Amer. J. Bot. 64(1): 24–32. 1977.

A COMPARISON OF MERISTEMS AND UNEQUAL GROWTH OF INTERNODES IN VINY MONOCOTYLEDONS AND DICOTYLEDONS[1]

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ABSTRACT

The distribution of meristematic activity and cell length in the growing internodes of seven species of dicotyledonous vines and three species of monocotyledonous vines is described. In *Schlegelia*, *Ipomoea*, *Mucuna*, *Passiflora*, *Ficus*, *Thunbergia alata*, *Dioscorea*, *Smilax*, and *Vanilla* the loss of meristematic activity proceeded from the base to the top of the internode. The absence of isolated meristematic regions is typical of the uninterrupted meristem. In *Thunbergia grandiflora* a small peak of residual meristematic activity is located at the base of the internode, which is typical of the intercalary meristem. The same region of the internode is swollen and functions as a pulvinus. The young internodes of the seven dicotyledonous vines and an additional eight species of monocotyledonous vines with uninterrupted meristems were marked into three segments for growth studies. The upper part of the internode grew more rapidly and for a longer time than the basal part of the internode, except in *T. grandiflora*. The relative amounts of unequal growth in various species differed widely. Greater growth of the upper region was not correlated with comparable increases in final cell length in the upper region. It is concluded that the uninterrupted meristem is a common feature of shoot extension in many monocotyledons and dicotyledons.

A RECENT SURVEY of the development of internodes in the vegetative axes of 17 families of monocotyledons has failed to support the concept that the presence of an intercalary meristem at the base of an internode is a general feature of monocotyledons (Fisher and French, 1976). Instead, the survey revealed that in shoots of many monocotyledons the subapical meristematic region is uninterrupted by mature tissues. In shoots with this pattern of meristematic activity, termed the uninterrupted meristem, the maturation of tissues progresses acropetally from the base to the top of the internode. Thus, in many monocotyledons there is a resemblance to the pattern of internode development reported for dicotyledons (Garrison, 1973; Enright and Cumbie, 1973). However, detailed comparisons of patterns of cell division in internode development between monocotyledons and dicotyledons are not possible because there is no comparable information on internode development in dicotyledons. Only semi-quantitative or indirect measurements of meristematic activity have been made, i.e., the use of numbers of cell divisions (Jahn, 1941) or cell number per internode, or surface marking experiments (Garrison, 1973).

The present study extends the quantitative histological methods used in the previous paper (Fisher and French, 1976) that was oriented toward tropical monocotyledons (which included many vines) to selected species of viny dicotyledons. In addition, surface marking studies on both monocotyledons and dicotyledons have been incorporated to gain an appreciation of the amount of unequal growth within the developing internodes of both groups of plants.

This paper is the first part of a survey comparing the development of internodes in monocotyledons and dicotyledons with the viny habit. Vines were selected because: (1) shoot extension receives considerable emphasis in vines, often through the production of long internodes, which are more convenient to study than short internodes; (2) vines present interesting and little-studied morphological modifications for climbing supports. The relationship between the method of climbing and the patterns of leaf and internode development in various species of angiosperm vines that are described in this study is explored in a subsequent paper (French, in press).

MATERIALS AND METHODS—The plants used in this study were growing in a greenhouse or in outdoor plantings in Miami, Florida, from November through June. Shoots exhibited continuous growth at the relatively uniform temperatures that prevailed in this period. The daily range in temperature was usually between 15 and 28 C, except for occasional lower temperatures at night.

The growth of visible internodes on shoots during a two day interval was measured to determine the extent of the region of elongation. For histological studies the shoot tip and shorter inter-

[1] Received for publication 8 April 1976.
This study was supported by NSF Grants GB-40065 and BMS73-01226. The authors thank Mary French and Jan Wassmer for their valuable technical assistance, and Mrs. Nelly Dijkman for her translation of Burkom (1913) from the original Dutch.

nodes (less than 3–4 cm) were cut into 1-cm segments for fixing. For the longer elongating internodes only 1-cm segments from the upper (U), middle (M), and lower (L) regions of the internode were fixed. Except for the lower segments of the internode of *Thunbergia grandiflora*, these regions were relatively uniform histologically. The upper and lower segments were sampled below and above the node, respectively; the middle segment was sampled in its mid-region. The tissues were processed, embedded in Paraplast, sectioned longitudinally at 10–15 μm and stained with haematoxylin, safranin, and fast green as described in the previous paper (Fisher and French, 1976).

As in the previous paper the assumption is made that sequentially developing internodes exhibit qualitatively similar patterns of development. For successive internodes the final internode length and width remained relatively constant during the period of study. The numbering of internodes is the same (Fisher and French, 1976) so that an internode is given the same number as the suprajacent leaf; thus, the youngest leaf primordium was considered P 1, and the internode below it was In 1. For species with helical phyllotaxis, the sequence of the congested internodes immediately below the apex was determined by examination of serial longitudinal sections.

The methods used to determine cell length and mitotic index are as before (Fisher and French, 1976). Cell length was measured by counting the number of cells in a file of known length. Only parenchyma cells of the pith or central ground tissue were measured, and five replicates were made for the most median longitudinal sections of internodes in the shoot tip. Cell length was also determined in mature internodes by using freehand sections. Twelve replicate measurements in adjacent files of cells were made. Mitotic index was used to locate regions of mitotic activity in the shoot. No attempt was made to estimate rates of cell division from mitotic index. The nuclei of ground parenchyma cells in entire microscope fields were counted, and the percentage of nuclei in a phase of mitosis from metaphase to telophase was determined. Except where the apex or young internodes were too small, the sample size for mitotic index values was approximately 1,000 cells. The mitotic and cell length data were pooled for internodes which were too small to contain sufficient numbers of cells or give meaningful counts, and this is indicated, for example, as A + 1 or In 3–4.

For markings studies, young internodes (see Table 1 for length) were divided into three segments of equal length by short lines of India ink by using a #1 Rapidograph pen, and the growth of these regions was measured at two day intervals until elongation was completed. The marking studies were made simultaneously with measurements of leaf and internode growth described in a subsequent paper (French, in press). The marks at the base of each internode were located opposite the upper limit of the leaf base; the marks at the top of the internode were located opposite the lower limit of the leaf base. Each segment was considered mature when no total change in length greater than 1 mm was detected for two succesive periods of measurement. At least four internodes were marked for each species. During elongation marks were redrawn, if necessary, in the center of the dispersing particles of ink. Leader shoots of seedlings (*Thunbergia alata*, *Mucuna*, *Ipomoea*) or established plants were selected for studies of the distribution of growth. The drawings are by Priscilla Fawcett. Voucher specimens have been deposited at Fairchild Tropical Garden herbarium (FTG).

RESULTS—*Species of dicotyledons examined*—The measurements of mitotic index and cell length for the seven species of dicotyledonous vines are presented in Fig. 1–7. The pattern of meristematic activity in six of the species of dicotyledons is typical of the uninterrupted internodal meristem described for monocotyledons (Fisher and French, 1976). In the uninterrupted meristem mitotic index declines to zero first at the base of the internode, and subsequently throughout the entire internode in an acropetally moving wave. The decline in mitotic index is often, but not always, accompanied by a sharp increase in mean cell length, which likewise progresses toward the top of the internode. These features are recognizable in *Mucuna* (Fig. 1), *Thunbergia alata* (Fig. 2), *Ipomoea* (Fig. 3), *Passiflora* (Fig. 4), *Ficus* (Fig. 5), and *Schlegelia* (Fig. 7). *Thunbergia grandiflora* (Fig. 6) shows a different pattern and will be discussed further individually.

Mucuna sloanei Fawc. and Rendle (Fabaceae), Fig. 1, is a twining vine with alternate leaves (Fig. 11A, C) and hollow internodes. Mitotic activity has ceased in lower In 10 and upper In 11, but a few divisions still occur in middle In 10. In upper In 10 mitotic index reaches a higher value and remains relatively uniform for a number of internodes. Mean cell length remains relatively uniform from In 1 to In 9 and then rises abruptly in middle In 10. These data are typical of the uninterrupted meristem in which there is an acropetal wave of development within each internode and the shoot as a whole.

Thunbergia alata Bojer (Acanthaceae) Fig. 2, is a twining vine with decussate leaves and hollow internodes. Mitotic index is highest in A and in lower In 5, then falls to zero in middle In 6. Cell length increases gradually below the apex, with the largest increases taking place after meristematic activity is lost. Internode 6 was the last elongating internode.

Ipomoea purpurea (L.) Roth. cv. Heavenly

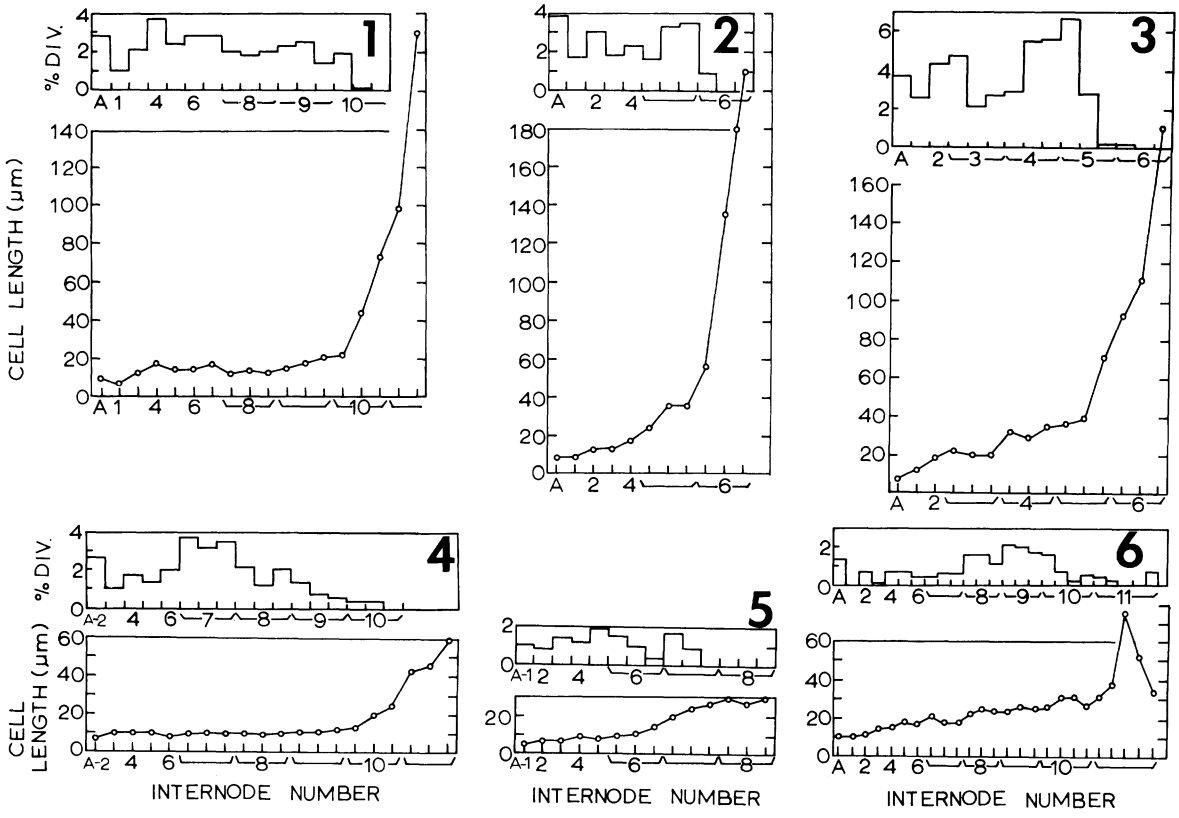

Fig. 1–6. Mitotic index and cell length vs. internode number in species of dicotyledonous vines. **1.** *Mucuna.* **2.** *Thunbergia alata.* **3.** *Ipomoea.* **4.** *Passiflora.* **5.** *Ficus.* **6.** *Thunbergia grandiflora.* A, apical dome. Data are from individual shoots.

Blue (Convolvulaceae), Fig. 3, is a twining annual vine with alternate leaves. Mitotic index reaches a peak in upper In 5 and then declines to low values in lower In 5 and upper In 6. Data for A and an undetermined number of adjacent internodes were pooled. The average cell length exhibits a gradual irregular increase from A to middle In 5 followed by a sharp increase starting in lower In 5, which is correlated with a decline to a low mitotic index in the same region. Internode 7 had completed elongation, while In 6 was approaching the declining phase of elongation.

Passiflora laurifolia L. cv. Jamaica 6 (Passifloraceae), Fig. 4, is a vine climbing by means of tendrils from the axils of the alternate leaves. Mitotic index reaches high values in In 7, followed by a decline to zero in lower In 10. Data for A-In 2 were pooled. Mean cell length remains essentially uniform from A through In 9 followed by an increase in middle In 10, which is the last internode with a detectable mitotic index. Internode 11 was probably elongating at the time of collection.

Ficus pumila L. var. *minima* Bailey (Moraceae), Fig. 5, is a vine attaching by means of roots; leaves are alternate. There is no defined peak in mitotic index. Mitotic index declines to zero in lower In 7, while cell length shows an increase from A onward. The data for A + In 1 were pooled. Internode 8 had completed elongation, and In 7 was approximately one-half elongated.

Thunbergia grandiflora Roxb. (Acanthaceae), Fig. 6, is a twining vine with decussate leaves and hollow internodes. Mitotic index rises to a peak in In 9, followed by a decline to zero in middle and lower In 11, with an isolated peak of mitotic activity located in the extreme base of In 11. This region of the internode is without a lacuna and is somewhat swollen (Fig. 11B). The same region also accounts for localized growth at the base of the internode which can reorient the stem to a more upright position (Fig. 11B, D). This feature is absent from the other species, e.g., *Mucuna* (Fig. 11A, C). The slope of the increase in cell length below the apex is gradual; then larger increases in net cell length take place in older internodes, especially in In 11. Cell length remains lower at both ends of In 11, which are sites of meristematic activity. Internode 11 was undergoing rapid elongation; the next four internodes below In 11 were also elongating.

Schlegelia parasitica (Sw.) Miers ex Griseb. (Bignoniaceae), Fig. 7, is a vine with opposite

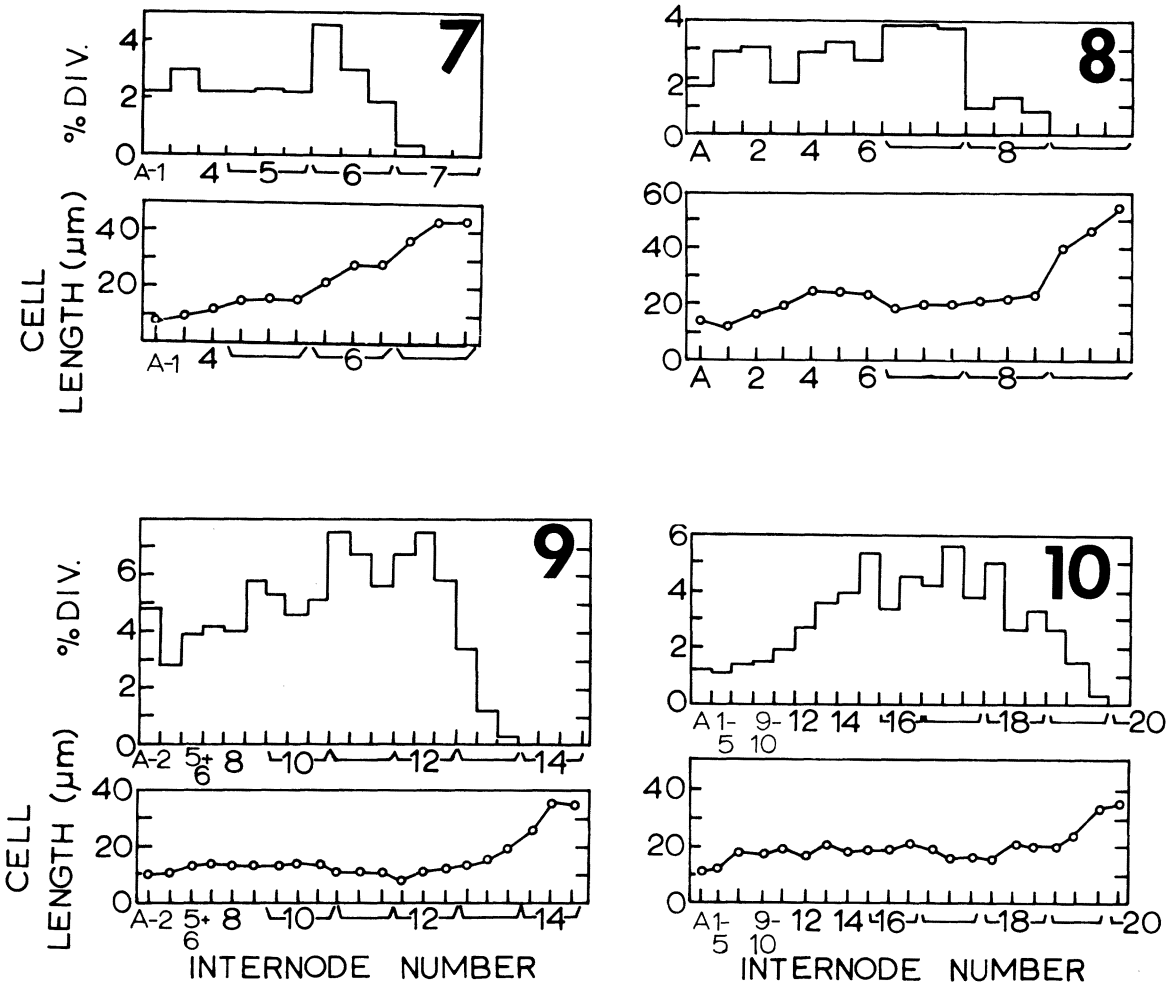

Fig. 7–10. Mitotic index and cell length vs. internode number in species of dicotyledonous (Fig. 7) and monocotyledonous vines. **7.** *Schlegelia.* **8.** *Vanilla.* **9.** *Smilax.* **10.** *Dioscorea bulbifera.* A, apical dome. Data are from individual shoots.

leaves; it attaches by roots. There is a peak of mitotic index in upper In 6, followed by a decline to zero in middle In 7. Data for A + In 1–3 were pooled. Mean cell length follows a stepwise increase in In 5 through In 7 with the shortest cells in each internode located in the upper part. Internode 7 was the lowest elongating internode on the shoot and was nearing the end of elongation, i.e., In 8 was not elongating. Examination of the primary xylem in In 7 revealed pitted metaxylem elements in the middle and lower regions only which indicates these regions had completed elongation. This result is consistent with marking studies reported later for *Schlegelia* which demonstrate considerably greater growth in the upper region.

Additional species of monocotyledons examined —These vines are included as supplements to the previous survey of internode development in monocotyledons (Fisher and French, 1976).

Vanilla sp. (Orchidaceae), Fig. 8, is a vine climbing by means of roots. Mitotic index declines to zero in In 9 after reaching a broad peak in In 7. Cell length declines slightly in In 7 and rises sharply in In 9, in which mitotic index is zero, and which was elongating.

Smilax bona-nox L. (Smilacaceae), Fig. 9, is a vine with alternate leaves bearing stipular tendrils. Mitotic index reaches the highest values ca. 0.2 to 2.8 cm from the apex in In 11 and In 12, and then declines sharply to zero in In 14. The data for A + 2, In 3–4, 5–6 were pooled. Cell length increases through the first seven internodes, then declines to its lowest value in In 12, in a region of high mitotic index. A sharp rise in cell length is associated with the decline in mitotic index in In 13.

TABLE 1. *Patterns of differential growth of internodes of 15 angiosperms*[a]

Species	Length of internode at marking (cm)	Final internode length (cm)	Relative final length of segments[b]			Duration of growth of segments (days)		Rate of growth of segments (cm/d)	
(Dicotyledons)			*L*	*M*	*U*	*L*	*U*	*L*	*U*
Ipomoea	0.8	25.4	1.0	1.5	3.4	4.0	5.2	0.8	2.8
Thunbergia alata	1.0	14.9	1.0	1.4	3.1	4.4	7.8	0.7	1.1
Schlegelia	0.9	8.6	1.0	1.6	2.9	6.5	8.5	0.2	0.5
Ficus	0.9	3.2	1.0	1.4	2.7	2.0	5.0	0.2	0.3
Mucuna	0.9	22.4	1.0	1.5	2.0	4.5	6.5	1.2	1.4
Passiflora	0.6	7.3	1.0	1.5	1.8	5.0	6.6	0.3	0.4
Thunbergia grandiflora	1.2	15.4	1.0	1.1	1.0	7.7	7.6	0.7	0.7
(Monocotyledons)									
Rhaphidophora	1.9	18.7	1.0	1.8	2.4	6.0	11.6	0.5	0.7
Luzuriaga	1.2	23.8	1.0	1.7	2.3	5.2	7.6	0.9	1.4
Vanilla	1.2	8.2	1.0	1.7	2.2	14.6	20.2	0.1	0.2
Dioscorea bulbifera	0.8	9.5	1.0	1.3	1.8	6.0	7.0	0.4	0.5
Smilax bona-nox	0.9	11.6	1.0	1.1	1.6	5.4	7.4	0.5	0.7
Philodendron	3.8	10.8	1.0	1.3	1.5	21.0	28.0	0.1	0.2
Gloriosa	1.0	4.4	1.0	1.2	1.4	4.0	4.9	0.2	0.3
Dioscorea alata	0.8	6.4	1.0	1.3	1.3	6.0	6.5	0.3	0.3

[a] Species are arranged by class and then by order of decreasing value of U/L.
[b] Lower (1); Middle (M); Upper (U).

Dioscorea bulbifera L. (Dioscoreaceae), Fig. 10, is a twining vine with alternate leaves. A large number of growing internodes are present on the shoot. Mitotic index is relatively low in A and progressively increases to a broad region of high values in In 13–18, then declines to zero in upper In 20. Net cell length remains relatively constant from In 6 to upper In 19, except for a slight decline in middle In 17, lower 17 and upper 18. Net cell length then increases in middle and lower In 19 and in upper In 20 as mitotic index declines. Two internodes below In 20 were elongating.

Marking studies—Young internodes of 15 species of dicotyledons and monocotyledons were marked with ink into three equal segments: lower (L), middle (M), and upper (U) (See Table 1 for internode length at the time of marking). In addition to the seven dicotyledons and three monocotyledons just described, five species of monocotyledonous vines are included for which mitotic data were presented in Fisher and French (1976).

The initial and final length of the internode are presented in Table 1. For comparative purposes the ratio of the upper and middle to lower final segment length was also calculated.

With the exception of *Thunbergia grandiflora*, all of the species examined showed the same qualitative distribution of growth in the internodes. In essence, the duration and rate of growth are greater in the top segment than in the basal segment, and regions of basal residual growth are absent. In the various species quantitative differences exist, so that the upper part of the internode may attain an average ranging from 1.0 (in *Thunbergia grandiflora*) to 3.4 (in *Ipomoea*) times the length of the lower segment. In *T. grandiflora* there is considerable variation in the pattern of growth with respect to the relative contribution of U, M, and L. In nine marked internodes of *T. grandiflora* no consistent pattern of unequal growth in U was found. An additional marking study in *T. grandiflora* revealed the presence of a small region of residual elongation at the base of the internode. The basal thirds of five internodes which were from 28 to 73% of their final lengths were marked into 4–8 additional subsegments. The extreme basal subsegments of the internode continued to elongate longer than both the adjacent subsegments and the middle and upper segments. The residual growth contribution was not large, amounting to at most 6% of the length of the internode. This region corresponds to the swollen portion (Fig. 11B) which was described previously as the site of a residual peak of meristematic activity (Fig. 6).

The unequal growth of the upper segments of the species shown in Table 1 may be examined further to find the (1) duration of growth, (2) rate of growth, and (3) the final cell length in the upper and lower segments. The length of each of the three segments was measured every two days, and from these data the duration of growth of each segment was calculated. An examination of the data reveals that the upper segment usually grows for a longer time than the lower segment (Table 1), though in some species the differences are rather small or are absent. Calculations of

TABLE 2. *Final length of ground parenchyma cells in the lower and upper segments of internodes*

Species	Final length of cells (μm)[a]		Ratio of final length of cells (U/L)	Ratio of final length of segments (U/L)
	L	*U*		
Ipomoea	168.4 ± 5.1	208 ± 8.2	1.27	3.4
Schlegelia	44.6 ± 1.5	43.5 ± 1.3	0.98	2.9
Ficus	42.1 ± 1.8	45.0 ± 1.3	1.06	2.7
Rhaphidophora[b]	113.0 ± 2.8	96.4 ± 1.9	0.85	2.4
Luzuriaga	173.5 ± 11.4	142.1 ± 7.8	0.82	2.3
Vanilla	142.1 ± 3.8	152.6 ± 4.3	1.07	2.2
Mucuna	211.6 ± 11.6	177.6 ± 7.4	0.83	2.0
Passiflora	120.0 ± 6.5	95.2 ± 4.8	0.79	1.8
Dioscorea bulbifera	57.7 ± 3.3	59.8 ± 6.9	1.04	1.8
Smilax bona-nox	44.8 ± 3.0	45.3 ± 2.1	1.01	1.6
Philodendron	49.5 ± 1.5	51.5 ± 0.7	1.04	1.5
Gloriosa	247.2 ± 31.2	238.4 ± 10.8	0.96	1.4
Dioscorea alata	63.0 ± 1.6	74.7 ± 3.7	1.19	1.3
Thunbergia grandiflora	66.1 ± 4.5	63.5 ± 3.1	0.96	1.0

[a] Values include ± SE mean, n = 12 replicates.
[b] Equals *Scindapsus aureus* (Lind. & Andre) Engl. in Fisher and French (1976).

growth rates show that the upper segment elongates at a greater rate than the lower segment in nearly all species (Table 1).

The average length of a ground parenchyma cell in the upper (U) and lower (L) segments from mature internodes was measured to determine if greater final cell length was associated with the greater length of U. The boundaries of U and L were either calculated from the ratios of Table 1, or the original marked internodes were used. The data in Table 2 reveal that the cell length in U is generally close to the cell length in L, and the ratio of cell length in the upper/lower (U/L) segments is less than the ratio of final segment length. In species with much greater growth in the upper segment, e.g., *Ipomoea*, *Schlegelia*, more cell divisions take place in U than in L, and cell length in the upper segment does not differ markedly from cell length in the lower segment.

DISCUSSION—A comparison of the results of an earlier survey of the development of internodes in monocotyledons (Fisher and French, 1976) with results presented here for dicotyledons and three additional monocotyledons allows us to emphasize some important points of similarity with regard to patterns of meristematic activity. During the early development of internodes in these angiosperms, the entire internode is meristematic; it is only in the later phases of development that the two distinctive patterns of localization of meristematic activity have been recognized: (1) the uninterrupted meristem, in which the decline in mitotic index to zero begins at the base of the internode and spreads acropetally to the top of the internode; and (2) the intercalary meristem, in which a region of meristematic activity becomes restricted to the base of the internode, and is surrounded by mature tissues. The previous study (Fisher and French, 1976) revealed that the uninterrupted meristem is found in a wide range of monocotyledons that have elongated internodes, i.e., representatives of 11 families, including the Costaceae, Pandanaceae, Orchidaceae, Liliaceae, Agavaceae, Dioscoreaceae, Araceae, Philesiaceae, Smilacaceae, Arecaceae, and Zingiberaceae. The present results confirm that the uninterrupted meristem occurs widely in dicotyledons as well, since all of the dicotyledonous vines examined here show the typical features, with the exception of *Thunbergia grandiflora*. *Thunbergia grandiflora* and certain other dicotyledons which exhibit alternate patterns of internode development are discussed below in more detail.

The acropetal decline of meristematic activity within dicotyledons is expected from the findings of other authors who have reported an acropetal wave of growth and maturation in internodes of dicotyledons, based on both anatomical data and surface marking techniques (Grisebach, 1843; Harting, 1845; Burkom, 1913; Jahn, 1941; Wetmore and Garrison, 1966; Millet, 1970; Garrison, 1973, and Enright and Cumbie, 1973). The studies of Burkom (1913), Millet (1970), Garrison (1973), and Enright and Cumbie (1973) established that the basal region of internodes stopped elongating prior to the upper region. Burkom (1913) reported detailed marking studies which showed a shift in the maximum rate of growth from the base to the upper part of the internode. However, with the exception of Jahn (1941), who counted numbers of mitoses in in-

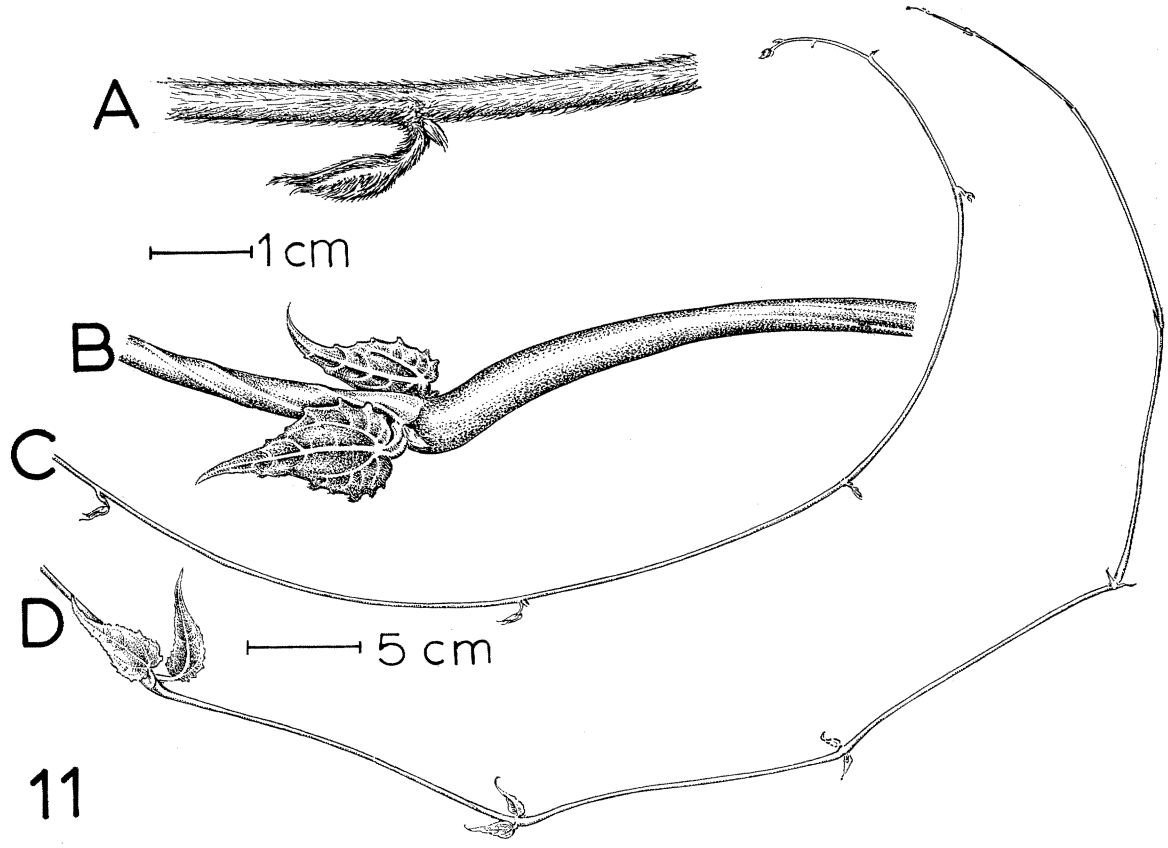

Fig. 11. Searcher shoots and nodal regions of two species of dicotyledonous vines. **A.** Nodal region of *Mucuna*, with the base of the internode unthickened. **B.** Nodal region of *Thunbergia grandiflora*, with the base of the internode thickened. **C.** Searcher shoot of *Mucuna*. **D.** Searcher shoot of *Thunbergia grandiflora*, with angular bends at the bases of internodes.

ternodes of *Vicia faba*, investigators have avoided an examination of cell division as presented in our study. The principle advantage of data on mitotic index is its directness, since it does not depend on a comparison between the average cell numbers of several samples to locate meristematic activity. Our findings are consistent with the data of Jahn (1941) which show a decline in cell division prior to large increases in cell elongation.

Sachs (1965) chose to emphasize the important role of subapical meristematic activity in sustaining stem elongation by calling it a "primary elongating meristem." In our previous paper, the extent of subapical meristematic activity was confirmed for the first time in monocotyledons with actual counts of mitoses (Fisher and French, 1976). The most extensive primary elongating meristems were found in climbing monocotyledons such as *Gloriosa*, *Korthalsia*, *Luzuriaga*, and *Dioscorea*, in which the meristematic region extended from 1.9 cm to 18.1 cm below the apical dome. In the dicotyledonous climbers examined here, large uninterrupted elongating meristems were also present in such species as *Ipomoea*, *Mucuna*, *Schlegelia*, and *Passiflora*, in which meristematic activity extended 4.3, 4.2, 5.4, and 2.4 cm below the apical dome, respectively.

Sachs (1965) also stated that a region of lower meristematic activity usually separates the apical dome from subapical meristematic tissues. This is consistent with our observations that in the meristematic regions of many species the mitotic index increases to a maximum value some distance from the apex and then declines in both dicotyledons (Fig. 3, 4, 6, 7) and in monocotyledons (Fig. 8–10; also see *Gloriosa*, *Luzuriaga*, *Alpinia*, in Fisher and French, 1976). The subapical peak in mitotic index may represent a regular feature of some shoot meristematic regions; however, more detailed studies are required to establish this point. Additional studies are also required to determine if mitotic index accurately reflects the rate of cell proliferation (Gifford and Corson, 1971). In other species of angiosperms, the subapical meristematic region extends a number of internodes below the apex, although the highest mitotic index is found in the apex.

In the uninterrupted meristems examined here, growth is more rapid and prolonged in the upper part of the internode, and consequently the amount of growth is greater than in the lower part of the internode. The upper part of the internode is not an intercalary meristem in the sense that it is a region of isolated meristematic activity. The decline in mitotic index progresses from the top of an internode into the lower part of the next internode above. Burström (1974) has described the stem of *Pisum sativum* as growing in the apical ends of the internodes "in a number of separated intercalary meristems." We have marked adjacent young internodes of *Pisum sativum* into three equal segments and measured growth increments (unpublished observations). A wave of growth progresses acropetally through the internodes. Isolated regions of residual growth, which are typical of our concept of intercalary meristems, are absent, even though the apical regions of the internode were sites of greater growth. Although the value of U/L in various species differed widely (from 1.0 to 3.4), the differences were not correlated with the ratio of final cell length in U vs. L. Final cell length in *Helianthus* is also reported to be relatively uniform throughout the internode, although the upper region contributes more to final internode length (Garrison, 1973).

At this time, we feel it is appropriate to comment on certain aspects of the relationship between cell division, cell elongation and growth. As Haber and Foard (1963) have reemphasized, an increase in organ size cannot result directly from cell division alone, and in that sense the term "growth by cell division" has no meaning. Instead, the growth of internodes can be divided into an initial phase with both cell division and elongation, and a second phase without cell division. The end of the cell division phase precedes the rapid period of internode elongation in *Vicia faba* (Jahn, 1941) and *Avena* (Kaufman, Cassell and Adams, 1965), while cell division in *Helianthus* is reported to continue up until the end of internode elongation (Garrison, 1973). Enright and Cumbie (1973) made an attempt to evaluate the relative "importance" of cell division versus cell elongation in the growth of long and short internodes of *Phaseolus*. For short internodes, the cell length increased 4 × from young to mature internodes, while cell number increased 1.7 ×. It was concluded that cell elongation was the dominant factor in the growth of short internodes. In long internodes, cell elongation and division were considered equally important because the ratios of length and number increase were about equal, 4.5 × and 4 ×, respectively, between young and mature internodes. These data actually reflect differences in the duration of the phase of internode growth with cell division, which is longer in the long internodes. It is a matter of coincidence that the ratios of cell number increase and cell length increase are similar for long internodes, i.e., extremely high ratios of increase in cell number could be obtained by selection of much younger internodes.

The only vine found to have an internodal intercalary meristem was *Thunbergia grandiflora*. In *T. grandiflora*, a small region of residual meristematic activity is located at the base of the internode. Although this basal region is capable of reorienting the stem in the manner of a pulvinus (as in some other members of the Acanthaceae; Rentschler, 1929), it does not make a significant quantitative contribution to the overall growth of the internode (less than 10% of the final internode length). In this respect the development of the internode in *Thunbergia grandiflora* differs from the intercalary meristems found in grasses and sedges. These intercalary meristems account for a considerable proportion of the internode (Buchholz, 1920; Evans, 1969).

There is some indication in the older literature that the organization of internodal meristems in dicotyledons is at least as diverse as in monocotyledons. Grisebach (1843) long ago showed that residual basal growth of internodes takes place in certain families, e.g., Polygonaceae and Caryophyllaceae. Basal growth of internodes in *Silene* (Caryophyllaceae) contributed less than basal growth in *Polygonum*, which accounted for much of the final length of the internode. The basal regions of internodes in both families have been reported to function like pulvini (Rentschler, 1929) and seem to be similar to *Thunbergia grandiflora*. Unequal growth in the basal regions of *Polygonum* has been reported by Burkom (1913). The presence of an intercalary meristem in the Chenopodiaceae has been cited by Fahn (1967). Biopolar growth of *Astrantia* (Apiaceae) was described by Grisebach (1843), with growth more pronounced in the upper part of the internode.

In *T. grandiflora* the region of residual growth is also the site of a stem swelling. Swollen regions of internodes have been correlated by Troll (1937) with regions of residual primary growth in other dicotyledons at the base of an internode (Caryophyllaceae, Polygonaceae), or at the top of an internode (*Galeopsis*, Lamiaceae, and presumably some Apiaceae). For all of these species, definitive information on the distribution of meristematic activity which would confirm the presence of an intercalary meristem is lacking. A broader survey of meristematic organization during internode development in dicotyledons should prove useful for comparison with monocotyledons.

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