The Heterophylly of Hemiphragma heterophyllum, Wall.

BY

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With four figures in the text.

A NATIVE of the temperate Himalayas, *Hemiphragma heterophyllum* is a diffuse prostrate perennial herb, growing at altitudes between 4,000 and 12,000 feet.

From a slender horizontal creeping stem, which may reach a length of 60 cms., upright shoots are produced, and from the bases of the largest of these, bunches of roots arise. The leaves are markedly dimorphic, those arising directly on the larger upright shoots being flattened structures — the so-called " summer " leaves—whilst on the branches borne in their axils, and on the smaller offshoots of the main horizontal stem, there appear dense tufts of small inrolled acicular " winter " leaves.

The production of these two types of leaves takes place alternately at definite periods throughout the life of the plant, and would appear to be due to seasonal fluctuations in the climatic environment, each form of leaf being expressive of the external conditions at the time of its inception, and therefore not to be regarded as being either juvenile or adult in the strictly accepted sense of these terms. To support this view of the nature of the heterophylly in *Hemiphragma,* an examination of material collected in the neighbourhood of Darjeeling at different times of the year was made, the type of leaf on each particular specimen being specially noted in an endeavour to correlate leaf form with external conditions of temperature and rainfall. In this connection, " The Climates of the Continents "* was particularly helpful.

The first specimens, collected in the month of August, showed only the broad cauline summer leaves. This is the season of general monsoon rains, the heaviest rainfall and highest temperature for the year being recorded in July (Rainfall : 31.7 ins.; Temperature : 61.5° F). Plants collected in October still bore summer leaves, but in the axils of these, small shoots bearing winter leaves were beginning to appear. This is the season of the retreating monsoon, the rains have practically ceased, and the average rainfall for the month is as low as 5.3 ins., while the temperature has fallen to 55.2° F.

* W. G Kendrew, " The Climates of the Continents," 1922, pp. 190, 194.

[Notes, R.B.G., Edin. No. LXXI, June 1925.]

During the winter months the climate is cold and very dry, with a mean temperature of 44.2° F., and an average rainfall of .64 ins.; but in April, which marks the beginning of the hot-weather season, continuing till the breaking of the monsoon in mid-June, the rainfall has risen to 4.1 ins. and the temperature to 56.2° F. Plants collected in April still bore the remains of some summer leaves, but in their axils there were strong healthy shoots of winter leaves which had functioned during the cold dry months of the year. Towards the apices of some of these shoots, however, the narrow inrolled leaves were already being replaced by broader forms resembling in shape the summer leaves on the main stem.

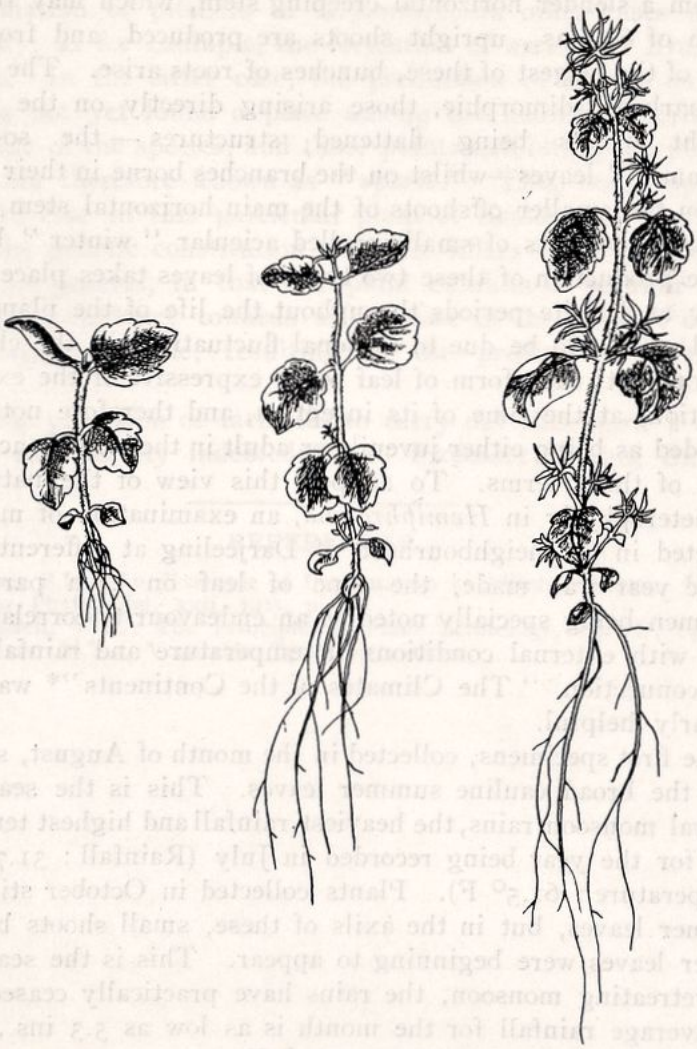

FIG. 1.—Seedling stages: 1, Seedling of Oct. 6th; 2, Seedling of Dec. 21st; 3, Seedling of Feb. 7th. Natural size.

Thus it would seem that variation in the foliage of *Hemi-*

phragma heterophyllum corresponds with the seasonal variations of the climate. During the season of the monsoon, from mid-June to mid-September, when moisture is plentiful, only the broad summer leaves are present, and the maximum amount of leaf-surface is exposed for the purpose of photosynthesis and transpiration. The monsoon rains cease in September and the summer leaves die off, while shoots with small setaceous leaves are produced, and these serve the plant during the dry winter months. The approach of the hot-weather season in April, and with it the first rains which herald the breaking of the monsoon in June, synchronises with the production again of summer leaves which appear at the apices of the winter twigs and on the tall vertical shoots which arise in summer from the horizontal creeping stem.

A similar variation in the form of the foliage is seen also in the seedlings of *Hemiphragma*. In Fig. 1 are shown three successive stages which have resulted from the germination of seeds out of August fruits. The first seedling was collected on October 5th, and at that time there were two pairs of summer leaves on the seedling stem. Germination had evidently taken place towards the end of the season of monsoon rains, and the leaves produced were similar to those of the adult plants of this period. The second seedling represents the stage reached on December 21st, and has summer leaves still predominating, but winter leaves are beginning to form at the apex and on the axillary shoots. This change in the foliage of the seedlings is similar to that which also takes place in the adult plants before the cold dry season in the early part of the year. On February 7th, the seedling had reached the stage shown in the third drawing, and the winter shoots by this time had reached their maximum development. Had a later stage in seedling growth been available it would in all probability have shown the winter leaves replaced by broader leaves towards the apices of the shoots, and a gradual transformation taking place in the appearance of the young plant prior to the wet months of mid-summer.

Thus in both adult and seedling conditions a regular alternation in the form of the foliage of the plant takes place. These variations in leaf form occur with such regularity as to lead one to suppose that the plant responds in this manner to the changing external conditions. During the rainy season, the broad summer leaves are present, then as the monsoon passes, shoots bearing inrolled winter leaves appear. The latter persist throughout the dry winter months and in the early summer are again replaced by the broad type of leaf. The broad leaves are obviously an adaptation to an environment in which mois-

ture is plentiful, while in winter their place is taken by the narrow acicular leaves which serve the plant through the dry season.

The summer leaves are shortly stalked and more or less ovate in shape, from 0.5–1.5 cms. in length, and from 0.25–1.25 cms. broad. The margin of the leaf is crenate, and there is a sparse coating of simple hairs on both surfaces. In transverse section (Fig. 2) the epidermis, both upper and lower, is seen to be covered with a fairly thick cuticle, while the long stout hairs, each consisting of two elongated cells on a broad base, appear at intervals in the sections. Short-stalked capitate glandular hairs are also present here and there on the epidermis. Stomata are entirely confined to the lower epidermis, and are not unduly prominent, while the mesophyll is differentiated into a rather poorly-developed palisade parenchyma above, and a loose spongy tissue below.

The structure of this leaf is such as might be found in any mesophyte where the leaves are exposed during their period of growth to conditions which afford sufficient moisture, and do not necessitate the development of any special mechanism to inhibit transpiration.

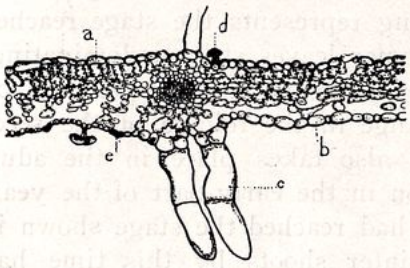

Fig 2.

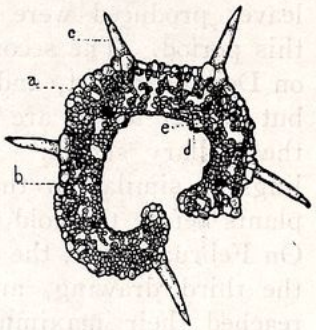

Fig. 3.

FIG. 2.—Transverse section of summer leaf: a. upper epidermis; b. lower epidermis; c, long hair; d, glandular hair; e, stoma. × 50.

FIG. 3.—Transverse section of winter leaf: a, upper epidermis; b, lower epidermis; c, hair; d, stoma; e, air-space behind stoma. × 50.

The acicular winter leaves vary from 0.3–1.0 cms. in length, and are about 1 mm. in breadth. They are rigid and acute, and have a convex lower surface due to the inrolling of the margins, while the upper exposed surface is covered with stiff simple hairs. A transverse section (Fig. 3) shows that the epidermis is again covered with a cuticle which is slightly thicker on the upper surface of the leaf. The cells of the upper epidermis are much larger than those of the lower epidermis, and only from the upper surface do hairs arise. These are stiff and sharp and usually consist of two cells. Stomata,

as in the summer leaf, are confined to the lower epidermis, but each stoma is here situated at the summit of a small eminence, and opens into a large sub-epidermal air-chamber. The general ericoid construction of the leaf is obviously an adaptation to prevent excessive loss of water, and contrasts strongly with the mesophytic character of the summer leaf. There is little distinction however in the amount of differentiation in the mesophyll.

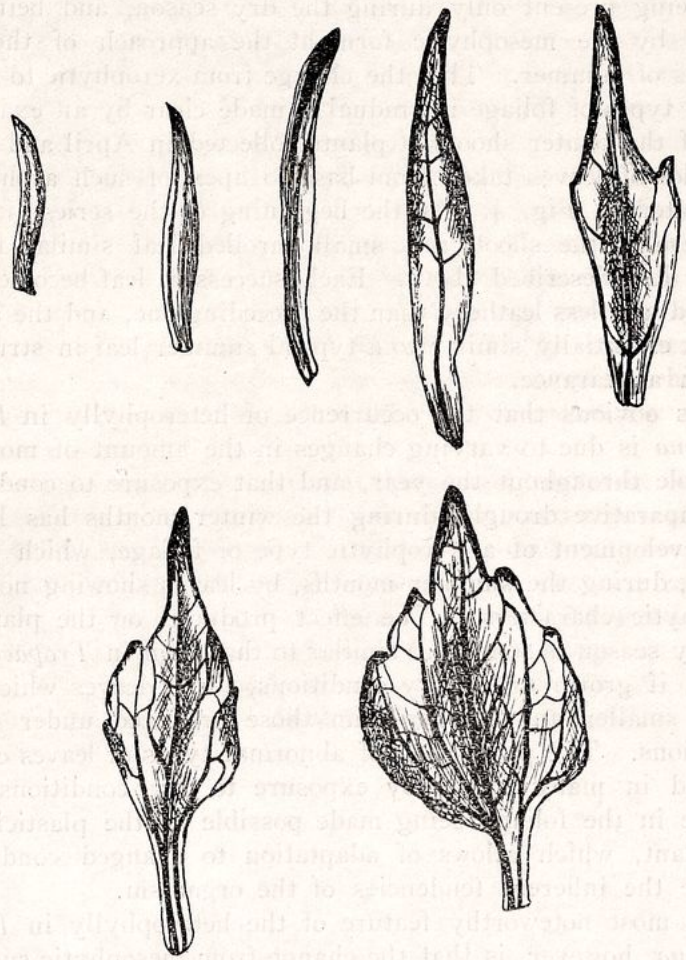

FIG. 4.—Series of leaves from base to apex of a winter shoot. × 10.

It will be seen from the above descriptions that in structure the winter leaf is on the whole a xerophytic type. The lamina is greatly reduced in size and by the inrolling of the margins until the leaf becomes almost tubular it presents a minimum of surface to the agents which accelerate transpiration. The cuticle is specially thickened to protect the exposed upper surface, and a covering of hairs minimises the drying effects of

air-currents, while the stomata are confined to the sheltered under surface. This type of leaf is clearly adapted to an environment in which the amount of moisture available is small, and where special mechanisms, such as reduction of leaf-surface, protection of stomata and development of a thick cuticle have been evolved to prevent the plant from losing too much water.

The foliage of *Hemiphragma heterophyllum* is thus closely correlated with the external conditions, the xerophytic type of leaf being present only during the dry season, and being replaced by the mesophytic form at the approach of the wet months of summer. That the change from xerophytic to mesophytic types of foliage is gradual is made clear by an examination of the winter shoots of plants collected in April and May. A series of leaves taken from base to apex of such a shoot is illustrated in Fig. 4. At the beginning of the series, i.e., at the base of the shoot, is a small inrolled leaf similar to the winter leaf described above. Each successive leaf becomes less inrolled and less leathery than the preceding one, and the apical leaf is essentially similar to a typical summer leaf in structure and in appearance.

It is obvious that the occurrence of heterophylly in *Hemiphragma* is due to varying changes in the amount of moisture available throughout the year, and that exposure to conditions of comparative drought during the winter months has led to the development of a xerophytic type of foliage, which is replaced, during the summer months, by leaves showing no such xerophytic characters. The effect produced on the plant by the dry season is somewhat similar to that seen in *Tropaeolum,* which, if grown under dry conditions, forms leaves which are much smaller and thicker than those produced under moist conditions. The production of abnormal types of leaves can be induced in many plants by exposure to dry conditions, the change in the foliage being made possible by the plasticity of the plant, which allows of adaptation to changed conditions despite the inherent tendencies of the organism.

The most noteworthy feature of the heterophylly in *Hemiphragma,* however, is that the change from mesophytic summer leaves to xerophytic winter leaves and vice versa takes place with unceasing regularity throughout the entire life of the plant, whereas in the majority of cases plasticity is lost with increasing age, and the power to respond to changes in environment slowly disappears. Thus the submergence of an old plant of *Sium,* which has hitherto been grown entirely on land, does not result in the formation of the dissected water-leaves below the water level, but merely in the continued production of the entire air-leaves. In *Hemiphragma,* however, xerophytic and

mesophytic types of leaves appear alternately, season after season, irrespective of age.

Because this alternation of foliage corresponds with climatic changes it might be said that this type of heterophylly is not an adaptation to environment, but is rather an annual return to a juvenile state of the foliage. It is a well-known fact, that following the cotyledons, many plants produce leaves which are known as juvenile leaves, and which are later replaced by the true adult foliage. No flowers appear in the axils of these juvenile leaves and normally they do not occur again unless the plant sustains a shock, such as a sudden change of environment, when reversion to the juvenile conditions may take place. In *Hemiphragma*, however, flowers occur in the axils of both winter and summer leaves, so that neither of these can be considered to be juvenile. The fact that summer leaves were produced first by the September seedlings is in all probability due to the seasonal conditions since adult plants also possess summer leaves at this time of the year. It was also found that flowers were even more frequent in the axils of the summer leaves, contrary to the statement in the original description which associates the flowers with the winter leaves and rarely with the summer leaves.

Annual reversion to a juvenile condition cannot be considered therefore as the true explanation of the occurrence of heterophylly in *Hemiphragma*. Indeed all the evidence goes to prove that the phenomenon is really a response to variation in climatic conditions during the year, whose regular changes lead to a constant alternation of summer and winter foliage.

In conclusion, I wish to express my thanks to Professor Wright Smith who provided the material and facilities to carry out this research.

Printed under the authority of His Majesty's Stationery Office by
JOHN PELLOW, 3 Lintrathen Street, Dundee.

(113D) Wt9948/1 375 11/25 G7.