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Internodal Meristems of Monocotyledons: Further Studies and a General Taxonomic Summary

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ABSTRACT

The occurrence of uninterrupted (UM) and intercalary (IM) meristems in the internodes of vegetative and/or reproductive axes is reported for 90 species in 34 families of monocotyledons. Meristem type was determined by measuring regions of surface elongation and cell division in developing internodes. Many aquatic and predominantly tropical families are included. These new data and previously published information are presented in a summary of 45 families in 19 orders of monocotyledons (*sensu* Takhtajan, 1969). The distribution of UM's and IM's is about equal among families and orders. Phylogenetic trends are not apparent in the distribution. Generally, UM's tend to predominate in vegetative internodes, and IM's tend to predominate in reproductive internodes.

INTRODUCTION

Internodal extension is particularly significant in establishing shoot form in the monocotyledons, since most species lack secondary growth. Grasses and sedges have localized meristematic regions at the bases of their internodes—intercalary meristems (IM) that are often cited as 'typical' of internodal development in monocotyledons. However, IM's are absent in many families, and the IM may be another example of the inaccurate grass stereotype of the group which was noted by Tomlinson (1970).

We have found two basic types of meristematic organization in internodes of monocotyledons—the uninterrupted meristem (UM) and the above-mentioned IM, both widely distributed among tropical families (Fisher and French, 1976; French and Fisher, 1977). We now present new information on internodal development for both temperate and tropical families, including many aquatics. Both reproductive and vegetative axes are examined in our present survey.

The descriptions of UM and IM are clearly applicable to most of the species examined, demonstrating the usefulness of those terms. New observations are combined with those of previous reports to give a general taxonomic summary of the distribution of internodal meristems among the families and orders of monocotyledons.

MATERIALS AND METHODS

Material for both anatomical and marking studies was collected from a number of locations. Vigorous horticultural specimens were studied and collected at Fairchild Tropical Garden (Miami), University of California Botanical Garden (Berkeley) and the Royal Botanic Gardens (Kew). Native species were also studied and collected in the field in California, Florida and Louisiana. All material is vouchered in the Fairchild Tropical Garden herbarium (FTG).

Species with well-developed, long internodes in the vegetative and/or reproductive axes were chosen for study. In many species little distinction was observed between the vege-

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TABLE 1. *Types of internodal meristems found in various species of monocotyledons arranged alphabetically by family* (after Takhtajan, 1969).

Family/Species	Uninterrupted meristem*	Intercalary meristem*
Agavaceae		
Agave braceana Trelease	Rb	
Manfreda (*Agave*) sp.	Rb	
Sansevieria sp.	Rb	
Cordyline terminalis (L.) Kunth	Rb	Rb
Alismaceae		
Echinodorus ranunculoides Engelm.	Va	
Echinodorus cordifolius (L.) Griseb.	Ra	
Sagittaria latifolia Willd.	Va	
Sagittaria lancifolia L.	(Rb)†	Rb
Alliaceae		
Agapanthus africanus Beauverd.	Rb	
Allium cepa L.		Rb‡
Allium tuberosum Rottl. ex K. Spreng.		Rb
Amaryllidaceae		
Hippeastrum evansiae (Traub & Nelson) H. E. Moore	Va	Rab
Stenomesson variegatum MacBride		Rb
Araceae		
Anthurium andraeanum Lind.	Rb	
Anthurium salviniae Hemsl.	Rb	
Anthurium sp.	Rb	
Zantedeschia aethiopica (L.) Spreng.	Rb	
Aglaonema robelinii Hort. ex Gentil.		Ra
Pistia stratiotes L.		Va
Spathiphyllum floribundum N.E.Br.	(Rb)†	Rb
Spathiphyllum cochlearispathum Engl.	(Rb)†	Rb
Spathiphyllum kochii Engl. & Krause		Ra
Arecaceae		
Chamaedorea elegans Mart.	Ra	
Chamaedorea (*oreophila* Mart. × *sartorii* Liebm.)	Ra	
Thrinax morrisii H. Wendl.	Ra	
Calamus australis Mart.		Ra
Calyptrogyne ghiesbreghtiana (Linden et H. Wendl.) H. Wendl.		Ra
Paralinospadix hollrungii (Becc.) Burret		Ra
Phoenix reclinata Jacq.		Ra
Ravenea sp.		Ra
Syagrus oleracea Becc.		Ra
Bromeliaceae		
Aechmea (*racinae* L. B. Sm. × *victoriana* var. discolor M. B. Foster)	Ra	
Dyckia rariflora Schult.	Ra	
Tillandsia utriculata L.	Rb	
Tillandsia usneoides L.		Vab
Burmanniaceae		
Burmannia disticha L.	Rb	
Cannaceae		
Canna warscewiczii Otto & Dietr.		Rab
Cyclanthaceae		
Ludovia sp.		(Vab ?)§
Cymodoceaceae		
Halodule wrightii Aschers.	Va	
Syringodium filiforme Kuetz	Va	Ra
Cyperaceae		
Cyperus rotundus L.	Va	Rb
Eleocharis cellulosa Torr.	Va	Rb
Eriocaulaceae		
Eriocaulon compressum Lam.		Rb
Haemoridaceae		
Anigozanthos flavida DC	Rb	

TABLE 1—(*continued*)

Family/Species	Uninterrupted meristem*	Intercalary meristem*
Heliconiaceae		
Heliconia crassa Griggs	Ra	
Heliconia psittacorum Sessé & Moc.		Rb
Hydrocharitaceae		
Halophila baillonis Aschers.	Va	
Vallisneria americana Michx.	Va	
Hydrilla verticillata Royle		Va
Iridaceae		
Iris chamaeiris Bertol.	Rb	
Iris confusa Sealy	Vab	
Iris pseudacorus L.	Rb	
Sisyrinchium striatum Sm.	Rb	
Trimezia martinicensis (Jacq.) Herb.	Rb	
Tritonia hybrid	Rb	
Watsonia versfeldii Mathews & L. Bolus	Rb	
Neomarica sp.		Rb
Watsonia sp.		Rab
Juncaceae		
Juncus effusus L.		Rb
Juncaginaceae		
Triglochin striata Ruis & Pav.	Rb Va	
Lilaea scilloides (Poir.) Haum.		Ra
Liliaceae		
Aloe ferox Mill.	Rb	
Aloe vogstii Reynolds	Rb	
Aloe umfoloziensis Reynolds	Rb	
Arthropodium cirrhatum R. Br.	Rb	
Bulbine aloides (?) Willd.	Rb	
Dianella sp.	Ra	
Hemerocallis sp.	Rb	
Ornithogalum caudatum Jacq.	Rb	
Limnocharitaceae		
Hydrocleys nymphoides Buchen.		Va
Marantaceae		
Calathea lindeniana Wallis		Rb
Najadaceae		
Najas mariana L.		Va
Orchidaceae		
Epidendrum ibaguense HBK	Ra Vb	
Paphiopedilum sp.	Rb	
Phalaenopsis lueddemanniana Rchb. f.	Rb	
Phaius tankervilliae (Ait.) Blume	Rb	
Phragmipedium longifolium (Rchb. f.) Rolfe	Rb	
Pholidota imbricata Lindl.		Rb
Pontederiaceae		
Eichhornia crassipes (Mart.) Solms-Laub.		Vab
Pontederia lanceolata Nutt.		(Rb†)
Potamogetonaceae		
Potamogeton illinoensis Morong.	Va	Ra Va
Ruppiaceae		
Ruppia maritima L.		Ra Vab
Sparganiaceae		
Sparganium androcladum (Engelm.) Morong.	Ra Va	
Strelitziaceae		
Strelitzia reginae Ait.	Ra	
Taccaceae		
Tacca chantrieri André	Rb	
Tacca leontopetaloides (L.) O. Ktze.	Rb	
Typhaceae		
Typha domingensis Pers.	Ra Va	Ra

TABLE 1—(*continued*)

Family/Species	Uninterrupted meristem*	Intercalary meristem*
Xyridaceae		
Xyris jupicai L.C. Rich.		Rb
Zingiberaceae		
Globba bulbifera Roxb.	Ra	
Zosteraceae		
Zostera marina L.		Ra Va

* R = reproductive axis, V = vegetative axis, a = based on anatomical data, b = based on surface marking data.

† Bipolar growth, mostly basal growth but small amount of distal growth during geotropic bending of inflorescence.

‡ Unpublished data supplied by D. DeMason, University of California (Berkeley).

§ Uncertain meristem type because of very diffuse IM which was unlike any other IM.

tative shoot axis and the reproductive axis; such axes were considered reproductive. Thus, long internodes in species having terminal inflorescences closely associated with foliage leaves (*Canna*, *Iris*) were listed as reproductive (Table 1). In order to compare a wide range of plant habits, single long internodes, scapes below compact inflorescences (*Anthurium*, *Ornithogalum*, *Xyris*), and the numerous internodes in terminal (*Agave*) or lateral (*Chamaedorea*) inflorescences were all designated as reproductive internodes.

Young axes and internodes used for anatomical studies were fixed in FAA, or CRAF, embedded in Paraplast, sectioned at 10 μm, and stained with safranin, haematoxylin, and fast green. Average ground parenchyma cell length and mitotic index were determined for the upper, middle, and lower regions of internodes as in French and Fisher (1977). Young intact internodes were marked either by fine India ink lines or by fine needle pricks made when sheathing leaves obscured the immature internode. Most internodes were marked into thirds, and the growth of each region was noted weekly until elongation stopped. Sampling size varied greatly depending upon the availability of young growing axes. In this report, a species with a minimum replicate size of one or two axes is listed only if the localization of growth or mitotic index is not ambiguous. Many species which did not clearly show regions of growth or meristematic activity in limited samples have been omitted. Wherever possible, both anatomical and marking methods were used for the same species. Both methods gave consistent qualitative results in terms of general meristem type.

RESULTS

Criteria used in classifying meristem types are based on our previous and more detailed studies of internodal development. All internodes are initially meristematic throughout their length. The uninterrupted meristem (UM) is defined by a region of cell division that is confined progressively to the upper (distal) region of a developing internode. Therefore, internodes with mitoses localized in the distal region of the internode have a UM. This distal meristematic region is continuous with the sub-apical meristem of the shoot and is not isolated from the apex by mature tissues. The UM is correlated with an acropetal gradient of decreasing cell size due to acropetal tissue maturation within the growing internode. The steepness of the acropetal gradient of cell length varied considerably in different species. Surface markings also show that growth continues longer in the upper region than in the lower. Total elongation of the upper third of the internode may be equal to or greater than that of the lower third (see French and Fisher, 1977 and French, 1977 for specific examples).

The intercalary meristem (IM) is defined by a localized region of cell division in the lower (proximal) region of the developing internode. This region is discontinuous with the sub-apical meristem since it is isolated above and below by mature tissues. Tissue maturation is basipetal, and the gradient of cell size within the growing internode is, accordingly, opposite that of the UM. Surface markings also show that there is pronounced basal growth in the IM in which the elongation of the lower third is greater and more long-lived than that of the upper third.

These two types of internodal meristems represent clearly defined categories, and most anatomical and surface marking data fitted into one or the other. The species examined and the meristem types which they exhibit are listed alphabetically by family in Table 1. However, there were several species in which meristem type was not clearly defined, and these are reported on in greater detail.

Certain scapes exhibited pronounced and prolonged growth in the distal region of the single long internode as shown by marking studies. In *Anthurium*, *Bulbine* and *Ornithogalum* the ratios for the upper: lower segment lengths were equal to or greater than 3:1. The maturation of the inflorescence axis above the long internode, including the flowers, was also acropetal. The pattern of tissue maturation in these scapes qualified them as UM's, although only one elongated internode is present. The terminology is a convenient way to distinguish between the above conditions and inflorescences with prolonged basal growth (i.e. the IM's in the scape of *Spathiphyllum* or the long internode of *Phoenix*). This terminology is an outcome of our concept of *intercalary* which stresses the isolation of meristematic regions by mature tissues. However, this usage of IM has not been followed by some workers. Therefore, a note should be made of differences in usage.

A broader definition of IM has been used for any primary meristematic region removed from the apical meristem (Esau, 1965). The distal growth regions in the long internodes of scapes in the Asteraceae (Sachs, 1968), the gynophores of *Arachis* (Jacobs, 1947), and the fertile spikes of *Ophioglossum* (Peterson and Cutter, 1969), have been referred to as IM's. This conflict in terminology seems to be one of semantics, dependent upon the definition of intercalary and one's frame of reference. We considered the entire growth region of the shoot, including the apex, while the above authors were primarily concerned with a single internode. In an attempt to be consistent in our comparative survey, we refer to such meristems as localized UM's because these regions are not isolated from the meristematic regions of the inflorescence or floral axis by mature tissues.

In rhizomes of *Cyperus* and *Eleocharis* the internodes at the appropriate phase of growth exhibited well defined UM's with very localized distal meristematic regions. In marked contrast to the internodes of their rhizomes, the aerial axes of *Cyperus* and *Eleocharis* exhibited IM's. The presence of UM's in underground vegetative axes and IM's in upright reproductive and/or vegetative axes of the same plant was also found in *Hippeastrum*, *Potamogeton* and *Syringodium*.

In *Zantedeschia*, growth continued throughout the length of the single long internode of the inflorescence (scape) for a long time, presumably after cell division stopped. Growth first stopped at the base of the scape but continued slightly at the distal end after the inflorescence opened and until the spathe began to wither. In contrast, growth of the single long internode of the inflorescence of *Anthurium* (another species of Araceae) was much more localized in the distal region of the internode. In other Araceae with single long internodes, basal IM's were present (*Spathiphyllum*, *Aglaonema*).

Several other variations of internode development should be noted. The upper internodes of the inflorescence of *Pontederia* exhibited typical IM's with some slight growth in the distal regions of each of the several internodes at the end of internodal elongation. This renewed distal growth (= bipolar internode growth) was related to bending behavior of the inflorescence. The inflorescence became inverted by a series of bends at the nodes; the regions immediately above and below the node elongated. This striking geotropic behavior resulted in the late growth recorded in the upper region of the internode. In the scape of *Spathiphyllum*, which had a well developed IM, the distal region immediately below the spathe showed a slight amount of growth after basal growth had stopped. This may have been related to a reorientation of the inflorescence. Bipolar growth was also exhibited by the long basal internode of the *Sagittaria* inflorescence which stopped growing first in the middle, then at the distal end, and finally at the base. In *Cordyline* the basal and most elongated internode had an IM, while the remaining shorter internodes had UM's. In *Typha* the shorter basal internodes associated with foliage leaves had UM's, and the greatly elongated internode below the inflorescence had an IM.

The only species examined in which internodal meristems could not be categorized was *Ludovia* (Cyclanthaceae). The internodes grew very slowly, and growth in the lower region was greater than in the upper region (for details see French, 1977) suggesting the presence of an IM. It was not possible to determine meristematic localization, because there were few dividing nuclei in any particular internode. The average ground parenchyma cells in rapidly expanding internodes were longest in the midregion and shortest in the upper and lower regions. The direction of tissue maturation was weakly basipetal, since raphid cells and metaxylem elements were slightly more mature in the upper region than in the lower. However, the strong basipetal gradient in tissue maturation and decreasing cell size seen in all other IM's was absent in *Ludovia*. For convenience, we tentatively consider *Ludovia* (Table 1) as having a very diffuse (or poorly defined) form of IM. We realize that this could possibly represent an intermediate type of internodal meristem for which a future detailed developmental study is necessary. This species is omitted from the summary Table 3 because of the uncertainty of meristematic organization.

DISCUSSION

The internodal meristems of all monocotyledons examined to date (with the single exception of *Ludovia*) fall into two broad classes, the IM and UM. The two categories are distinguishable both by localization of growth regions (via surface markings) and by regions of cell division and maturation (via anatomical observations), although the degree of localization and the intensity of cell division and growth may vary quantitatively.

Certain inherent limitations of the research methods used in this broad survey should be kept in mind. Only those axes with elongated, and therefore easily measured, internodes were selected for study. We presume that the relatively short internodes of thick stemmed axes (as in many palms) and of rosette plants develop by UM's, although our methods of study could not quantitatively demonstrate a distal localization in such short internodes. This may be a moot point with regard to rosette species in which the axis is basically composed of the leaf insertions with no internodes. The distinction between vegetative and reproductive axes may be somewhat arbitrary in determinate shoots (e.g. *Canna*, *Heliconia*, *Typha*) in which there is no clear boundary between the purely vegetative and reproductive regions.

The features distinguishing UM from IM may occur in a particular internode of a shoot for only a short time, since all internodes are uniformly meristematic in their early stages of development. For this reason, care must be taken to include the critical stage when studying an individual internode or shoot. It is reasonable to assume that sequential internodes of an indeterminate axis or a young determinate axis with homogeneous internode morphology represent approximate stages in the ontogeny of a single internode. However, in many determinate or heterogeneous axes only a developmental series of equivalent internodes can establish the type of meristematic organization. These procedures were carried out in the present study and in previous ones of this series.

The only morphological feature associated with meristem type is the presence of a completely sheathing leaf base in all species with IM's (this has been discussed in greater detail in Fisher and French, 1976). Sheathing leaf bases may or may not be associated with UM's. We assume that the main function of the sheathing leaf which is correlated to meristem type is support of the shoot in the unlignified IM region (as noted by Haberlandt, 1914). Protection is probably only a secondary function since the elongated and highly meristematic primary elongating meristems of vines (i.e. UM's) are for the most part unprotected by leaves (French and Fisher, 1977).

Stebbins (1974) has speculated on the adaptive and evolutionary significance of many vegetative features of monocotyledons. He stressed the important adaptive advance of IM's in the evolution of the monocotyledons. His meaning of IM is, however, similar to Esau's (1965) and quite different from our restricted use of the term. Stebbins (1974, p. 110) uses IM broadly to distinguish meristems that cause elongation of shoots (internodes), leaves, flower parts and other organs, in contrast to apical meristems. Thus, both the UM and IM described in our study would fall under his general meaning of IM.

Some botanists might over-estimate the significance of internodal IM's (our usage) in the monocotyledons because of their grass orientation (a point forcefully made by Tomlin-

TABLE 2. *Types of internodal meristems found in the families of monocotyledons arranged after Takhtajan* (1969)

Order/Family (gen./sp.)*	Uninterrupted meristem†	Intercalary meristem†
Alismales		
Butomaceae (0/0)	—	—
Limnocharitaceae (1/1)	—	Va
Alismaceae (2/4)	Ra Va	Ra
Hydrocharitales		
Hydrocharitaceae (3/3)	Va	Va
Najadales		
Scheuchzeriaceae (0/0)	—	—
Juncaginaceae (2/2)	Ra Va	Ra
Aponogetonaceae (0/0)	—	—
Zosteraceae (1/1)	—	Ra Va
Posidoniaceae (0/0)	—	—
Potamogetonaceae (1/1)	Va	Ra Va
Ruppiaceae (1/1)	—	Ra Va
Zannichelliaceae (0/0)	—	—
Cymodoceaceae (2/2)	Va	Ra
Najadaceae (1/1)	—	Va
Triuridales		
Triuridaceae (0/0)	—	—
Liliales		
Liliaceae (11/14)	Rahj Vbcd	Rei
Xanthorrhoeaceae (0/0)	—	—
Aphyllanthaceae (0/0)	—	—
Alliaceae (2/2)	Ra	Ra
Agavaceae (4/4)	Ra Vb	Ra
Amaryllidaceae (2/2)	Va	Ra
Alstroemeriaceae (1/1)	Vd	—
Haemodoraceae (1/1)	Ra	—
Hypoxidaceae (0/0)	—	—
Velloziaceae (0/0)	—	—
Philesiaceae (1/1)	Vbcd	—
Tecophilaeaceae (0/0)	—	—
Cyanastraceae (0/0)	—	—
Asparagaceae (1/1)	Vd	—
Smilacaceae (1/2)	Vbcd	—
Stemonaceae (0/0)	—	—
Dioscoreaceae (1/2)	Vbcd	—
Taccaceae (1/2)	Ra	—
Pontederiaceae (2/2)	—	Ra Va
Philydraceae (0/0)	—	—

TABLE 2—(*continued*)

Order/Family (gen./sp.)*	Uninterrupted meristem†	Intercalary meristem†
Iridales		
Iridaceae (6/9)	Ra Va	Ra
Geosiridaceae (0/0)	—	—
Burmanniaceae (1/1)	Ra	—
Corsiaceae (0/0)	—	—
Zingiberales		
Strelitziaceae (1/1)	Ra	—
Musaceae (0/0)	—	—
Heliconiaceae (1/2)	Ra	Ra
Lowiaceae (0/0)	—	—
Costaceae (1/1)	Vb	—
Zingiberaceae (2/2)	Ra Vab	—
Cannaceae (1/2)	—	Rae
Marantaceae (2/2)	—	Ra Vb
Orchidales		
Orchidaceae (10/10)	Ra Vabcd	Ra Vb
Juncales		
Juncaceae (1/1)	—	Ra
Thurniaceae (0/0)	—	—
Cyperales		
Cyperaceae (3/6)	Va	Ra Vbefkm
Bromeliales		
Bromeliaceae (3/4)	Ra	Va
Commelinales		
Commelinaceae (3/5)	—	Vbel
Mayacaceae (0/0)	—	—
Xyridaceae (1/1)	—	Ra
Rapateaceae (0/0)	—	—
Eriocaulales		
Eriocaulaceae (1/1)	—	Ra
Restionales		
Restionaceae (2/2)	—	Vbn
Centrolepidaceae (0/0)	—	—
Flagellariaceae (1/1)	—	Vb
Hanguanaceae (0/0)	—	—
Poales		
Poaceae (17/25)	—	Rfg Vbef
Arecales		
Arecaceae (10/12)	Ra Vb	Ra
Cyclanthales		
Cyclanthaceae (1/1)	—	(Vad ?)‡
Arales		
Araceae (7/12)	Ra Vbcd	Ra Va
Lemnaceae (0/0)	—	—
Pandanales		
Pandanaceae (1/1)	Vb	—
Typhales		
Sparganiaceae (1/1)	Ra Va	—
Typhaceae (1/1)	Ra Va	Ra

* Number genera/number species cited in the information source noted.

† R = reproductive axis, V = vegetative axis, letters indicate source of information as follows: a, original observations given in Table 1; b, Fisher and French (1976); c, French and Fisher (1977); d, French (1977); e, Buchholz (1921); f, Schmalfuss (1930); g, Kaufman, Cassell and Adams (1965); h, Kaldewy (1957); i, Hanks and Rees (1975); j, Kelder, Benschop and De Hertogh (1971); k, Evans (1965); l, Scott and Priestley (1925); m, Fisher (1970); n, Botha and Schijff (1976).

‡ Very diffuse IM unlike all other IM's. Omitted from Table 3 because of uncertainty.

TABLE 3. *Frequency of types of internodal meristems occurring in the families and orders listed in Table 2**

	Uninterrupted Meristem†			Intercalary Meristem†		
	R	V	Total	R	V	Total
Families	18	23	30	24	16	31
Orders	10	12	13	14	12	17

* Cyclanthaceae (Cyclanthales) omitted because of uncertainty of meristem type.
† R = reproductive axis, V = vegetative axis.

son, 1970). The rapid elongation of shoots, especially in reproductive structures of grasses (Poaceae) and sedges (Cyperaceae), is a consequence of one or more active IM's. However, long internodes or rapid shoot extension is not always associated with IM's. The long and rapidly growing internodes of rattan palms and other viny monocotyledons develop by UM's. The long reproductive axes of *Aloe*, *Agave*, *Iris*, *Tillandsia*, etc., and the scapes of *Agapanthus*, *Anthurium*, *Ornithogalum*, *Tulipa*, etc. also develop by UM's.

The taxonomic distribution of meristem types is presented in Table 2. Original data and previously published information are summarized for 45 of the 68 families of Takhtajan (1969) that are in 19 of his 20 orders. Many omitted families consist of predominantly or entirely saprophytic species (Triuridaceae, Corsiaceae, Geosiridaceae) or reduced aquatic species (Aponogetonaceae, Lemnaceae); their inclusion in an internodal survey may be inappropriate.

The IM is characteristic for the Cyperales, Commelinales, and Restionales. The IM is not particularly characteristic for the Liliales (with the exception of Amaryllidaceae and Pontederiaceae), Iridales, Bromeliales, Arecales, and Pandanales, although a few species possess IM's (see Table 1). Rosette plants often have an IM present in their scape, the only elongated internode of the shoot (Xyridaceae, Eriocaulaceae). There appears to be a diversity of internodal meristems in the Orchidales and Arales. An expanded study of these two large orders may be very useful in correlating meristem type with habitat or with ecological strategies of related species. For example, IM's have only been found in terrestrial orchids (*Sobralia* and *Pholidota*) among the small number of orchid species that have been studied.

In reviewing the taxonomic distribution of meristem types, there appear to be some broad trends at the superordinal level. The Juncanae and Commelinanae of Takhtajan (1969), or the Commelinidae of Stebbins (1974), have a predominance of IM's. The Arecanae (of Takhtajan) or the Arecidae (of Stebbins) tend to lack vegetative IM's. The remaining superorders (Alismanae and Lilianae or Alismatidae and Liliidae) have a wide variety of IM's and UM's and cannot be characterized by one or the other type. We feel that no phylogenetic trends can be seen in the distribution of meristem types other than in the uniformity of type in obviously natural families (e.g. Poaceae, Commelinaceae, etc.).

The distribution of meristem types for monocotyledons as a whole is presented in Table 3. The total number of families and orders with IM's and UM's is approximately equal. The UM is more frequent in vegetative axes, and the IM is more frequent in reproductive axes. This may be misleading since many rosette species (presumably with UM's in their short vegetative axes) are only recorded by the single long internode of the scape which has an IM. In conclusion, this survey shows that IM's are widespread among monocotyledons and are more common than among dicotyledons. However, UM's are also characteristic of monocotyledons and are about equally distributed throughout the group. One must take care, as noted by Tomlinson (1970), not to generalize all monocotyledons by the characteristics of grasses.

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LITERATURE CITED

BOTHA, D. J. and SCHIJFF, H. P. VAN DER, 1976. The structure and ontogeny of the chlorenchyma in the stems of *Elegia* L. (Restionaceae). *J. S. Afr. Bot.* **42,** 57–62.

BUCHHOLZ, M., 1921. Über die Wasserleitungsbahnen in den interkalaren Wachstumszonen monokotyler Sprosse. *Flora* **14,** 119–86.

ESAU, K., 1965. *Plant Anatomy,* 767 pp. 2nd edn. John Wiley and Sons, New York.

EVANS, P. S., 1965. Intercalary growth in the aerial shoot of *Eleocharis acuta* R. Br. Prodr. I. Structure of the growing zone. *Ann. Bot.* **29,** 205–17.

FISHER, J. B., 1970. Development of the intercalary meristem of *Cyperus alternifolius*. *Am. J. Bot.* **57,** 691–703.

—— and FRENCH, J. C., 1976. The occurrence of intercalary and uninterrupted meristems in the internodes of tropical monocotyledons. Ibid. **63,** 510–25.

FRENCH, J. C., 1977. Growth relationships of leaves and internodes in viny angiosperms with different modes of attachment. *Am. J. Bot.* **64,** 292–304.

—— and FISHER, J. B., 1977. A comparison of meristems and unequal growth of internodes in viny monocotyledons and dicotyledons. Ibid. **64,** 24–32.

HABERLANDT, G., 1914. *Physiological Plant Anatomy,* reprint Edn. of 1965, Today and Tomorrow's Book Agency, New Delhi, 777 pp.

HANKS, G. R. and REES, A. R., 1975. Scape elongation in *Narcissus*: the influence of floral organs. *New Phytol.* **75,** 605–12.

JACOBS, W. P., 1947. The development of the gynophore of the peanut plant, *Arachis hypogaea* L. I. The distribution of mitoses, the region of greatest elongation, and the maintenance of vascular continuity in the intercalary meristem. *Am. J. Bot.* **34,** 361–70.

KALDEWY, H., 1957. Wachstumsverlauf, Wuchsstoffbildung und Nutations—bewegungen von *Fritillaria medeagris* L. im Laufe der Vegetations-periode. *Planta* **49,** 300–44.

KAUFMAN, P. B. CASSELL, S. J. and ADAMS, P. A., 1965. On nature of intercalary growth and cellular differentiation in internodes of *Avena sativa*. *Bot. Gaz.* **126,** 1–13.

KELDER, P. OP DEN, BENSCHOP, M. and DEHERTOGH, A. A., 1971. Factors affecting floral stalk elongation of flowering tulips. *J. Am. Soc. hort. Sci.* **96,** 603–5.

PETERSON, R. L. and CUTTER, E. G., 1969. The fertile spike of *Ophioglossum petiolatum*. I. Mechanism of elongation. *Am. J. Bot.* **56,** 473–83.

SACHS, R. M., 1968. Control of intercalary growth in the scape of *Gerbera* by auxin and gibberellic acid. Ibid. **55,** 62–8.

SCHMALFUSS, K., 1930. Untersuchungen über die interkalare Wachstumszone an Glumifloren und dicotylen Blütenschäften. *Flora* **124,** 333–66.

SCOTT, L. I. and PRIESTLEY, J. H., 1925. Leaf and stem anatomy of *Tradescantia fluminensis* Vell. *Bot. J. Linn. Soc.* **47,** 1–28.

STEBBINS, G. L., 1974. *Flowering Plants: Evolution above the Species Level,* 399 pp. Belknap Press of Harvard University Press, Cambridge.

TAKHTAJAN, A., 1969. *Flowering Plants: Origin and Dispersal,* 310 pp. Smithsonian Institution Press, City of Washington.

TOMLINSON, P. B., 1970. Monocotyledons—towards an understanding of their morphology and anatomy. *Adv. Bot. Res.* **3,** 207–92.