AN APPRECIATION OF MONOCOTYLEDONS

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ABSTRACT. Monocots are characterized for the student who has studied dicots as the angiosperm type. Due to only limited secondary growth from an intercalary meristem, monocots are linear in form rather than cubic, and shoots are determinate with existence continued through a sympodial succession of shoots which forces the monocot to be motile as seen on a compressed time scale. Intercalary growth separates the plant into phytomer units, which, unlike the phyton units of 19th century dicot morphologists, are useful units for study and analysis of monocot plants. Most common movements of orientation are leaf movements with the stem carried passively.

The monocot embryo may be regarded as a highly determinate shoot of one leaf and one root with further growth from the bud growing point.

Considering some monocot sub-groups, plants in some families develop a group of primordia in a tightly welded nursery above the apical meristem. In Araceae, absence of vessels in stems, their presence in roots, suggests that prop roots function as substitute stems in both conduction and support.

INTRODUCTION

The purpose of this paper** is twofold. First, in working with monocots the author has developed views of monocot morphology which he would like to express. Second, he feels that botany students, and often teachers too, are so strongly oriented to dicot structure, they see monocots with only peripheral vision. This paper takes a *direct* look at some monocot features.***

The already ancient monocots became a significant part of the fossil flora in the Cretaceous. Attempts have been made to propose dicot-monocot relationships, but the fossil records are lacking. Here I propose that some monocot features can be interpreted by hypothesizing an aquatic origin—a second or separate emergence onto land from an aquatic beginning.

The following adaptations to an aquatic existence appear to me to contribute to monocot character. First, roots of aquatics function primarily in anchorage and their function in water and mineral uptake is reduced. Second, movements of waves and currents tend continually to tear plants apart, and in many water plants fragmentation takes place in a fashion such that pieces torn off are able to survive and carry on as individuals—that is, fragmentation becomes a means of vegetative reproduction.

It is also a water environment that could confer survival advantage on the development of an intercalary meristem, with production of extended leaves from an often condensed stem. Extended leaves can reach the greater light at the water's surface. There wave action tends to bruise and injure those extremities. In water, bruised areas are quickly pruned by fungi and other organisms. The whole plant suffers less if injured portions are older worn plant parts that can be replaced from a protected core, than if they are young or growing regions with a growth contribution still to make.

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*** In considering the generalized monocot, attention is not given to the many exceptions which will come to mind.
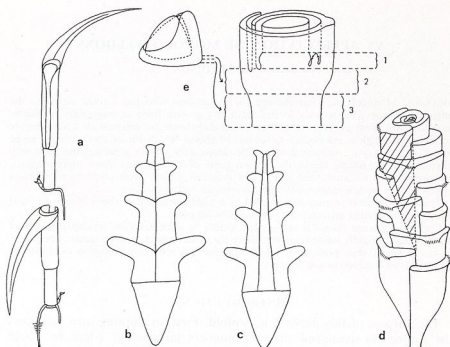
FIG. 1.**a**, the phytomer idea pictures a monocot plant as made of chains of repeating units; each unit consists of leaf blade, sheath, internode, and node with shoot bud and adventitious roots.

b–c, the phyton concept tried in various ways to see a unity of stem and leaf; in one version, **b**, the stem consisted of adnate decumbent leaf bases; in another version, **c**, leaf bases formed the cortex around a central axis. (After McLean & Ivimey-Cook).

d, phytons formed a pseudoaxis in a hypothesis of Priestley. As the median bundle of one leaf connected with a marginal bundle nine leaves below, he pictured in *Alstroemeria*, a stem of fitted leaf bases as the one shaded. (After Priestley et al).

e, at the left a leaf primordium and growing point are illustrated. The nodal plate of the leaf primordium is shown divided into two portions. The internode will be intercalated between these by divisions of the lower portion. The mature node will consist then of two parts. Part 2 is the top of the nodal plate associated with the leaf, and part 1, with root and shoot buds is the basal plate from the leaf above. Part 3 is intercalated internode. (After Sharman).

In going from land to water, the ancestral plant lost some adaptations to survival on land. In emerging a second time from water, new modes were evolved for enduring the stresses of a land environment. This new attack on an old problem produced what I should like to call a new philosophy of plant organization, but—to avoid teleology—I shall say it produced features providing effective adaptations for survival, which differed in salient respects from those of dicots.

One mode that distinguishes the monocot is that its development is essentially *linear* instead of cubic. The monocot growing point moves to generate a line. Limited secondary growth by the intercalary meristems is along the axis formed, and extends the line of growth. The apical growing point of dicots also generates a line, but the cambium is a plane, rolled into a cylinder, and secondary growth by this plane generates a solid. The dicot

builds solidly in three dimensions centering on an axis which branches to permeate the soil below ground, and the air space above.

In the water, monocots lost the (need for a) structural supporting cone, and developed a fragmenting structure. The presence of intercalary meristems divided the axis into a series of repeating units. Each unit consists of a leaf, internode, a shoot bud and a basal node with buds of adventitious roots; each unit is capable of food manufacture, storage, growth, water and mineral uptake, and reproduction of similar chains of units by growth of the bud (fig. 1a).

The idea of a plant as made of repeating units has had a long history. Goethe proposed phyton units as early as 1817. In 1841, Gaudichaud hypothesized that the shoot is of segments, each composed of a portion of stem and the leaf belonging to it (fig. 1b). Hofmeister (1863) considered that there were both phytons and a shoot axis; that the decurrent leaf bases formed the cortex of the stem (fig. 1c). Priestley (1935) was among those who favoured the idea of a pseudoaxis of overlapping units. This idea is shown diagramatically in fig. 1d from one of his papers. The *Alstroemeria* shown has a pattern in which the midrib of one leaf crosses the central ground tissue and joins with a marginal leaf bundle nine nodes below. This was presumed to define a pseudoaxis, formed, at any point, by the adnation of nine leaf bases. Several of Priestley's students examined other plants for similar relations. One student, Sharman (1942) failed to find a uniformly repeating vascular connection in maize (*Zea*) though he gave us a classic study of monocot morphology.

One point of grass morphology that Sharman clearly stated was the dual nature of the node. The intercalary meristem divides so as to intercalate the internode between two portions of the original nodal plate.* Hence at a mature node, the bud and root initials are associated with the leaf above rather than the leaf to which they are axillant (fig. 1e). The association of bud and roots of *Zea* with the internode and leaf above had also been noted by Weatherwax (1923) earlier, and Skutch (1927) had noted that in *Musa* the bud associated with a leaf was not the one axillary, but that at the union of the sheath margins at their insertion. Weatherwax applied the term *phytomer* to the structure shown in fig. 1a and analyzed the maize plant in terms of repeating units of phytomers. Phytomer was originally used by Asa Gray (1879). He defined phytomer as a structure, which, when produced in a series, results in a structure of higher grade.

The phyton concept has not been productive in dicot studies where the effort has been to study the stem in terms of leaf related structures. But in monocots the intercalary meristem cuts off repeating units and Weatherwax, Evans (1940), and Etter (1951) have all used the phytomer idea to advantage in studying *Gramineae*. Fig. 2 illustrates variations on the phytomer theme in *Poa pratensis* L. A wave of development begins at the leaf tip, and development proceeds from leaf blade to leaf sheath, to internode, to bud, and finally to the adventitious root growing point. As each part in turn develops more or less extensively, or fails to develop, we can get the variety of structures illustrated in fig. 2, from the same initial basic phytomer unit.

When a monocot seed germinates, the initial axis is small in diameter.

* Mr. B. L. Burtt notes that on this view we should perhaps speak of an *intranode* in monocots.
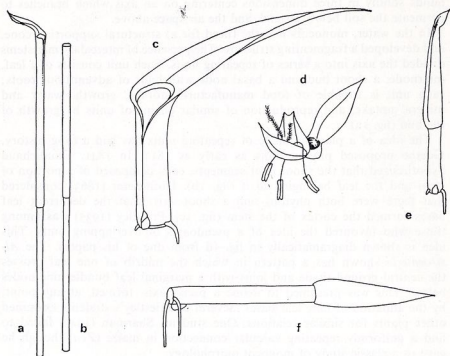
FIG. 2. The basic phytomer unit can take different forms in a grass plant. Culm phytomer **a** shows extensive development of the sheath and internode, but no development of root or shoot buds. Even blade development may be supressed—**b**. In the vegetative phytomer **c**, all parts are developed except the internode. In the floral phytomer **d**, the shoot bud is the only extensively developed part and forms the flower. In a rhizome phytomer the sheath comes to a point and there is no development of the blade **f** until the rhizome turns up, then a rudimentary blade appears—**e**. After emergence into the light the **c** type phytomer again predominates. (Based on *Poa pratensis* L.)

But each succeeding nodal plate is larger, and soon a "normal" size leaf and stem for that species is being produced. After a time however, added phytomers tend to decrease in diameter. The result is that the monocot axis tends to a spindle shape, tapering at each end. This is illustrated in fig. 3a–c which also sketches the basal taper of the *Pandanus furcatus* growing at the north end of the orchid house at the Royal Botanic Garden, Edinburgh. The spindle shape results from a determinate axis, and continued existence of an individual monocot is by growth of branch shoots.

[The necessity of a determinate axis in a plant without secondary growth is discussed in an excellent article by Holttum (1955) which looks keenly at monocots. He notes monopodial growth in some palms and grasses, and in a few orchids. But I know of no investigation as to whether monopodial monocot shoots are determinate. Shoot life of palms is long but in time a decreasing taper foretells death—perhaps because water transport from a fibrous root system can no longer support full secondary growth. Goethe based some of his ideas on portions of a palm (*Chamaerops humilis* L.) from Padua which is said to date from 1584 and which was alive in 1945. But there is no evidence of the time a single axis of this palm endured. I should guess old axes have been removed many times to make room for basal shoots.]
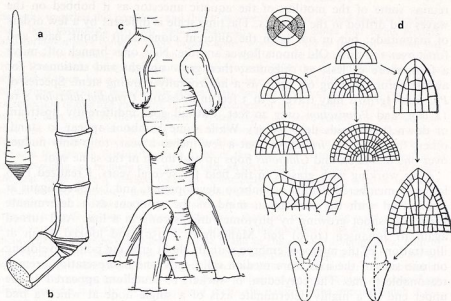
FIG. 3. The spindle-shaped axis of the determinate monocot shoot. The axis is shown diagrammatically in **a** and the basal portion is illustrated in **b** by a rhizome bud of *Phyllostachys*, and at **c** by *Pandanus*.
d, embryo development after similar octant stages, development of the embryo differs in dicots (left) and monocots (right). Two quarters divide more extensively in dicots whereas the whole monocot terminus divides uniformly. (After Swamy, 1962).

Thus far I have tried to develop the picture of a monocot plant as having a linear determinate shoot made up of repeating functional units named phytomers. Because an individual shoot is linear and determinate, a plant is motile.* To illustrate this, consider the grasses in a *Poa* lawn. An individual shoot is determinate, producing on the order of 14–20 leaves at about 8–18 day intervals over one or two growing seasons. A vigorous shoot will likely terminate in an inflorescence in June or July. If a shoot fails to flower, it terminates in time with production of one or two enfeebled phytomers.

Each branch shoot soon grows independently of the parent shoot. Each phytomer is capable of independent growth (and may be independent for a moment as it changes from a sink to an organ exporting excess photosynthate). Along the vegetative axis of *Poa* there are only three or four phytomers active at one time. Soon after the oldest phytomer fails to contribute, it is, in effect, discarded, and micro-organisms rapidly return it to humus.**

Because the small functioning part of the axis moves ahead by growth while the older part of the axis falls away in death, the functioning region

* Some dicots are motile, e.g. strawberry and many species of *Saxifraga*, but lack of secondary growth compels most monocots to keep moving.

** When one considers the limited life of a single phytomer and its independent ability to form root and shoot, and how it is set off by the intercalary meristem, the occasional serious effort to graft monocots is seen as inconsidered and irrelevant. Holttum (1955) notes a similar inconsidered redundancy when the botanist writes in his notebook, about a monocot, "fibrous root system".

retains some of the motility of the aquatic ancestor as it bobbed on the waves and drifted in the currents. The time scale is different by a few orders of magnitude; but in our lawn the different clones shift about, back and forth over the yard. Old shoots flower and die. New ones branch off; move a foot, more or less, as rhizomes; then grow upright and stationary for awhile before snaking off again as a horizontally growing stem. Species of *Poa* and *Agrostis* may travel 2 to 3 feet in a season, *Cynodon dactylon* 8 to 12 feet, and *Pennisetum* over 20 feet. Cat-tail goes indifferently upstream or down (but avoids deep water). While some bamboos appear to stand, others fairly gallop. *Iris* moves but a few inches a year, tulip only nudges over one diameter, and *Gladiolus* hops up and down in the same spot.

After working with grasses in the field for several years, I realized I no longer remembered details of embryo development, and I looked again at books, but with the concept in mind of the monocot as a determinate branching shoot growing by phytomer units strung in a line. As I turned again to Johansen (1950) and Maheshwari (1950) and looked again at illustrations of the monocot embryo with its shoot growing point developing on one side of the axis from median cells, only one interpretation seemed reasonable to me. The cotyledon, or sucker, or scutellum appeared as the upper end of a highly determinate axis of a single node at which a bud arises to produce a "normal" multifoliate shoot.

[There is, of course, no problem about one cotyledon except in the minds of men. In developing a picture of the plant kingdom as resulting from an evolutionary process, he has tried to visualize the relationships among plants. He found evidence that suggests to some that monocots are related in time to dicots, and the question has naturally been asked as to the nature of the change from two cotyledons to one. Fusion, splitting, suppression, displacement, reduction and so on have been examined as means that have been observed to result in changes in various plants. Each has been set forth as a hypothesis for cotyledonary change, and evidence gathered for or against such a hypothesis. For an example of a hypothesis of this kind see Boyd (1931) or Eames (1961).

There have been problems with words and their meanings. What is geographically a side may physiologically be a top or bottom (Randolph, 1936). Souèges (1954) and Maheshwari (1958) have adequately demonstrated that the monocot growing point arises from median layers to the side of the geometrical axis; that the embryo leaf arises from the apical layer.

Swamy (1962) has recently presented a related viewpoint in which he develops his thesis as follows: monocots and dicots are alike to the octant stage, though in both classes various groups reach the octant by dividing in different sequences. In each instance the resulting octant is quartered with respect to the long axis. In dicots, two opposite quarters develop more rapidly to produce the two cotyledons; the epicotyl develops in the depressed portion between. In monocots all four quadrants develop together and cotyledons and epicotyl both fail to differentiate from the structure which becomes terminal (fig. 3d). A growing point develops from the median layers rather than the apical layers of the octant.

Swamy concludes that, ". . . the essential differences between the dicotyledonous and monocotyledonous embryo will have to be looked for, neither in the number of cotyledons nor in their topographical relationships, but in the morphogenetic potentialities of the primary terminal meristems, especially the one at the shoot pole. In the dicotyledons these tissues develop into the functional root and shoot systems. In the monocotyledons on the other hand, the primary shoot meristem should be assumed to have become sterile and reduced to a stub-like termination in which are consolidated the derivative of the two cotyledons as well; the activity of the terminal root meristem is also similarly suppressed or is only transitory."

Swamy allows for the existence of two cotyledons in the determinate embryo axis. Arber (1925) argued somewhat differently 45 years ago. Of the need for cotyledonary equivalence she says, "I have myself come gradually to the conclusion that no logical

necessity underlies this postulate, and that it has been taken for granted because botanists have been hypnotized by their own terminology." She then notes that terms *prophyll* and *cotyledon* have come to imply organs apart, when they are in fact just the first leaf of a shoot or seedling. She goes on, "But why should it (the argument) be there at all? Herb Paris has its foliage in a four-membered whorl, while the related trinity flower has a whorl of three, but no one argues that *Paris* is derived from *Trillium* by splitting of one of its three leaves, or that *Trillium* comes from *Paris* by fusion of one of the two leaves, or reduction of one to a rudiment, or by displacement of one to another node. Why should we not, then, look at the cotyledonary system from the same standpoint and suppose that one section of the flowering plants is monocotylar—not because there has been a fusion of two seed leaves, nor because there has been a supression or displacement—but because the growth rhythm happens to be of the type that produces a single leaf at a node. Nothing can be more natural than such an occurrence in a group of plants in which the leaf bases have a marked tendency, completely to ensheath the axis—a character which, in itself, absolutely precludes the production of two leaves at a node."

What Arber, and Swamy, and I are saying is that none of the hypotheses for deriving one cotyledon from two has been satisfactory—that they are dealing with plant form at the wrong level of organization; that the answer to the question of the difference between dicotyledony and monocotyledony is to be found in the area of developmental control that explains why the sweet pea raises a standard, the poplar hangs a catkin. We are up against the problem of plant form, into which we have not yet driven any substantial wedge. Until we can move beyond our present limitations we will be most effective if we simply describe how the thing appears of itself—the nature of the impulse which it expresses.]

What I suggest is that the nature of growth and development in monocots is such that we can describe the embryo axis as a highly determinate axis of one node in which the growing point is the bud associated with the single seedling leaf (i.e. cotyledon). Such a description is agreeable with both the plant facts and many of our human abstractions, and it is also economical (Occam's razor). It proposes a description of the monocot impulse but offers no hypothesis of how it came to be that way.

It would be tidy to be able to demonstrate the monocot growing point as the bud of a single phytomer—the embryo. At the present, I suspect the lineage of monocots is too ancient for us to expect to find a simple picture of the embryo, uncomplicated by contradictory evidences from embryology, vascular anatomy, and developmental morphology. One can reasonably argue that the embryo is a single phytomer if one considers only the morphologically simpler grasses. In the simpler grasses there is no development of internode between the scutellum and root.* The vascular connection of root, shoot and bud occurs in a thin plane as it would in the nodal plate of a later phytomer in which the internode fails to grow in length. In a primitive type grass, *Streptochaeta spicata*, the coleoptile is not a cylinder but a flattened foliar leaf, and it is positioned between the scutellum and the growing point, the position of the bud prophyll (Reeder, 1953).

Development of the gramineous embryo has been described by Roth (1961). In the process of differentiation, first development is of the growing point and coleoptile which arise at the side of the long axis. The pattern of development is the same as that of an axillary bud. Next the scutellum develops at the apical end of the embryo following a leaf pattern of development. (In *Gramineae* the embryo apex produces the *scutellum*, a modified first cotyledonary leaf. The coleoptile or first green functioning leaf is

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* In some more extensively evolved monocots, including some grasses, the cotyledon doubles back on itself to form a *mesocotyl* by adnation with the internode of the first foliar phytomer.

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anatomically comparable to a prophyll or first bud leaf.) Lastly, growth of tissue below the bud forms the coleorhiza. The first root initial forms inside this tissue.

Grasses are specialized and the picture is broadened by looking at the onion. There the apex develops a leaf in which only the tip is specialized and remains within the seed as a sucker, the rest being very much green leaf. The leaf is divided into blade and sheath. At one side of the base of the hollow sheath is a growing point with leaf primordia, and the second leaf emerges from a pore in the sheath of the seedling leaf. The basal area of the seedling leaf is meristematic and the leaf continues to elongate for a time. The first root of onion differs from that of grasses, but before considering that difference I should like to consider seedling roots of dicots vs monocots.

The dicot seedling has an order of development with strong survival potential for a land plant. The root tip is immediately beneath the micropyle where water first enters the germinating seed. Thus it is the root which receives the first moisture stimulus. A wave of growth is initiated which begins with the root and passes up the axis successively to the hypocotyl, the cotyledons, and finally to the epicotyl. The significant point is that the water-gathering organ, the root, grows first and is well developed before any water losing organs (leaves and cotyledons) are developed. The ancestral monocot lost (or never developed) this precocious root development, and the seedling is at a disadvantage with respect to water uptake and anchorage.

Fig. 4 illustrates degrees of development that have taken place in the monocots. Fig. 4a illustrates a seedling of a number of the Alismales such as Naias, Alisma, or Butomus. I interpret this as the primitive monocot condition in which formation of an embryonic root has been lost. The basal end of the embryo produces root hairs which serve for anchorage and some uptake, and a root forms only after considerable development of the first or cotyledonary leaf. As these are water or bog plants, they are successful in spite of a lag in root development.*

In onion (4b) root and shoot emerge and begin development together. Development is balanced.

In grasses (4d) the coleorhiza, and where it occurs, the epiblast, are root tissue (Foard & Haber, 1962). While neither develops much at germination (there is elongation without division) every cell can produce a vigorous root hair so that in a tiny seed such as one of Agrostis, the seed can draw water from a soil volume many times the seed volume. These functioning root hairs provide one reason I consider the coleorhiza (and epiblast) to be a vestige of the first axile root, and the first active root to be already adventitious. A second reason is that the embryo root of grasses originates below the surface and digests its way out as either a branch root or adventitious root would. In the maize used in the classroom, the first root emerges from the end of the coleorhiza, but in many other grasses it emerges at random through the coleorhiza wall. In grasses, the coleorhiza may be an effective organ of water uptake at germination, and provides some anchorage while

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* Klebs (1885) notes several dicot seedlings similar in development to figure 4a, (his type 5) but the instances are isolated and terminate offshoot lines of evolutionary development.
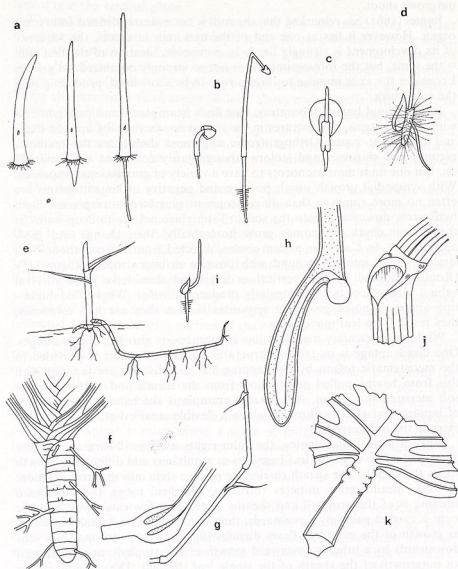
Fig. 4. Seedling development of monocots. In many plants of the Alismales the shoot develops ahead of the root **a**. In most seedlings, root and shoot develop simultaneously (**b**, *Allium*; **c**, *Zea*). In *Gramineae* root hair production by the coleorhiza and epiblast may provide moisture uptake for initial growth (**d**, *Poa*). **e–k**, stem orientation in monocots: **e**—down bending and upturning of the *Poa* rhizome is effected by differential growth of leaf sheaths. In *Cordyline* **f**, a basal bud grows vertically downward forming an upside down stem (after Arber). **g**—Grass rights itself by differential growth at the base of the sheath. **h**—A tulip dropper stem is directed downward by an outgrowth of the leaf sheath. **i**—The oat shoot is directed upward by response of the coleoptile (leaf) to gravity. **k**—At the upper end of the leaf sheath a collar or pulvinar region grows differentially to provide leaf orientation movements (**j**, *Poa* collar; **k**, *Monstera* petiole).

the coleoptile and first active root develop simultaneously. Root soon outgrows shoot.

Eames (1961) has remarked that the root is not a clearly defined embryonic organ. However it lies at one end of the axis and, in dicots, the sequence of its development is strongly fixed. In monocots, location of the first root is the same, but the rooting impulse is not so strongly organized. In grasses I consider the axile impulse to form a root to be short lived, producing only the coleorhiza.

In the school botany laboratory, one finds bean plants and pelargoniums with upright stems, and pictures in the school books showing upright stems and downright roots. Orthogeotropic alignment dominates the textbook picture, and rhizomes and stolons (though fairly common) are remarked on. But one finds most monocots to have a variety of gravitational responses. With sympodial growth usual, positive and negative orthogeotropisms are often no more common than diageotropic or plagiotropic responses. Stem buds grow downwards into the soil to form rhizomes, or to drop bulbs at the correct depth. Rhizomes grow horizontally, then change and grow upright (4e). In *Cordyline* a stem grows, directed from a basal shoot bud, straight down into the ground with positive orthogeotropism (figure 4f). (Roots produced by this vertical underground stem have good survival value.) Many dicot families regularly produce rhizomes. What I find interesting about monocot geotropic responses is that they are leaf responses, they result from leaf movements.

While an intercalary meristem has advantages, it also has disadvantages. One disadvantage is its lack of structural strength. Support is provided to the meristematic region by overlapping leaf sheaths. We are familiar with this from having pulled grass culms from the sheath and chewed on the soft meristematic region. An extreme example is the banana "tree" made of lapping leaf sheaths through which a flexible stem eventually snakes to extrude the infloresence.

When a wind lodges barley, the culm rights itself as illustrated in figure 4g. A pad of tissue at the leaf base acts as a pulvinus and differential growth rights the sheath. The sneath carries the passive stem into the erect position.

When meadowgrass initiates rhizomes, (Fischer, 1965), the downward bending is of the prophyll and sheaths of the first few cataphylls, and the stem is carried passively downwards, then horizontally, and finally upwards as growth of the cataphyll bases dictates (fig. 4e). Tulip droppers are sent downwards by a tubular downward growth of the prophyll, or in seedlings, an outgrowth of the sheath of the single leaf (fig. 4h). The nodding spring boquet of snowdrop is held upright in a prophyll's fist. It is the first leaf sheath, or coleoptile, that directs the emerging oat shoot upwards in response to gravity or light (figure 4i). Orientation movements to light are generally made at the base of the leaf blade in the ligular region where again pulvinar tissue remains at the site of a former meristem (figure 4j and 4k). Put differently, support and movement are provided by a leaf sheath which is capable of making orienting growth movements at either end. It is astonishing to me how much we appear to have learned about the bending of dicot stem from studies of monocot leaf sheaths.

There is one geotropic stem response that is independent of leaf control. In some grasses the rhizome growing point makes a quarter turn which

brings the plane of bilateral symmetry of the growing point from the horizontal into the vertical plane.

The pattern of monocot leaf growth results in a leaf remarkably resistant to adversity. The intercalated growth leads to an essentially linear form. When the end of a leaf blade is removed by grazing or cut off by necrosis from *Helminthosporium*, the remainder functions without impairment. Independence of parts is carried even further in some grasses (e.g. *Cynodon*). There chlorenchyma is arranged radially about each bundle with a layer of hyaline bubble cells separating components of each vascular strand. An infection of *Ustilago* may spread the length of a vascular strand and blast it while adjacent strands continue to function. Wind may whip a banana leaf to shreds after which it continues to contribute for months with only slightly reduced efficiency.

The relation of the growing tissues of the apex, one to another, forms an intriguing feature of many monocots. The cone of tissue consisting of several leaf initials grows as a unit. Even though the parts are differentiated, there is no slippage, and the whole cone grows as if it were welded. I first noted this when making a key to identify grasses in the vegetative condition. I found a constriction near the end of the leaf blade in *Poa*. Wanting to know if this were a reliable characteristic, useful for keying, I looked into its origin. I found that a leaf developed, clasped in the fold of the previous leaf, and that pressure from the developing blade of the older clasping leaf restricted development of a portion of the enclosed leaf.

Unity of the growing apical cone is readily seen in the *Agavaceae* where the leaves often have a waxy coating. An unfolding leaf carries the impression of adjacent leaves firmly pressed into the waxy coat where it endures for years. Further, the pattern is accurately carried on a four foot leaf, even though contact may have been lost when the two pressing leaves were an inch or two long.* We appear to find growth and differentiation taking place in an apical nursery where a wave of differentiation passes inward from leaf to leaf. The growing point sits below this cone, expanded visible organs lie above it. In examining development within this cone of tissue, one feels strongly the unity of the whole plant, the subservient function of parts, such as genes, for example.

In dicot buds there is neither the proximity nor pressure to bring parts together into a collective whole. Nor does this proximity obtain in those monocots that have margins inrolled, as for example, *Commelina* or *Potamogeton* (persons with their arms folded over their breast cannot embrace).

In *Poa pratensis* a similar but looser relationship of parts is seen. A vigorous plant growing in a friable, weed-free soil will, in time, produce a flush of rhizome initials. While the axillary buds from which the rhizomes develop are arranged in two ranks, the rhizomes develop so they are distributed in a circle (Etter, 1951). After a period of later growth the rhizomes turn up and emerge in a circle around the parent plant. Later a wave of second generation rhizomes is initiated from the ring of offspring plants. These continue to orient themselves in a circle moving out from the original central plant. But if the rhizome connection of an offspring plant is severed, its rhizomes will circle around it, instead of around the grandparent plant.

* This can be seen in a number of *Agaves* in the desert collection at the Royal Botanic Garden greenhouses.

I should like to conclude with a little fantasy based on the *Araceae*. This fanciful speculation illustrates the ideas of linearity, motility and phytomer units.

During its aquatic existence the monocot ancestor lost its ability to differentiate vessels except for primitive vessels in the roots. Evidence suggests that after re-emergence on land, vessels were independently evolved by a number of monocot groups, but not by the *Araceae* (Cheadle, 1953). The *Araceae* today have vessels in the roots only. They are primitive in that they have perforate end-walls rather than full lacunae.

This suggests to me that "prop" roots in the *Araceae* are substitute stems with respect to conduction as well as support. It is questionable whether a few stem bundles without vessels could supply water at a rate needed by a large actively transpiring plant. But each prop root provides vessels as direct channels of conduction from soil to leaf.

Leaves of an araceous plant, such as *Monstera* for example, develop, ensheathed by a membrane on the adaxial side of the petiole (sheath) of the previous leaf. The emerging leaf bends to one side and its adaxial side is that nearest the leaf which formerly ensheathed it. The plant appears distichous with leaves emerging alternately to one side, then the other.*

If we now consider an old mature *Monstera*, high above the ground—one in which the original stem connection to the ground has rotted away—and if we imagine a time lapse movie in which a year is reduced to a minute—and if we further imagine this plant treated with a fluorescent dye so we see but this single plant on our film, then we can imagine the plant dropping prop roots like pencil-thin legs on which it moves ahead, tiptoing, as it were, through the trees. But at the same time as it walks, it also appears to swim as successive leaves sweep back from the axis on alternate sides.

So here is a monocot, typical of many as I picture them: motile; of linear associated units which can survive independently—in this instance each leaf and bud on its own stalk. Here is the descendant of an ancient water plant. The Cretaceous seas and marshes have dried and left it stranded. Its descendant floats now, in the air, but rooting still in the ooze below.

References

Arber, A. (1945). *Natural philosophy of plant form*. Cambridge. 247 pp. (p. 42 ff).

— (1925). *Monocotyledons*. Cambridge. 258 pp. (p. 179). (Reprinted 1961. Hafner. N.Y.).

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* The phyllotaxy of *Monstera* and many other araceous plants is of two spirals—a double helix—so at any point two successive leaves are almost opposite. There is a *Monstera* along the wall east of the greenhouse pool at the Royal Botanic Garden. The double helix is more clearly seen looking at *Schismatoglottis lavallei* north of the pool. A triple helix of closely set leaves gives *Pandanus furcatus* its common name, screw-pine.

Boyd, L. (1931). Evolution in the monocotyledonous seedling: a new interpretation of the morphology of the grass embryo. *Trans. Bot. Soc. Edinb.* 30: 268–303.

Cheadle, V. I. (1953). Independent origin of vessels in the monocotyledons and dicotyledons. *Phytomorph.* 3: 23–44. (Also in other papers.)

Eames, A. J. (1961). *Morphology of the angiosperms.* McGraw-Hill Book Co. Inc. New York. 518 pp.

Etter, A. G. (1951). How Kentucky bluegrass grows. *Mo. Bot. Gard. Annals* 38: 293–375.

Evans, M. W. & Grover, F. O. (1940). Developmental morphology of the point of the shoot and the inflorescence of grasses. *Journ. Agric. Res.* 61: 481–520.

Fischer, J. E. (1965). The growth of rhizomes in Kentucky bluegrass. *Greenhouse-Garden-Grass* 5, 3: 1–7; 5, 4: 1–6. (See also *Can. Journ. Bot.* 42 and 43).

Foard, D. E. & Haber, Alan H. (1962). Use of growth characteristics in studies of morphologic relations. I. Similarities between epiblast and coleorhiza. *Am. Journ. Bot.* 49: 520–523.

Gaudichaud, C. (1841). Récherches générales sur l'organographie, la physiology, et l'organogénie des végétaux. *Mem. Acad. Sci. Paris VIII.* (in McLean et al.).

von Goethe, J. W. (1817). Morphologische Hefte (in Arber and McLean et al.).

Gray, A. (1879). *Structural Botany.* New York. 442 pp. (p. 7).

Hofmeister, W. F. B. (1863). (in McLean et al.).

Holttum, R. E. (1955). Growth-habits of monocotyledons—variation's on a theme. *Phytomorph.* 5: 399–413.

Johansen, D. A. (1950). Plant Embryology. *Chronica Botanica.* Waltham, Mass. 305 pp.

Klebs, G. (1885). *Beiträge zur Morphologie und Biologie der Keimung.* In W. Pfeffer. Untersuchungen aus dem Botanischen Institut zu Tübingen. Leipzig. 1: 536–635.

Maheshwari, P. (1950). *An introduction to the embryology of angiosperms.* McGraw-Hill Book Co. Inc. New York. 453 pp.

Maheshwari, S. C. & Baldev, B. (1958). A contribution to the morphology and embryology of Commelina forskalaei Vahl. *Phytomorph.* 8: 272–298.

McLean, R. C. & Ivimey-Cook, W. R. (1951). *Textbook of theoretical botany.* Vol. I. Longmans, Green & Co. London.

Priestley, J. H., Scott, L. I. & Gillette, E. C. (1935). The development of the shoot in Alstroemeria and the unit of shoot growth in monocotyledons. *Ann. Bot.* 49: 161–179.

Randolph, L. F. (1936). Developmental morphology of the caryopsis in maize. *Journ. Agr. Res.* 53: 881.

Reeder, J. R. (1953). The embryo of Streptochaeta and its bearing on the homology of the coleoptile. *Am. Journ. Bot.* 40: 77.

Roth, I. (1961). Histogenesis and morphological interpretation of the grass embryo. *Recent Adv. in Bot.* 1: 96–99. Univ. of Toronto Press.

Sharman, B. C. (1942). Developmental anatomy of the shoot in Zea mays L. *Ann. Bot.* N.S. 6: 245–282.

Skutch, A. F. (1927). Anatomy of the leaf of banana. *Bot. Gaz.* 84: 337–391.

Souèges, R. (1954). L'origine du cône végétatif de la tige et la question de la "terminalita" du cotylédon des monocotylédons. *Ann. Sci. Nat. XI* (*Bot.*) 15: 1–20.

Swamy, B. G. L. (1962). The embryo of monocotyledons: a working hypothesis from a new approach. *Plant embryology.* Maheshwari, editor. Council Sci. Indust. Res. New Delhi. Pp. 113–123.

Weatherwax, P. (1923). *The story of the maize plant.* Chicago. 247 pp. (p. 40) (see also *Torrey Bot. Bull.* 57: 211: 1930).

Plant families for Malayan students. Here is a book* to which an unreserved welcome can be given. Taxonomic teaching in the tropics has long been hampered by a lack of texts designed to cover the plants a student actually has a chance of seeing around him. Dr. Hsuan Keng has wisely included a good many cultivated plants in his account, so that it may well have a much wider area of utility than the Malay Peninsula and Singapore, for which it is designed.

One interesting feature is the attempt to use the order as a teaching unit. Dr. Keng admits that some of these are rather a mixed bag—he is not proposing a new system, merely adapting the best of what is to hand—but thinks that on the whole they are useful teaching guides. The 188 families that he includes are thus grouped into 41 orders. Most of these are reasonable enough and a help to the student; perhaps the merit of Geraniales is just that it does provide a sharp contrast. Personally, to stand up and tell a class anything useful about an order including Meliaceae, Polygalaceae and Euphorbiaceae would defeat me entirely; but the fact that the dicotyledonous families cannot all be grouped into satisfactory orders is a taxonomic fact which the student should learn.

It is good to have an entirely new set of illustrations, and Dr. Keng's wife is to be congratulated on these. A few are rather thin (e.g. figs 82, 126) and just occasionally (*Lagerstroemia flos-reginae:* fig. 91) they fail to conjure up the plant; here, and in a few others the floral detail is too small. On the whole, however, they are just what is needed for a book at family level.

The main part of the work is, of course, the family descriptions and the keys and these are admirable. There is a key to the orders, to families under each order and often to genera or tribes within the families. There is also a brief description (c. 10 lines) for each family and a few notes of general interest. All this adds up to a very solid body of information.

One part, however, I would like to see completely re-written for a second edition. This is the Introduction. As it stands this is simply an "introduction explanatory" for teacher, taxonomist or reviewer: what is needed is an "introduction exhortatory" for the student; a few words to arouse his enthusiasm for finding out about the plants around him. In fact I would happily sacrifice some of the taxonomic detail in the main text for a few more items of biological interest. Araceae and Annonaceae, Dipterocarpaceae and Orchidaceae and many others all deserve a few lines to bring them alive.

B. L. Burtt.

* Orders and families of Malayan seed plants. By Hsuan Keng. Pp. xxiii + 429, 1 pl., 207 figs. Kuala Lumpur & Singapore, University of Malaya Press. 1969. 25 cm. Price M$ 60. (Sole distributor: University of Malaya Cooperative Bookshop Ltd., Kuala Lumpur.)