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ABSTRACT — An analysis of internode lengths in the *Hippuris* stem is represented by a four phase growth curve. The two parameters which influence this pattern of internode lengths are the number of cells per internode and the length of the individual cells within the internode. In the ontogeny of the *Hippuris* stem cell length and cell number influence internode length in the distal portion of the stem while in the basal portion of the stem cell number is the major factor affecting internode length. The pattern of stem growth in *Hippuris* differs from that of *Elodea* in that the cell number in *Elodea* reaches a maximum before cell length, and the major factor influencing internode length is cell length.

Textbooks often characterize plant growth as an irreversible process which involves an increase in size accompanied by an increase in biomass. Histologically this expansion is caused by both an increase in the number of cells produced and by enlargement of previously existing cells. As the plant grows, the tissues differentiate and the plant reaches a mature state. Sachs (1873) stated that the individual organs of a plant and the entire plant increase in size in such a fashion that when growth data for increment per unit time are plotted against time, three distinct stages of growth may be distinguished. The three stages which make up the so-called "grand period of growth" are 1) an early period of slow growth, 2) a central period of rapid growth, and 3) a final period of slow growth (Bonner and Galston, 1959).

The present study is concerned with the ontogeny of the stem and stem units in the aquatic macrophyte, *Hippuris vulgaris* L. In 1944 Pollock and Abbe conducted a study on the development of the stem units in *Elodea*, a plant which superficially resembles *Hippuris* but belongs to the monocotyledonous family Hydrocharitaceae, which is far removed taxonomically from the unique dicotyledonous family the Hippuridaceae, to which *Hippuris* belongs. The following work was undertaken to determine whether the two aquatic plants exhibit a similar type of growth pattern and to define clearly the mode of stem and internode growth in *Hippuris*.

Gross Morphology

Before an understanding of the quantitative aspects of the growth pattern in *Hippuris* can be attained, the qualitative form changes that occur during the early ontogeny of the stem unit must be considered. The gross morphology of *Hippuris* will be discussed and when relevant will be compared with that of *Elodea*.

Hippuris vulgaris is a rhizomatous, aquatic perennial which produces unbranched, erect stems with whorled leaves separated at maturity by internodes which may be as long as 4 cm. (Fig. 1). Because it has whorled leaves and lacks woody, or mechanical tissue, it is a favorable plant for the study of stem growth. The nodal and internodal regions in older portions of the shoot are easily defined externally (Fig. 1), and the internal arrangement of cells in the younger sections of the stem makes it possible to distinguish between the node and the internode. In this paper the node and internode are referred to collectively as a stem unit, as first proposed by Doak (1935).

The first recognizable stem unit in *Hippuris* is that portion of the shoot which is associated with the newest leaf primordium (Fig. 2). The ground meristem of this stem unit consists of rib-block meristem which is primarily derived from the corpus of the shoot apex plus derivatives of the inner daughter cell resulting from the first periclinal in the tunica layer. A nodal block meristem is present in the most recently formed stem units and is characterized by an increase in number of longitudinal cell walls (Fig. 2). The internodal region of this distal meristematic system is characterized by slightly larger cells. The appearance of transverse cytokineses in a few of these internodal cells results in the establishment of a typical rib meristem.

In the distal portion of the *Hippuris* stem there are long, continuous, schizogenous cavities each of which may extend through the nodal and internodal regions for a varying number of stem units (Fig. 2). These cavities interrupt the lateral continuity of the nodal block meristem.

Beginning with the seventh stem unit below the shoot apex, the internode becomes clearly defined, inasmuch as the nodal block meristem becomes laterally continuous and the large intercellular spaces remain only between the longitudinal rows of rib meristem of a given internode. Thus, the ground meristem of the slightly older stem units (excluding stelar precursors and protoderm) is composed of these internodal lacunae and the rows of longitudinal rib meristem.

The early ontogeny of the stem unit of *Elodea*, as described by Pollock and Abbe in 1944, is similar to *Hippuris* except for certain differences in detail. A single layer of rib meristem initials first becomes evident at about the seventh to thirteenth stem unit and only then may the internode be identified. Distal to that there is no internal differentiation of the node and internode. In the

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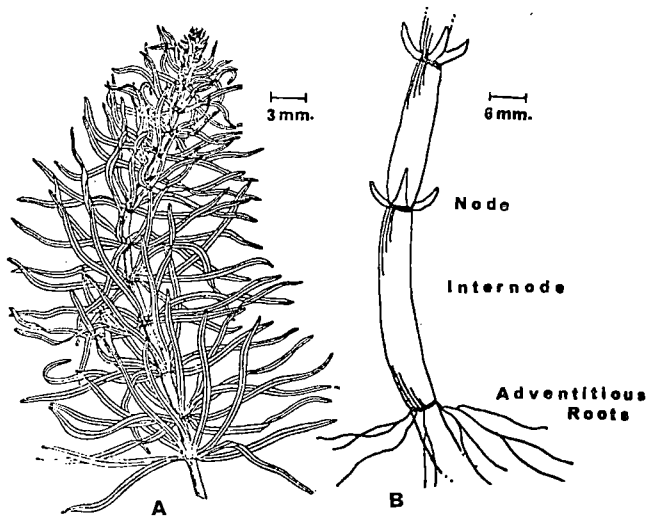

FIGURE 1. External morphology of *Hippuris vulgaris*. A. Distal portion of the stem. B. Basal portion of the stem.

distal portion of the shoot of *Elodea* there are, instead of the large and extensive lacunae of *Hippuris*, intercellular spaces of limited extent. In both genera the nodal region consists of closely packed block meristem cells. Older internodes in *Elodea* are characterized by an arrangement of cells and intercellular spaces which closely resembles that of *Hippuris*. Each stem unit in both plants consists of a nodal block meristematic system and an internodal rib meristem system with the internodal rib meristem inserted proximally to the nodal block cells.

Stem and Internode Development

The stems investigated for this study were collected in northern Minnesota from Lost Lake, Itasca State Park, on July 22, 1969, and from Fishhook Lake, Park Rapids on August 24, 1970. The stems were taken in their entire state and were preserved at the sampling site with FAA. The apical portions (approximately 4 cm. in length) were embedded in paraffin and sectioned longitudinally with a rotary microtome. These sections were subsequently stained with Fast Green (Sass 1958). The remaining portions of the stems were hand-sectioned and no stain was necessary. Measurements of cell size and internode length were made with an ocular micrometer appropriately calibrated, using a Wild M20 microscope. Other gross measurements were made with a Wild M5 dissecting scope and a millimeter rule scaled in 0.2mm. intervals.

Measurements of the internodes were completed in the following manner: a file of cells within an internode was selected, the length of this file was measured, and the cells within the file were counted. This procedure was repeated between six and eight times per internode, and from these data a mean internode length and a mean cell number were computed. An average cell length within a particular internode was then obtained by dividing the mean internode length by the mean number of cells. The mean of the above parameters are used in subsequent portions of this paper and in Figs. 3-5.

Fig. 3 is a graphic representation of the internode length data for five stems. The maximum internode length for each stem is represented as 100 percent and the other internodes are plotted in relation to this maximum internode length. The maximum number of internodes per stem is also referred to as 100 percent, with the other internode numbers represented as a percent of this total.

The curves in Fig. 3 suggest that there are four distinct regions of internode lengths which can be observed over the entire stem of *Hippuris vulgaris*. When all the stems are compared, the average number of internodes within each of these four growth regions is as follows: Zone A, 22.2; Zone B 10.0; Zone C, 84.6; Zone D 9.6.

The initial region (Zone A) includes the most recently initiated stem units and is located near the apex of the stem. The length of the internode in this region is consistent and relatively short as compared with the maximum observed internode length. The initial region is followed by Zone B in which the internode length increases rapidly. The above two areas are succeeded by a long region of gradual increase in internode length. This phase of internode lengths is followed by a region which is characterized by a very noticeable increase in internode length. The above phase terminates when the internode reaches the maximum observed length. Beyond this stage adventitious roots are seen in the nodal region (Fig. 1) and the length of the internodes is either slightly less or remains approximately the same as the terminal internode.

When analyzing the characteristic growth pattern of internode elongation, two parameters which influence the length must be considered, cell number and cell length. The former is a function of cell division and the latter is determined by the amount of cell elongation. Fig. 4 and 5 were plotted to show the relationship and effect of these two factors on internode length. In Fig. 4, cell numbers, cell lengths, and internode lengths from one *Hippuris* stem are plotted as a percent of their maximum observed size or number. In Fig. 5 the original data from the same stem is plotted semi-logarithmically.

As previously stated, little noticeable change in the internode length takes place in Zone A. Graphs 4 and 5 show that during this initial ontogenetic phase there is also little change in either cell number or in cell size. As compared with the above, however, the second phase exhibits a rapid increase in both cell number and in cell length concurrently with the increase in internode length.

Cell size reaches an upper asymptote at the end of Zone B (Fig. 5) and remains approximately constant from this point to the base of the stem. Neither internode length nor cell number reaches a maximum until the most basal internodes of the stem are reached. Both of the above parameters show a slow increase in Zone C and a rapid increase in Zone D. When the observed values for cell number and internode length are graphed as percent of maximum of each against internode number, they coincide in Zones C and D (Fig. 4). This may be interpreted to mean that the internode elongation during the growth of these stem units was directly proportional to the number of cells produced per internode, while the growth of the internodes in the distal stem

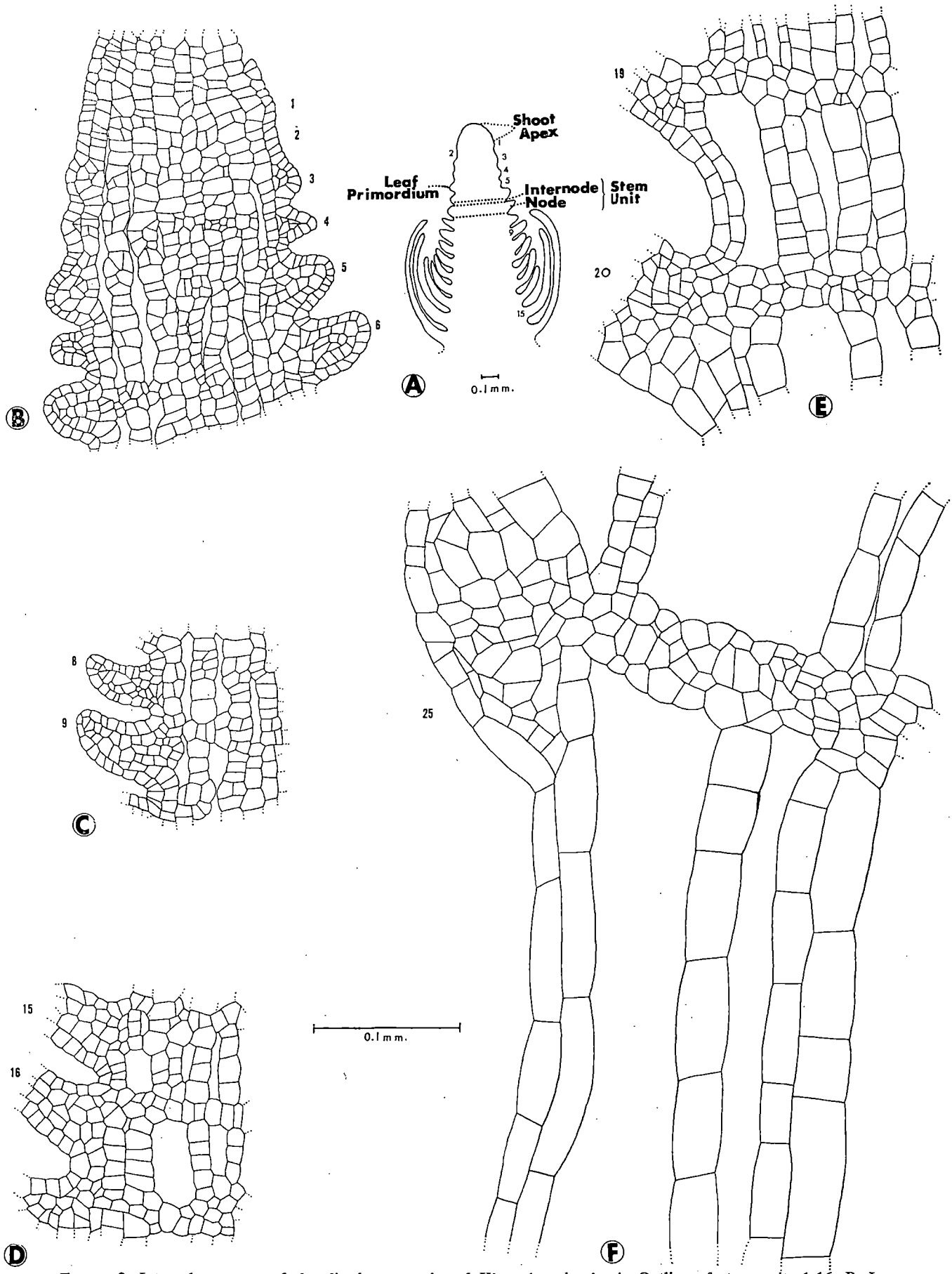

FIGURE 2. Internal anatomy of the distal stem units of *Hippuris vulgaris*. A. Outline of stem units 1-16. B. Internal structure of stem units 1-6. C. Stem units 8-9. D. Stem units 15-16. E. Stem units 19-20. F. Stem unit 25.

units was directly correlated with the number of cells produced plus the amount of cell elongation.

The above data may be explained by using the plastochronic concept which was first proposed by Askenasy in 1880. A plastochron represents the time interval between two successively similar events such as the initiation of leaf primordia or the successive formation of internodes (Abbe, 1941).

When considering time intervals or plastochrons, the youngest internodes are found in Zone A and the oldest are located in Zone D (Figs. 4 and 5). This means that the greatest amount of internode elongation has taken place in those plastochrons which occur first, and the least amount of elongation has occurred in the most recent plastochrons.

It must be remembered that when the plants were removed from their native habitat and fixed in FAA all growth processes ceased. The curves for internode lengths therefore represent a composite of the length achieved by each internode up to this point in time. It has been shown that the greatest amount of internode elongation has taken place in Zone D (the first-formed stem units) and that these have had the longest period of time in which to develop. It has also been pointed out that the maximum length of individual cells does not increase beyond Zone B. This means that cell length reaches a maximum size early in the development of internodes and that an increase in cell length is not a major factor affecting internode length beyond Zone B. Cell

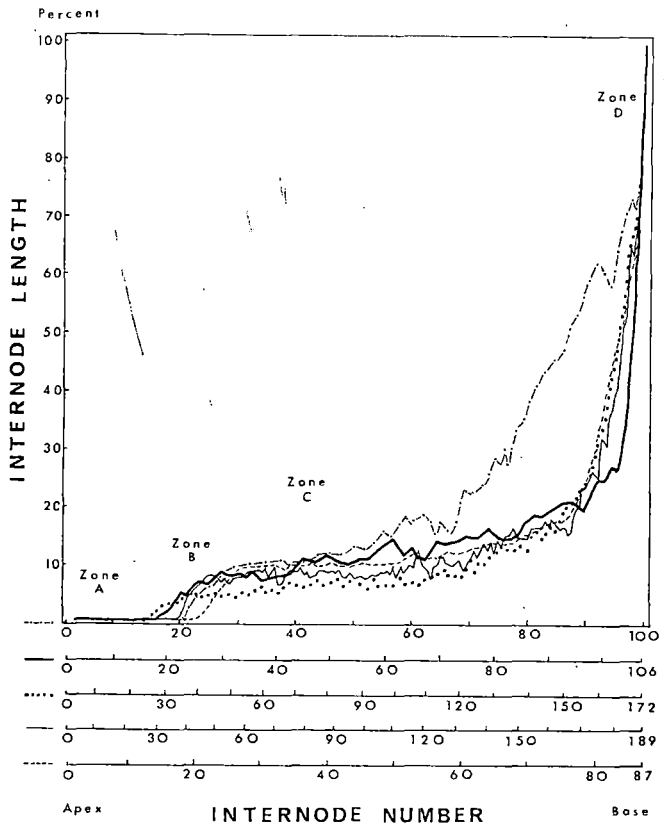

FIGURE 3. Internode lengths of five *Hippuris* stems plotted against internode number.

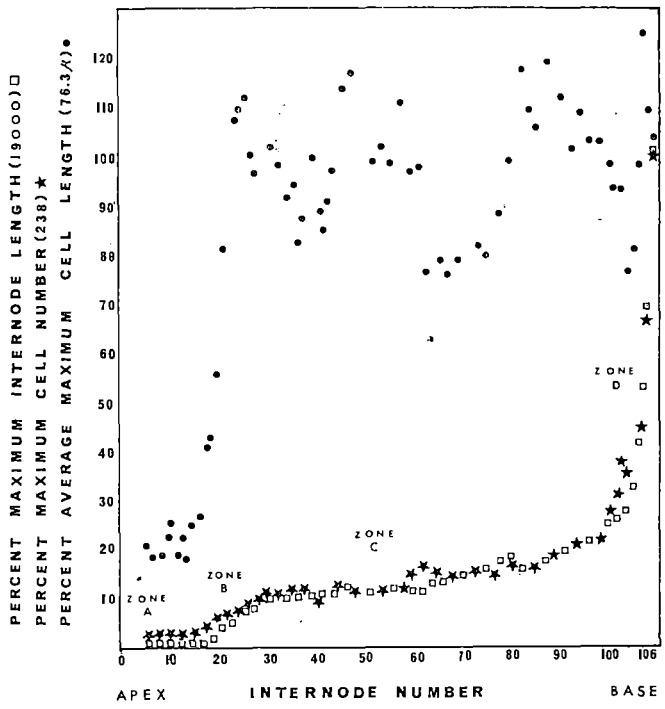

FIGURE 4. Cell numbers, cell lengths, and internode lengths of one *Hippuris* stem plotted against internode number.

number, however, increases to the base of the stem and is directly correlated with the length of the internodes in Zones C and D. Each time a cell divides, the resulting daughter cells may increase up to the maximum cell length, but the only factor influencing the length of the internodes in Zones C and D is the number of cells present.

As can be seen in Fig. 4, a typical sigmoid growth curve results from plotting the data for the most recently initiated stem units (Zones A and B). This is an indication that these stem units were actively growing when the samples were taken. It is questionable as to whether the internodes in Zones C and D were actively elongating at the time of collection or whether they had reached maturity. Until further research is completed, the growth pattern of individual internodes can not be completely defined and the question of the curious increase in the length of the basal internodes must remain unanswered. Internode growth must be followed from the beginning of the growing season and watched throughout the season in order to answer the above questions.

Besides significant differences in the early ontogeny of *Hippuris* and *Elodea* stem units, the method of internode elongation also differs markedly. During early ontogeny of *Elodea*, cell number, cell length, and internode length increase very slowly in the distal portion of the shoot. This growth phase coincides with Sach's first period of growth (1873). The second growth stage, which corresponds to Sach's rapid growth phase, is characterized by an increase in cell length as well as an increase in cell number. However, the cell number reaches its maximum before cell length does. Thus, after reaching a maximum cell number, cell elongation is the only factor which ac-

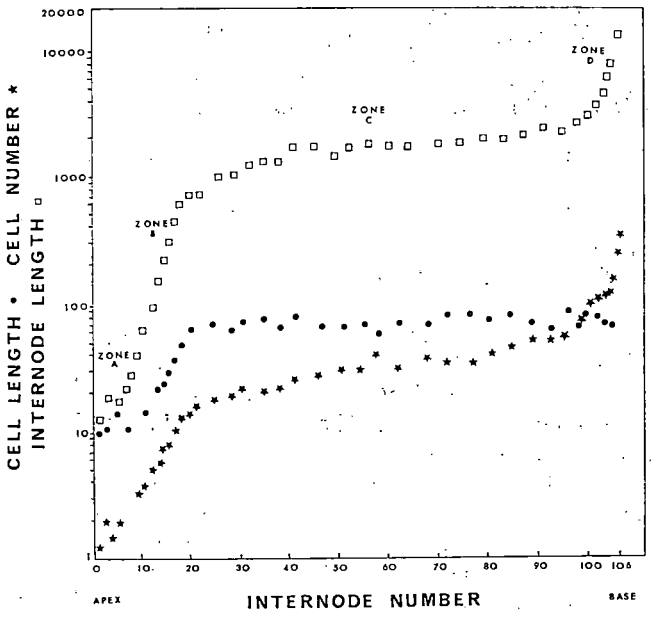

FIGURE 5. Semilogarithmic graph of cell numbers, cell lengths, and internode lengths of one *Hippuris* stem plotted against internode number.

companies increase in internode length. When cell length reaches its maximum, the internode has reached maturity. Although superficially somewhat similar, *Elodea* and *Hippuris* differ with respect to the primary histogenetic factors which influence internode length.

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