# VARIATION OF LEAF-FORM IN *POTAMOGETON PERFOLIATUS* L.

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AN opportunity to study the causes of form-variation in *Potamogeton perfoliatus* was afforded while studying the ecology of water plants in the English Lakes. Many other pond-weeds such as *P. praelongus*, *P. alpinus*, etc., also exhibit variations in the shape and size of their leaves in different lakes and even in the same lake at different places. Nevertheless, the variations in form are far more pronounced in *P. perfoliatus* than in these other species. Taxonomists usually split the natural forms into various sub-species on account of this feature (*cf.* Hagstrom, 1916). However, Fryer, Bennett and Morgan (1915) think that all the British forms of the species may possibly be mere states and not varieties. It was thought that the habitat might be partly responsible for the variations in the species and hence this study was undertaken as an aid to ecological study of the aquatic plants now published elsewhere (Misra, 1938).

*P. perfoliatus* is a characteristic species of silted zones in the lakes where organic matter decomposes readily. In shallower water, it grows only in land-locked bays but in deep water it can grow in exposed parts upto a depth of six metres. The plants growing in Lake Coniston have usually long internodes and narrowest leaves which are thin and olive green in colour. On the other hand, the plants of Ullswater and of the calcareous river Wharfe possess short internodes and broadest leaves which are usually thick, pale coloured and with well-developed veins. They are also usually larger in size than any other forms. The species collected from the rest of the lakes vary between these two extreme forms which differ from one another much as do shade and sun leaves. But, although the plants growing in deeper parts of a lake usually possess somewhat longer internodes yet there is apparently no correlation between depth and shape of the leaf. Thus light intensity as judged by the depth of the water has no obvious influence upon the shape of the leaf. Movement of water is also not responsible for the variations as the river forms are identical with many of the lake forms.

## SHAPE VARIATIONS IN ADULT LEAVES

A fully grown plant shows slightly broader leaves at the base and the top ends of the main axis than the leaves present at its middle part. The same sequence of leaf shape is found upon the individual branches although the leaves are usually much smaller in size. Since changes in the form of the leaves are mainly due to the relative variations of length and breadth the shape of the leaf can be expressed numerically by the ratio $\frac{\text{length}}{\text{breadth}}$ (or briefly, L/B) as suggested by Pearsall and Hanby (1925). The statistics of this ratio obtained from different localities are given in Table I. The mean L/B ratios of leaves borne on different plant organs are tabulated with the standard error along with the standard deviation with its error and the variance.

TABLE I

*Statistics of L/B ratios*

| Locality | Shoot parts | No. of leaves measured | Mean | Standard deviation | Variance |
|---|---|---|---|---|---|
| 1. River Wharfe . . . . | Main axis | 229 | 2·000<br>±0·019 | 0·283<br>±0·013 | 0·080 |
| 2. Lake Ullswater . . . . | Main axis | 52 | 2·920 | . . | . . |
| | Branch | 35 | 2·810 | . . | . . |
| | Flowering shoot | 8 | 2·310 | . . | . . |
| 3. Lake Coniston . . . . | Main axis | 156 | 3·776<br>±0·068 | 0·851<br>±0·048 | 0·724 |
| | Branch | 38 | 3·579<br>±0·147 | 0·903<br>±0·114 | 0·816 |
| | Flowering shoot | 11 | 2·750<br>±0·091 | 0·301<br>±0·064 | 0·099 |
| 4. Lake Windermere—<br>(*a*) Low Wray Bay . . | Main axis | 171 | 3·654<br>±0·019 | 0·346<br>±0·027 | 0·120 |
| | Branch | 114 | 3·877<br>±0·023 | 0·877<br>±0·032 | 0·770 |
| (*b*) Boat house (Wray Castle) | Main axis | 178 | 3·960<br>±0·012 | 0·154<br>±0·010 | 0·237 |
| (*c*) Sawpit Bay . . . . | Main axis | 115 | 3·210<br>±0·009 | . . | . . |
| | Branch | 34 | 2·560 | . . | . . |
| | Flowering shoot | 22 | 2·410 | . . | . . |
| (*d*) Greentuft Islands (Fisherty How Bay) | Main axis | 112 | 3·200<br>±0·003 | 0·356<br>±0·002 | 0·127 |
| | Flowering shoot | 38 | 2·070 | . . | . . |
| (*e*) Congo Bay . . . . | Main axis | 122 | 3·200<br>±0·050 | 0·553<br>±0·025 | 0·306 |
| (*f*) Pullwyke Bay (Deep, 3–4 metres) . . . . | Main axis | 56 | 2·700 | . . | . . |
| | Branch | 8 | 3·500 | . . | . . |
| (*g*) Pullwyke Bay (Shallow, 0·5–1 metre) | Main axis | 205 | 2·590<br>±0·020 | 0·285<br>±0·014 | 0·081 |
| | Branch | 17 | 1·660 | . . | . . |
| | Flowering shoot | 14 | 1·820 | . . | . . |

An examination of the data solely from the point of view of the types of leaf-form shows that the leaves on the flowering branches are normally and relatively broader than those on the main axis. The other branches bear leaves which are generally of a similar L/B ratio to the main axis, though not necessarily so (*cf.* Pullwyke and Sawpit Bay samples). The production of branches in *P. perfoliatus* sometimes precedes the actual appearance of flower buds (*e.g.*, Low Wray samples) and may sometimes be more nearly associated with it in time [*e.g.*, Pullwyke (shallow) and Sawpit Bay samples]. In the former case it may be that the leaf shape resembles that of the main axis, while in the latter case it might be expected that the internal conditions would produce similar leaves on all developing branches whether flowering or not. This suggestion, however, requires further detailed examination.

Another noteworthy fact is that the maximum range of shape variation is shown by Coniston and Low Wray forms which possess the narrowest leaves. The range of shape variation on the other hand in case of broad leaved forms, *e.g.*, Wharfe and Pullwyke Bay (shallow) forms is comparatively narrow. This plasticity of the narrow leaves may be on account of a prolonged meristematic activity during which changes in growth conditions might be affecting leaf shape.

## SHAPE VARIATION IN DEVELOPING LEAVES

A large number of young vegetative and floral buds was collected from stations at which variations in adult leaves were already studied. These buds were dissected and the young leaves measured by means of a micrometer under a microscope. The length of the developing leaves has been plotted against the breadth logarithmically for typical plant forms in Figs. 1 and 2. The curves apparently conform to the equation $x = cy^k$ as given by Pearsall (1927), where $x$ and $y$ are sizes of growing plant organs (corresponding to length and breadth in this study), $c$ is a constant expressing their relative initial sizes and $k$ is a quantity for their relative logarithmic growth rates. The value for $k$ can be easily estimated from the slope of the curves so plotted.

Coniston forms as indicated in Fig. 1 show an initial high rate of relative growth for length with a $k$ of the order of $\pm 6$. However, the value for $k$ falls down to $\pm 1 \cdot 1$ after the leaves have grown longer than 3 mm. The leaves mature so into the narrow forms. On the other hand the Wharfe type has a lower value of $k$ ($\pm 2$) in the early phase of growth and hence develops into the broader form.

Measurements from buds taken from the top of about 6 inches high seedlings growing in Congo Bay are plotted in Fig. 2. Here the longest leaves are those first formed by the seedling ($k = \pm 1 \cdot 8$). The latter leaves show great variation but an average $k$ of the order of $\pm 1$. This may be held to indicate that as products of carbon assimilation become abundant $k$ falls and this assumption would agree with the lower $k$ for flowering plants as plotted on the same figure and as is shown subsequently for plants growing from rhizomes.

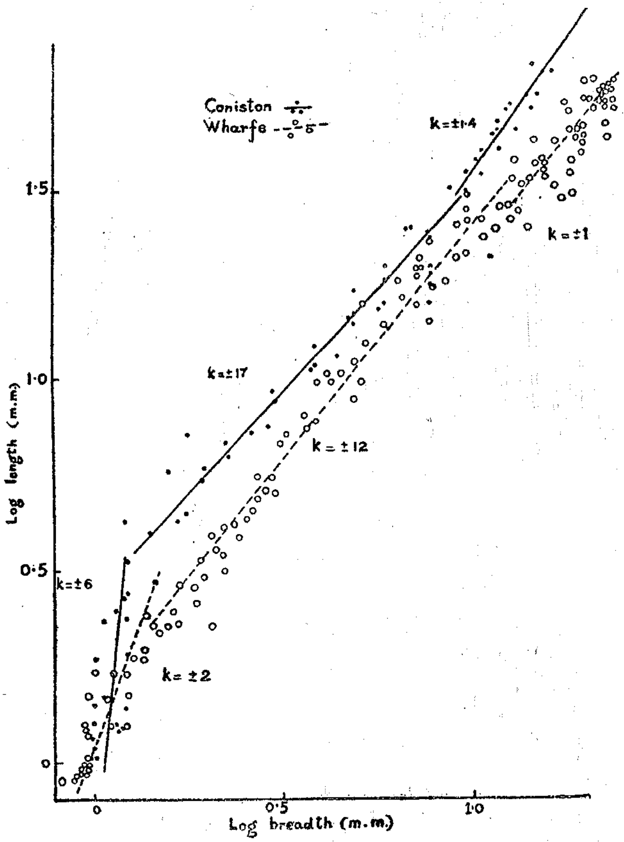

Fig. 1

Both of these in general possess broader leaves than the leaves upon a seedling or a non-flowering plant.

Two young plants apparently of the same age were found growing together from rhizome pieces of different thickness. The pieces were actually branches of the same parent rhizome. So the environmental conditions were identical for both of them. Nevertheless, the plant from the thicker rhizome had a thicker axis and the open leaves were also broader than those growing from the thinner rhizome. But on plotting logarithmic curves for the length and breadth of the young leaves from the two plants the same value for $k$ ($\pm 1\cdot 2$) was found for both the cases. Therefore differences in the shape of the leaves of the two plants must be on account of different values for $c$ (in the formula $x = cy^k$) which would possibly depend upon different amount or kind of food supply from the rhizome during the stage when the leaf primordium was formed. If the food supply from the thicker rhizome is quantitatively superior in some respect to that from the narrow

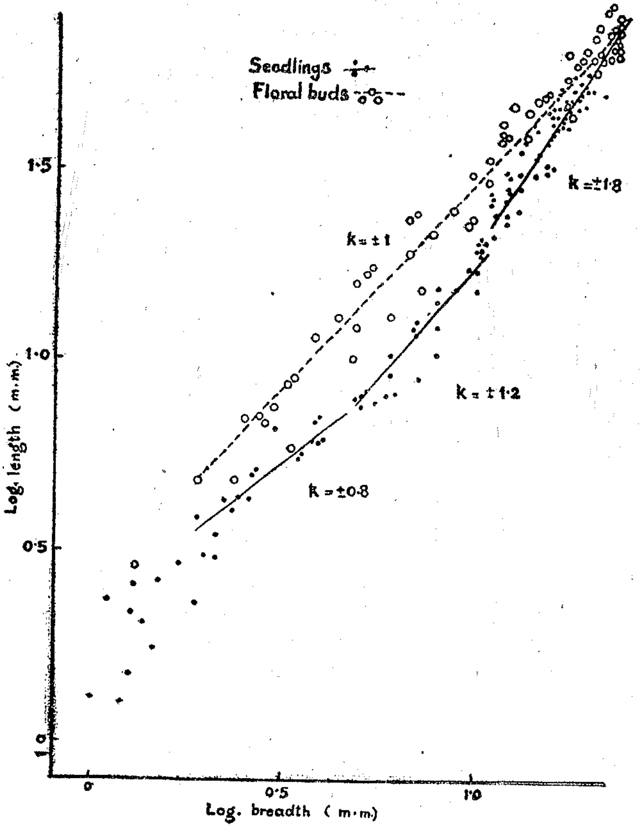

Fig. 2

one then the leaf-forms might be expected to be related to one another in much the same way as the successive leaves from a single rhizome. These become longer as they develop further from the rhizome. This is the difference observed in the examples between leaves from a narrow rhizome and those from a thick one.

As far as possible similar pieces of rhizome were obtained from Congo Bay and left in jars containing well water in the laboratory for a fortnight. The well water had a carbonate hardness two to three times more than the lake water. But when the buds developed from these rhizomes were dissected and the measurements were plotted against those developed at the same time in the lake no difference in the value of $k$ or the shape of the leaves could be discovered. Hence it is clear that changes in the environment for a short duration cannot induce changes in the shape of the leaves which are just developing from the rhizome.

## CHEMICAL ANALYSES OF PLANTS

In order to detect any obvious differences in chemical composition of the main food reserves air dried and pressed specimens were analysed for total nitrogen. The results are given in Table II. It is possible that soluble nitrogen may have been lost while pressing the plants between paper sheets and, during drying, some of the insoluble nitrogen might have been hydrolysed and redistributed in the plant. But such a preliminary study for the sake of comparison clearly showed that (*a*) buds of flowering plants have a lower nitrogen content than those from vegetative plants, (*b*) narrow leaves possess more nitrogen than broad leaves, and (*c*) the nitrogen content does not usually decrease much in older leaves of mainly vegetative plants.

TABLE II

*Total nitrogen contents of air-dried and pressed specimens*

(Expressed as percentage of dry weight)

| | No. of estimations | Average | Standard deviation |
|---|---|---|---|
| (*a*) Buds— | | | |
| Vegetative .. .. .. | 11 | 5·510<br>±0·170 | 0·556<br>±0·120 |
| Flowering .. .. .. | 7 | 4·550<br>±0·110 | 0·428<br>±0·160 |
| (*b*) Narrow leaves (Coniston, Low Wray and Sawpit ; L/B = 3·2-3·76)— | | | |
| Top leaves .. .. .. | 12 | 4·510<br>±0·101 | 0·350<br>±0·073 |
| Middle leaves .. .. .. | 5 | 4·330<br>±0·070 | 0·155<br>±0·049 |
| Bottom leaves .. .. .. | 3 | 3·970<br>±0·120 | 0·203<br>±0·084 |
| (*c*) Broad leaves (Pullwyke, shallow and Ullswater ; L/B = 2·59-2·92)— | | | |
| Top leaves .. .. .. | 7 | 3·810<br>±0·190 | 0·500<br>±0·130 |
| Middle leaves .. .. .. | 1 | 3·900 | .. |
| Bottom leaves .. .. .. | 1 | 3·600 | .. |

For more accurate determinations freshly collected plants of comparable age were hung on a string in a room and when sufficiently dry in air they were transferred to an oven kept at a temperature of 65° C., where these were finally dried to a constant weight. The nitrogen content of these along with their L/B ratios are shown in Table III. It will be seen here also that narrow-leaved forms are generally richer in nitrogen than the broad leaved forms.

Further analyses were made in order to obtain a comparison between the food supplies of the growing regions. In this case buds were collected and dropped into boiling alcohol and boiled for ten

TABLE III

*Total nitrogen content of whole plants*

(Expressed as percentage of dry weight)

| Locality | L/B of leaves from axis | Total nitrogen |
|---|---|---|
| Coniston .. .. .. | 3·776<br>±0·068 | 7·567 |
| Low Wray Bay .. .. .. | 3·654<br>±0·019 | 6·253 |
| Ullswater .. .. .. | 2·920 | 5·318 |
| Pullwyke .. .. .. | 2·590<br>±0·020 | 4·883 |

minutes, then cooled and stored. Subsequently the extract and the insoluble residue were analysed separately. The results are given in Table IV. The data clearly show that vegetative buds and their leaves have a higher proportion of soluble and insoluble nitrogen than developing leaves obtained from floral buds and branches and that the ratio total sugars/soluble nitrogen is higher for young leaves

TABLE IV

*Chemical analysis of buds preserved in alcohol*

(Results expressed as percentage of dry weight)

| Form (Locality) | Material | Dry weight, % of fresh weight | Soluble nitrogen | Insoluble nitrogen | Total sugars | Reducing sugars | Total sugars / Soluble nitrogen |
|---|---|---|---|---|---|---|---|
| Coniston .. | Vegetative buds | 3·083 | 1·897 | 8·690 | 17·490 | 7·703 | 9·217 |
| Ullswater .. | Young leaves from flower buds | 7·082 | 0·805 | 3·368 | 7·674 | 5·835 | 9·528 |
| Fisherty How Bay | Young leaves from branches | 3·699 | 2·317 | 8·245 | 11·330 | 4·196 | 4·890 |
|  | Flower buds | 3·623 | 0·778 | 5·525 | 7·047 | 4·919 | 8·851 |
|  | Branch buds | 5·269 | 0·909 | 6·243 | 8·307 | 5·388 | 9·139 |
| Congo Bay .. | Young leaves from seedlings | 6·348 | 0·399 | 3·417 | 10·940 | 4·169 | 27·370 |
|  | Young leaves from vegetative buds | 2·774 | 2·513 | 7·050 | 15·970 | 10·400 | 6·356 |
|  | Flower buds | 6·078 | 0·250 | 2·802 | 3·968 | 2·917 | 15·890 |

obtained from floral buds or seedlings than for those obtained from vegetative buds. Thus both floral buds and seedlings seem to possess a high C/N ratio and both of them ultimately develop broad leaves. It also agrees with the general assumption that flowering is associated with higher C/N ratios.

## DISCUSSION

It has been shown that shape variations in the leaves of *Potamogeton perfoliatus* are induced when they are still developing in the bud. The most potent factor likely to bring about such changes in the bud seemed to be the quantity and quality of food supply.

It is a well-known fact that the relative rates of growing plant organs can be altered by changes in the carbon to nitrogen ratio in the growing medium. For instance, Turner (1922) and Grist and Stout (1929) have obtained a high ratio of stem/root growth by supplying a high proportion of nitrogen to the plant. The behaviour of growth in length and that in breadth of the leaves can be taken to be of similar nature since they conform to the general equation $x = cy^k$ as formulated by Pearsall (1927) and discussed at great length by Huxley (1932). In the case of *P. perfoliatus* it is found that narrower leaves are developed in localities where the substratum contains well decomposed organic matter and as has been shown by Misra (1938) it contains more of nitrogen in the available form. Thus a high supply of nitrogen from the mud and its uptake by the plant seem to increase the relative rate of growth in the length of the leaves.

The most conclusive evidence of variation in the relative rate of growth by changes in the ratio of carbon/nitrogen supply comes from an analysis of the plants. This largely happens due to changes in the metabolic balance of the growing plant organs. A high C/N ratio for instance tends in dicotyledonous plants to turn meristem into vacuolating cells. This has been shown to some extent by Pearsall and Billimoria (1938) in case of sunflower. Pearsall (unpublished) has observed in case of Sycamore that a high C/N supply to vegetative buds gives rise to narrow, small and deeply lobed leaves and longer internodes. This phenomenon is attributed to early cessation of meristematic cell divisions and increased growth of the rippen meristem. But in monocots like *P. perfoliatus* where there is a basal meristem in the leaves for quite a long period it is difficult to see how increased post-meristematic growth can alter the shape of the leaf. Nevertheless, it seems very clearly from the data presented in this work that a high C/N supply tends to produce broad leaves in *P. perfoliatus* and not narrow ones as in the case of Sycamore.

The existence of a high C/N ratio in case of *P. perfoliatus* buds is possible in three different ways. Firstly low availability of nitrogen from the mud, secondly lower reserve of nitrogen in the young leaves when the plant is flowering as has been shown to exist and thirdly by a rapid translocation of carbohydrates from the rhizome to the developing young plant from it. In all these cases the leaf tends to develop broader.

Pearsall and Hanby (1925) have shown experimentally that the leaves of *P. perfoliatus* can be made to grow broader by an increased supply of calcium in their culture medium. Hence the rooting medium and the plant ash were also analysed in this work but the results are not recorded here since no significant correlation between these data and leaf shape could be established; yet there was some indication that replaceable calcium and iron in the mud favour growth in the breadth of the leaves. Soil conditions, if they have any effect upon leaf shape which must be very complex indeed, might control growth correlations through their effect upon carbon and nitrogen metabolism of the plant.

## SUMMARY

Morphological, developmental and chemical studies of plants collected from different lakes and localities indicate that form-variation in *P. perfoliatus* is caused by an early differential growth ratio which is affected by the supply of carbohydrates to the growing organs. It has been shown that a high C/N ratio tends to decrease the differential growth ratio between length and breadth thus producing a broad leaf.

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## LITERATURE CITED

Grist, J. W., and Stout, I. J. (1929) “Relation between top and root size in herbaceous plants,” *Plant Phys.*, **4**, 63.

Fryer, A., Bennett, A., and Morgan, R. (1915) *The Potamogetons (pondweeds) of the British Isles*, London.

Hagstrom, J. O. (1916) .. *Critical Researches on the Potamogetons*, Stockholm.

Huxley, J. S. (1932) .. *Problems of Relative Growth*, London.

Misra, R. (1938) .. “Edaphic factors in the distribution of aquatic plants in the English lakes,” *Joun. Ecology*, **26**, 441.

Pearsall, W. H. (1927) “Growth studies VI. On the relative sizes of growing plant organs,” *Ann. Bot.*, **41**, 163.

Pearsall, W. H., and Billimoria, M. C. (1938) “Effects of age and of season upon protein synthesis in detached leaves,” *Ann. Bot.* N. S. 11, **6**, 317.

Pearsall, W. H., and Hanby, A. M. (1925) “The variation of leaf form in *Potamogeton perfoliatus*, L.” *New Phyt.*, **24**, 112.

Turner, T. W. (1922) .. “Studies of the mechanism of the physiological effects of certain mineral salts in altering the ratio of top growth to root growth in seed plants,” *Am. Journ. Bot.*, **9**, 415.