenthera tomentosa* Nees., PC = *Pyrenacantha crenulata* (D. Don) Roem., DC = *Daphne cannabina* Sensu, BA_2 = *Boenninghausenia albiflora* Hook., DP = *Desmodium polycarpum* D. C., IG = *Indigofera gerardiana* Wall. ex. Baker, IC = *Inula cuspidata* Clarke, LL = *Leptodermis lanceolata* Wall., MA = *Myrsine africana* Linn., PP = *Pyrus pashia* Buch-Ham ex. D. Don., RM = *Rosa moschata* Miller, RE = *Rubus ellipticus* Smith, SP = *Sarcococca pruniformis* Lindl., SD = *Strobilanthes dalhousianus* Clarke, VC = *Viburnum cotinifolium* D. Don., PC = = *Parthenocissus semicordata* Wall. var Royal (Kind), Raizada and Saxena, WC = *Wikstromia canescens* Meissu.

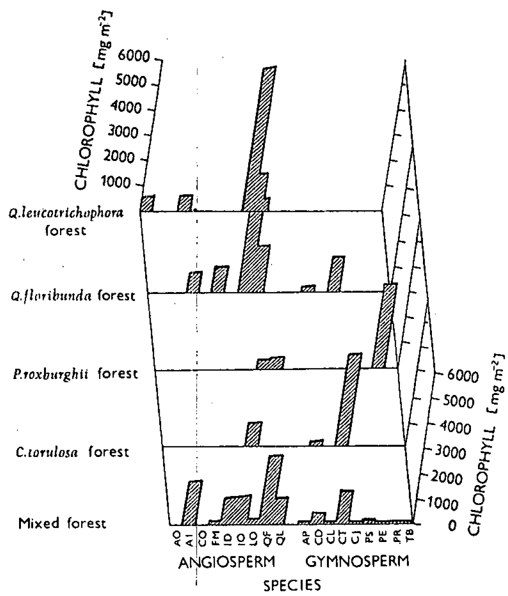

Fig. 2. Amounts of chlorophyll in different trees growing in various forests. Abbreviations: AO = *Acer oblongum* Wall. ex. D. D., AI = *Aesculus indica* Colebr., CO = *Cornus oblonga* Wall., FM = *Fraxinus micrantha* Lingelsh, ID = *Ilex dipyrena* Wall., IO = *Ilex odorata* Buch-Ham., LO = *Lyonia ovalifolia* Wall., QF = *Quercus floribunda* Lindl., QL = *Quercus leucotrichophora* A. Camus., AP = *Abies pindrow* Royle, CD = *Cedrus deodara* Roxb., CL = = *Cunninghamia lanceolata* Hook., CT = *Cupressus torulosa* D. Don., CJ = *Cryptomeria japonica* Linn., PS = *Picea smithiana* Wall., PE = *Pinus excelsa* Jackson, PR = *Pinus roxburghii* Sarg., TB = *Taxus baccata* Linn.

The tree foliage contributed from 4 to 10 g m^{-2} chlorophyll in various forests (Table 6). In all the forests the dominant biomass contributor accounted for most of the foliar chl (Fig. 2). In a mixed forest, however, there were several other species which contributed to total chl significantly. In all the five forest types the total amount of chl was in the order: the mixed forest 11.58 g m^{-2} > the *Q. floribunda* forest 10.44 g m^{-2} > the *Q. leucotrichophora* forest 9.04 g . . m^{-2} > the *C. torulosa* forest 6.11 g m^{-2} > the *P. roxburghii* forest 4.80 g m^{-2}, and the total above-ground biomass in these forest types was in the order: the *Q. leucotrichophora* forest 100 g m^{-2} > the *Q. floribunda* forest 87 g m^{-2} > the mixed forest 61 g m^{-2} > the *P. roxburghii* forest 47 g m^{-2} > the *C. torulosa* forest 42 g m^{-2} (Table 6). Thus the chl amount does not necessarily increase with an increase in total above-ground forest biomass.

The amounts of chl in different height strata for various forest types and for the grassland were calculated on the basis of foliage biomass and chl concentration (Fig. 3). The herb layer, the shrub layer and the forest layer chl contents were confined to 0–1, 0–2, and 5 m strata, respectively. A considerable amount of chl resides in the herb (including ferns) and shrub strata in all forests, with the maximum being in *Q. leucotrichophora* and *C. torulosa* forests and the minimum in the *Q. floribunda* forest. The height to which chl was projected vertically ranged in the order: *C. torulosa* forest > *Q. leucotrichophora* forest > *Q. floribunda* forest > mixed forest > *P. roxburghii forest* > grassland. Further, there was a considerable amount of variation in the vertical distribution pattern of chl among the different forest types (Fig. 3). On this basis, each forest seemed to constitute well-defined energy trapping layers.

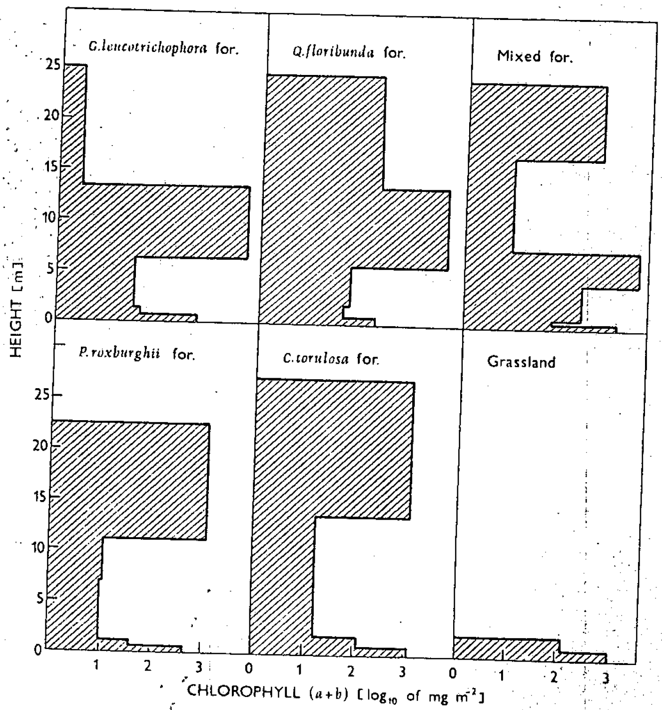

Fig. 3. Vertical distribution of total chlorophyll in different vegetation types.

The chl layering was maximum in the mixed forest (six) followed by *Q. leucotrichophora*, *Q. floribunda* and *P. roxburghii* (five) and lowest in the *C. torulosa* forest (four) (Fig. 3). In the coniferous forests (*C. torulosa* and *P. roxburghii*) the greatest amount of chl was found in the top part of the forest canopy. On the other hand, in the oak forests (*Q. leucotrichophora* and *Q. floribunda*) most of the chl was contained in the middle or lower middle parts of the canopy. In the mixed forest both the top as well as the lower part of the canopy were well developed as energy trapping layers. It would appear, therefore, that the broad-leaf canopies are more efficient energy trappers because of marked differentiation of layers. In such a multilayered canopy each quantum of incident light will have a greater chance of being trapped and utilized.

The amounts of chl for the different forests (Table 6, Fig. 3) were underestimated because the contribution of epiphytic flora was not considered. The amount of chl due to the epiphytic flora in a forest was calculated as follows: First the surface area of sample trees was determined from circumference readings by assuming the trunk and branches to be in cylindrical forms. Then the % area covered by epiphytic vegetation for different species was assessed. From the above two observations and from the data on chl content per unit area of epiphytic plant cover, total contribution of the epiphytic cover on the unit ground area basis was estimated for different forest types: the *Q. floribunda* forest, 2080.25 mg m^{-2}; the *Q. leucotrichophora* forest, 1755.07 mg m^{-2}; the *C. torulosa* forest, 1048.19 mg m^{-2}; mixed forests 685.72 mg m^{-2} and the *P. roxburghii* forest, 151.70 mg m^{-2}.

The percent of chl due to different life-forms, for an average forest (Fig. 4) was in the order: tree foliage (77.70%) > herbs (10.08%) > epiphytic ferns (8.32%) > epiphytic mosses (2.94%) > shrubs (0.96%). In the grassland (Fig. 4) herbs contributed 85.86% of the total amount of chl

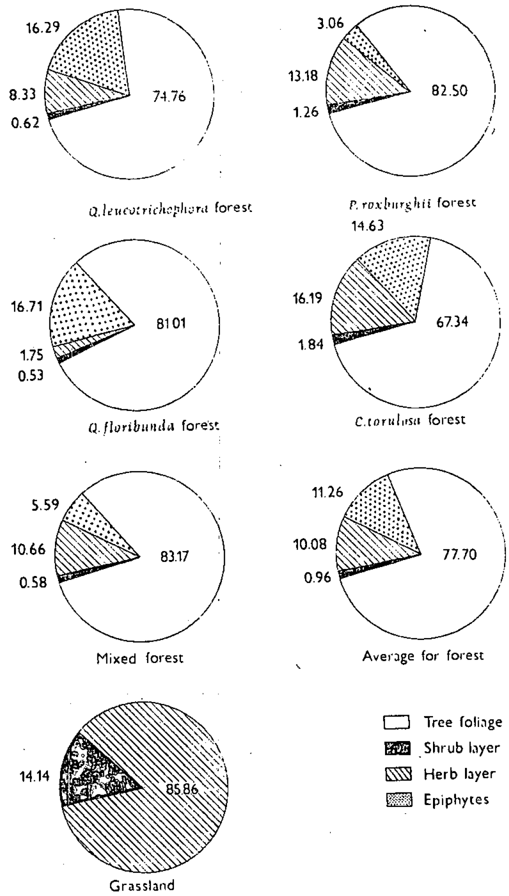

Fig. 4. Percent contribution to total amount of chlorophyll by herbs, shrubs, tree-foliage, and epiphytic flora in different vegetation types.

whereas shrubs contributed only 14.14%. The overall % contribution to chl amount by epiphytic flora was greater than or equal to the combined contribution of herb and shrub layers, except for *P. roxburghii* and mixed forests where the contribution by epiphytic vegetation was only 3.06 and 5.59%, respectively. This indicates that the epiphytes on tree trunks and branches may be playing a highly significant role in community functioning. For example, assuming a net photosynthetic rate of 0.56 g O_2 kg^{-1} (chl) s^{-1} (a medium ratio for stratified communities; Odum *et al.* (1958, 1970) and converting it to joules (Odum 1971) the primary productivity due to epiphytic plant cover in the *Quercus floribunda* forest would be 0.027 J m^{-2} s^{-1}. One has only to imagine the vastness of the surface area covered by such epiphytic flora in Himalayan forests in order to appreciate their significance. Unfortunately no attention has so far been paid to this plant cover.

The chl amount in the present forests ranged from 4.95—12.43 g m^{-2} which was nearly one and a half to four times higher than the value 3.14 g m^{-2} reported by Ovington and Lawrence (1967) for an oak forest at Minnesota, U.S.A., and 3.0 to 7.0 times higher than the value 1.87 g .

m^{-2} reported by Gopal and Bandhu (1972) (for trees and shrubs only) for a tropical forest at Varanasi, India. To sum up, the vast exposed surface area of the Himalayas becomes functionally a highly dynamic energy trapping system during the moist part of the year. The role of this active surface in terms of the carbon cycle remains unknown.

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