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UNROLLING OF LEAVES OF MUSA SAPIENTUM AND SOME RELATED PLANTS AND THEIR REACTIONS TO ENVIRONMENTAL ARIDITY[1]

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(WITH TWENTY-THREE FIGURES)

Introduction

In two previous publications the anatomy (5) and the development and morphology (6) of the leaf of the banana have been discussed. The present paper is devoted to a description of the unfurling of the lamina, and of the development of the tissues of the pulvinar band, by the agency of which the lamina halves fold together beneath the midrib in the middle of dry days and spread out again toward evening. For purposes of comparison, I shall discuss the same points in several other genera, representing each of the four families into which the Scitamineae is divided.

The first paper figured and described a peculiar hypertrophy of the cells of the upper water tissue at points where the longitudinal furrows in the surface of the lamina (caused by pressure exerted upon it while still rolled within the false stem) intersect one of the principal veins. At that time I was unable to explain the significance of the enormous anticlinal elongation of these cells, but merely recorded the anatomical peculiarity. During a recent visit to Panama experiments were performed on the mechanism of the unrolling of the lamina which make it clear that hypertrophy of the cells of the water

[1] Botanical contribution from the Johns Hopkins University, no. 109.

tissue at the points in question is the direct result of the difficulty in flattening out these folds when the leaf unrolls.

Since my earlier description of the banana leaf was written, Löv (3) has studied the mechanism of the unfolding of monocotyledonous leaves. In most families of this class the leaf, whether plicate, convolute, involute, or otherwise disposed in vernation, does not expand as a result of the properly modulated or harmonious growth of all of its tissues, but rather through the rapid enlargement of certain more or less specialized cells which up to the time of unfolding have lagged behind the others in development. These cells, which are designated "unfolding cells" (Entfaltungszellen) in the German literature on the subject, and for which I propose the term *expansion cells*, from their rôle in the expansion of the lamina, are of necessity situated on that surface of the leaf which is concave in vernation. In most monocotyledons this appears to be the upper or ventral surface, although in the plicate leaves of palms expansion cells are found alternately on the dorsal and ventral surfaces, as governed by the direction of the folds. Expansion cells may be either epidermal, hypodermal, or more deeply situated. In the Gramineae, Cyperaceae, Juncaceae, Liliaceae, Amaryllidaceae, and Commelinaceae the information at present available indicates that the expansion cells are typically epidermal, although in many cases they are aided by more deeply situated tissues. In the Pandanaceae, Palmae, and Scitamineae the expansion cells are almost always hypodermal (water tissue). The epidermis contributes at most a very subordinate aid in the process of unfolding, but the mesophyll (as distinct from the hypoderm) may in some cases be of substantial help. In the Orchidaceae there is considerable variation in the position of the expansion cells. In the whole order of the Helobiae they are apparently absent, as they are from the Bromeliaceae and the leaves of the Araceae (although present in the spathes of certain species) and from a series of genera in the Amaryllidaceae. In these leaves the unfolding is accomplished by the coordinate development of all of the tissues, the progressively increasing growth of all cells from the lower surface to the upper.

In this rapid survey it has been necessary to confine statements to the broadest generalizations; the numerous exceptions may be found in Löv's memoir. In some species great variation is found even between different regions of the same leaf. Thus in the upper portion of the leaf of *Homeria collina* the expansion cells are developed from the hypoderm and the mesophyll, while in the basal portion the epidermis also contributes to their number.

In regard to their distribution over the surface of the leaf, considerable variation exists. In the Commelinaceae, for example, the epidermis over the whole of the upper surface consists of expansion cells. In many grasses, palms, and other leaves with particular lines of folding, the expansion cells are more or less restricted to definite longitudinal series at these places.

Microscopically expansion cells are characterized by their thin, generally unsuberized walls and large clear lumina. Tannin, crystals, oil bodies, and leucoplasts are seldom present. Chlorophyll is present only in expansion cells which develop from the mesophyll, and even in these it typically occurs only in small amounts.

The expansion cells of the grasses, which generally contrast sharply with the neighboring epidermal cells, were apparently the first to receive the attention of botanists, and were described by DUVAL-JOUVE (1) in 1875. Later TSCHIRCH (7) devoted a special study to the inrolling of the leaves of xerophytic grasses, which is at least in part effected by their expansion cells. The expansion cells of grasses are apparently the only ones mentioned in the text-books, and then only in regard to the opening and closing of these leaves in response to wetting and drying, rather than in relation to their primary function in the unfolding of the young leaf. RUDOLPH (4) has described the mechanism of unfolding of the leaves of palms.

Unrolling of banana leaf[2]

At the moment the tip of the young leaf emerges from the top of the false stem, the lamina is practically full-grown. After tearing away the leaf sheaths, the tightly rolled lamina may be unfurled without

[2] The descriptions and drawings refer to apparently undescribed varieties of the subspecies *seminifera* of *M. sapientum* introduced to Almirante, Panama, from the Philippine Islands under various native names, but agreeing so closely in vegetative characters as to be indistinguishable from one another. The varieties of the banana are legion, and their names even more so, but there seems to be essential agreement within the species in anatomical characters, and the present account gives a description of the typical common cultivated varieties.

difficulty. The tissues, except perhaps at the extreme tip, are still ivory white, and the upper surface of the two sides of the lamina is perfectly smooth, without a trace of the transverse ribs so conspicu-

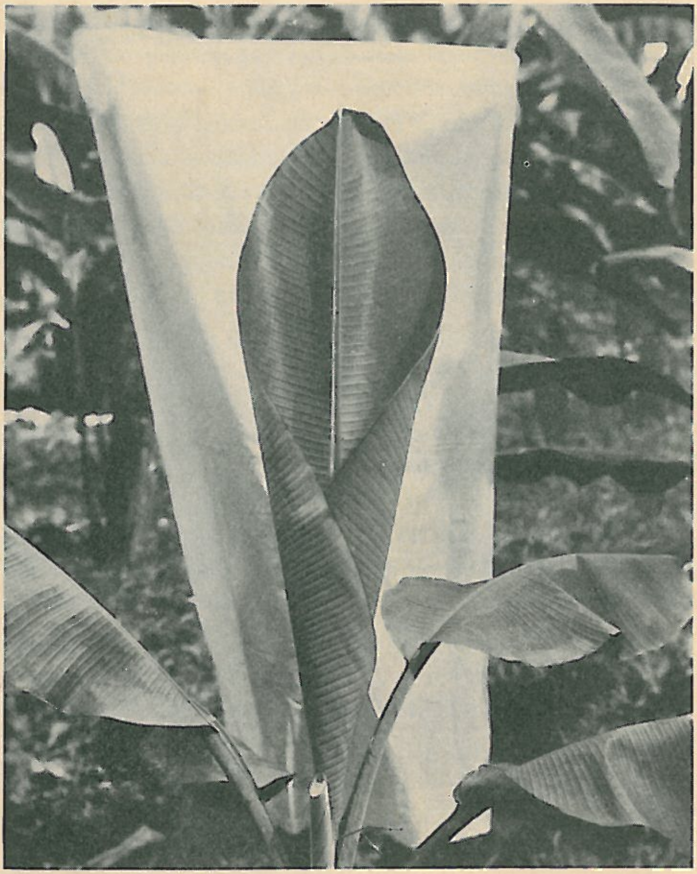
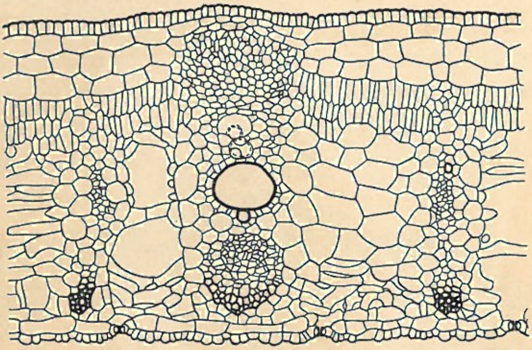


FIG. 1.—Partially expanded lamina of young banana plant (note prominent transverse ribs and reflexed position of sides of lamina at apex).

ous in the mature leaf (fig. 1). These ribs are not primarily places of greater thickness in the lamina, but merely corrugations, the result of the upward curvature of the tissues on either side of the principal veins, so that the latter lie above the general surface of the leaf. On the lower side each ridge is represented by a furrow. The ribs are formed as the leaf unrolls. They become apparent first at the apex of the left half of the lamina, which is always outermost in the convolute vernation. From this point their formation proceeds basally



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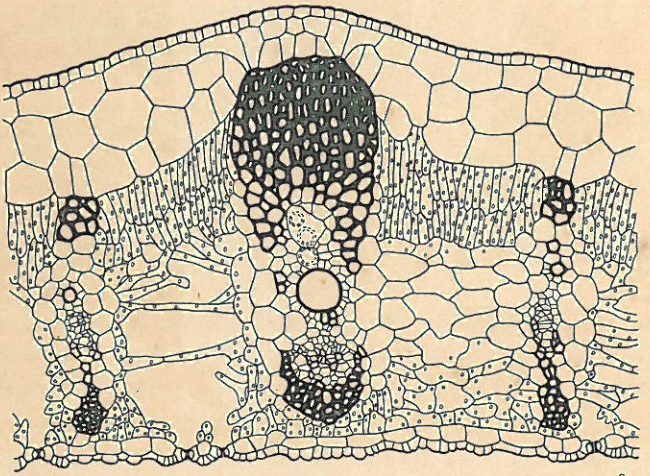

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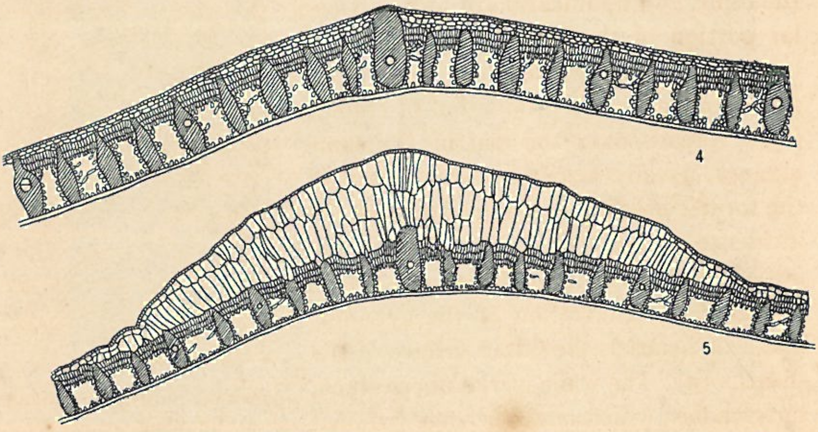
FIGS. 2, 3.—Fig. 2, transverse section through principal and two subordinate veins of lamina not yet unrolling; fig. 3, same, from mature lamina; ×135.

and to the right, keeping pace with the emergence of the leaf, which is effected by rapid elongation of the sheath, particularly its basal portion. Thus the regions of the lamina which are the first physically able to unroll are the first to show the formation of ribs.

Figs. 2 and 3 illustrate the alterations which occur in the cells themselves. Fig. 2 shows a cross-section through principal and subordinate veins of a large leaf just appearing above the false stem, but from near the center of the length of that leaf, and hence from tissues still far down the false stem. Fig. 3 was drawn by camera lucida on the same scale as the preceding, and gives the appearance of the corresponding portion of a mature expanded leaf. Certain evident changes have taken place during the interval between the stages represented by the two drawings, the most conspicuous of which are: (1) the



FIGS. 4, 5.—Fig. 4, transverse section through principal and neighboring subordinate veins of normally expanded lamina; fig. 5, same, from lamina bound 10 days; semi-diagrammatic, water tissue drawn with camera lucida; vascular bundles shaded; ×24.

great enlargement of the cells of the water tissue lying above and on either side of the principal vein; (2) the anticlinal elongation and thickening of the walls of the fibers on the upper side of the principal vein and the thickening of those above the subordinate veins. These cross-sections do not extend far enough laterally to show that the principal vein has been raised above the general surface of the lamina (fig. 4). The changes on the lower side are much less conspicuous. The fibers already show considerable thickening in fig. 2, while those above the xylem are extremely thin walled. The palisade cells have experienced a certain amount of elongation, and the upper epidermal cells have enlarged considerably, but both changes are overshadowed by those of the upper fibrous bundle and the water tissue. It is evident that the upper portion of the leaf lags behind the lower in its rapidity of differentiation until the moment of unrolling, at which time its development, in relation to a particular function, is greatly accelerated.

Lignification of the fibers lying on the lower side of the vascular bundles of the lamina proceeds *pari passu* with the unfurling of the lamina. The first trace of lignification is evident in the upper left corner shortly before the coils begin to loosen. Thence it proceeds basally and to the right, and lignification of any particular portion of the lamina has usually at least begun by the time that portion begins to unfurl. The production of chlorophyll spreads over the leaf in the same manner, usually keeping a step ahead of the former process, and suggests that the incidence of light is responsible for the initiation of lignification. The same is true in regard to lignification of the hypodermal cells beneath the outer surface of the sheaths (5). The walls of the fibers above the bundles, which never become lignified but at maturity give the reactions of suberized membranes, are at most very slightly thickened during the process of unfurling, and gradually increase in thickness after the leaf has expanded, until finally they are as thick as those of the dorsally situated fibers.

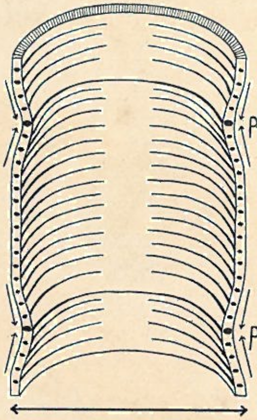
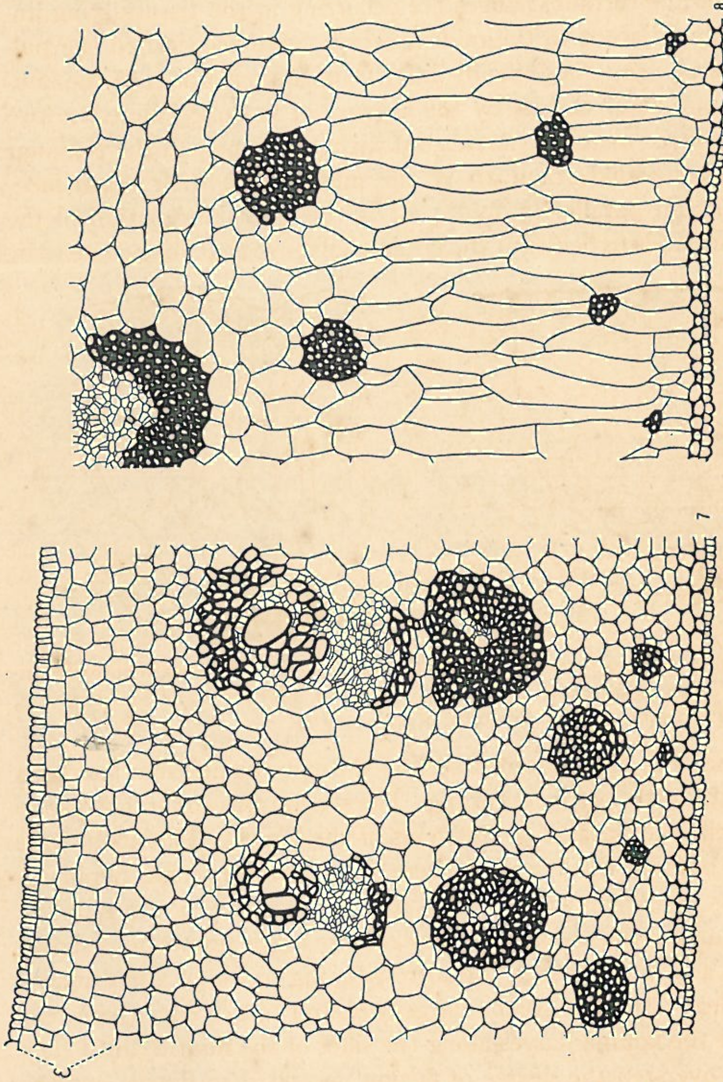


FIG. 6.—Illustrating method of leaf unrolling; arrows show direction of forces resulting from enlargement of expansion cells; *pv*, principal vein.

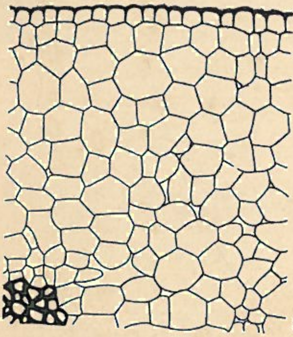
The great enlargement of the turgid cells of the upper water tissue above and particularly on either side of the principal veins results in pushing these veins above the general surface of the leaf. Since the upper surface is concave in vernation they are forced inward, and occupy, throughout the helix, a curvature of smaller radius than immediately adjacent tissues of the lamina (fig. 6); hence the whole principal vein is thrown into a state of compression in relation to the subordinate veins and the intermediate tissue. The turgid cells of the upper water tissue are most affected by this change, and eventually occupy a position enabling them to exert their expansive force to the greatest mechanical advantage. The lower side of the leaf,



FIGS. 7, 8.—Fig. 7, portion of cross-section of pulvinar band of leaf just appearing from false stem: *e*, expansion cells; fig. 8, lower portion of cross-section of pulvinar band of mature leaf, showing prismatic cells; ×112.

which contains fibers already showing lignification, is relatively resistant to stretching, while the entire upper portion, the fibers in which are still thin walled, is much more easily stretched. The divergent behavior of these two sets of fibers is accordingly of great importance in the unfurling of the leaf.

Meanwhile certain changes are occurring in the tissues lying immediately adjacent to the midrib, which have been called the pulvinar bands (5). These bands differ from the remainder of the lamina, among other things, by the absence of lacunae. Were the two lamina halves merely to flatten out without the help of the pulvinar bands they would stand above the midrib with their upper faces together and parallel (5, fig. 8). It is the primary function of the pulvinar bands to bend out the lamina halves so that they come to lie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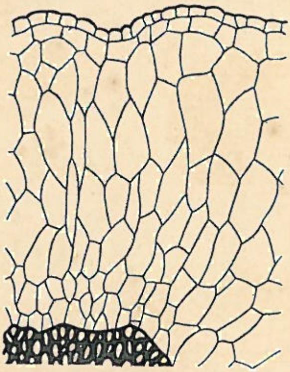
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FIGS. 9, 10.—Fig. 9, upper portion of cross-section of pulvinar band of normally unfolded leaf, showing expansion cells (cf. fig. 7*e*); fig. 10, same, from leaf bound 23 days, showing hypertrophy of expansion cells; ×112.

in a plane. Fig. 7 represents a section through the pulvinar band of a large leaf shortly before unfurling. The section was cut transverse to the midrib and parallel to the veins of the lamina. The fibers have already become thick walled (here they rarely become lignified). The cells of the upper water tissue, 4–5 layers deep, are still immature, and as the leaf unfurls they enlarge to the proportions shown in fig. 9, a section through the corresponding region of a mature expanded leaf. By their great enlargement and turgescence these cells bend out the lamina halves along the sides of the midrib, until they actually overstep the degree of flexion necessary to flatten out the leaf and are inclined backward (fig. 1, upper half of unfurling leaf). The process by which they are brought back to position is discussed in a later section of this paper.

Effect of preventing unrolling

By binding the apex of the leaf with soft twine when it first appears, and then continuing to wrap the twine basally as successive portions emerge, over a period of several days, it is possible to prevent unrolling of the lamina without injuring it. By this interference all of the growth processes which effect expansion of the leaf are greatly exaggerated.

By leaving the leaf bound for a week after it has completely emerged, striking results are obtained. When the cord is removed the left half slowly but visibly unrolls, and then begins to roll inward from the margin with the lower side concave (fig. 12), in just the opposite direction from vernation. The principal veins are marked by great welts which are lighter in color than the remainder of the leaf and are hard and turgid to the touch. The strongest of the subordinate veins, one of which lies between each pair of principal veins, are also sometimes swollen, but always to a much less degree, and not continuously. The leaf is much more strongly ribbed than normally. Microscopical examination reveals that the swollen appearance of the principal veins is caused by the great hypertrophy[3] of the cells of the upper water tissue, which elongate anticlinally, the only way they are free to grow. This hypertrophy extends over a variable number of the adjacent subordinate veins, but at its lateral margins the swollen portion of the water tissue is sharply delimited from the cells of normal appearance which occupy most of the interval between the principal veins (fig. 5).

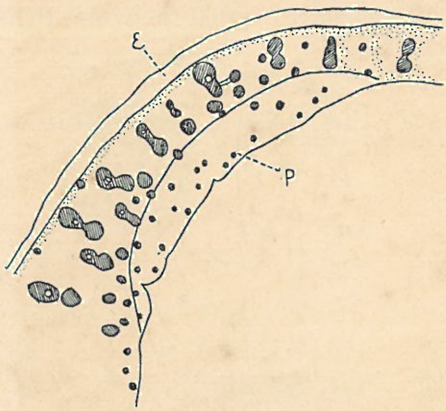


Fig. 11.—Diagrammatic cross-section through pulvinar band of normally expanded leaf, showing expansion cells (*e*) and prismatic cells (*p*); fibrovascular bundles shaded; ×11.

[3] The term hypertrophy is used merely to denote an enlargement of the cells of the upper water tissue, caused by experimental procedure, which is conspicuously above the normal.

Sometimes the tension set up by these enormously swollen cells is so great that the lamina is split inward from the left margin. At such places, or in strips torn by hand from the leaf, the torn margins roll inward over the lower surface, indicating that pressure of the hypertrophied water tissue tends to depress the portion of the lamina be-

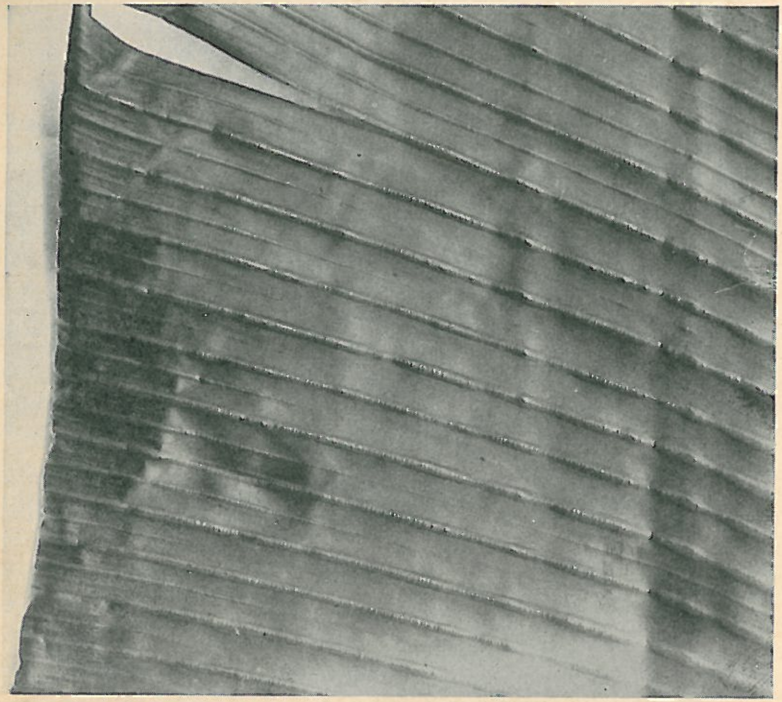


FIG. 12.—Upper surface of left side of lamina bound 12 days (note swellings above veins and backwardly rolled margin).

tween the principal veins, or to elevate the latter. The ribs formed on these bound leaves are always much stronger on the left or outer side of the lamina than on the right, and this difference persists even if the leaf is allowed to remain bound for a long period (three weeks or more). Near the right margin of a bound leaf the lamina never becomes strongly ribbed, and is in marked contrast to the opposite side. On each half of the lamina the ribbing is stronger next to the midrib than at the margin.

The thickness of the upper water tissue varies according to the region of the lam'na. Near the margins it is often single layered but usually double, near the midrib it becomes triple, and still closer to it, it is often quadruple. Immediately adjacent to a principal vein there is often one more layer of water tissue than elsewhere in the same region. The extra layer may extend as far as the fifth or sixth veinlet on either side of the principal vein. As seen in surface view, the cells of the water tissue are elongated transversely to the veins. The cell sap is perfectly clear, as in typical expansion cells, without chlorophyll or highly refractive bodies. In the bound leaves, at places where the water tissue consisted of two or three layers, the outermost layer was commonly much less hypertrophied than the one or two lying beneath it, and sometimes the cells comprising it were hardly deeper than normal. As a result of binding, the thickness of the water tissue above the principal veins may exceed that of all the remainder of the cross-section of the leaf. Thus at one point the water tissue became 480 μ deep, while the entire thickness of the lamina at this place was only 816 μ. The longest cell of the water tissue at this point measured 256 μ in depth, and cells 320 μ in depth have been observed. Cells of the epidermis do not aid in unrolling, and when the leaf is bound, do not exhibit any noteworthy hypertrophy, but are passively raised by the elongating cells of the water tissue. In some places swelling of the tissue above the principal veins was so great that the epidermis was split and a fissure extended into the cushion of tissue. The lumina of the fibers lying above the principal veins are strongly extended in the anticlinal direction, so that the fibrous bundle projects far upward into the cushion of water tissue. The palisade cells immediately adjacent to the principal bundle are also elongated somewhat more than normal. The tissues on the lower side of the leaf are not affected by binding it so that it cannot unroll.

On the plantation and in the jungle, one occasionally finds leaves of the Scitamineae with ribs abnormally swollen because the emerging lamina was caught in the embrace of a twining vine and unable to expand. If the plant is sickly, or if for any reason the leaf does not emerge normally and the lamina cannot unfurl at its due period, hypertrophy of the water tissue usually results. Local hypertrophy occurs wherever a sharp fold has been formed in vernation.

Prevention of the normal unrolling of the leaf also causes great hypertrophy of the water tissue on the upper side of the pulvinar bands (fig. 10). Here too the cells of the outermost layer are hardly swollen beyond the normal. The turgor of this tissue causes the lamina halves to become strongly deflexed beneath the midrib when unbound, even in moist weather and in the morning, when the other leaves are spread out horizontally; but after several days, by a process described later, they are raised to the normal position.

Unrolling of lamina in darkness

When a leaf has been constrained in the coiled condition by binding, even after a long period the right side remains yellowish, especially at the margin. The slight production of chlorophyll on this side seemed to be correlated with the very slight ribbing which was acquired, and suggested that light was essential to the unrolling of the leaf. To test this supposition, young suckers in the field were inclosed in light-proof portable houses, 90 cm. square by 2 m. high, which were equipped with light-proof ventilators at the top and bottom, and draped with white sheets to prevent their becoming too hot in the sun. The leaves which emerged in these houses unrolled normally, although they were without a trace of chlorophyll.

As in the leaves in the open, the formation of ribs began at the apex on the left side, and proceeded thence basally and to the right. The order of maturation of the expansion cells is thus an autonomic process, adjusted to bring about the harmonious unrolling of the leaf, and is not, as at first suspected, determined by the incidence of light. Their behavior in the banana is in entire agreement with the results of Löv's studies of a number of other plants. In leaves folded into a cylinder, with their edges in contact, such as those of *Luzula nemorosa*, the order in which the cells of the upper epidermis enlarge is from both margins toward the center. In simply folded leaves, such as those of *Hemerocallis*, enlargement of the expansion cells also proceeds inward from the margins. In convolute leaves the order of enlargement is from the exterior margin toward the interior. In involute leaves, as exemplified by species of the Commelinaceae, the order of enlargement is from the midrib toward both margins, while in the palms the expansion cells of the marginal folds are the first to enlarge.

Although it thus became evident that the beginning of the enlargement of the cells of the upper water tissue at the left margin was an autonomic process, not conditioned by the greater exposure of this portion of the leaf to the light, it remained to be seen whether light influences the degree of hypertrophy which can be attained by these cells. For this purpose leaves were bound as they emerged in the dark-house. After remaining bound for 16 days from the time it had completely emerged, a leaf was unbound and revealed a slight to moderate degree of hypertrophy of the cells of the upper water tissue in the neighborhood of the principal veins on the left side; but enlargement of the cells was not nearly so great as one would find in a leaf held bound for a similar period in the light. The anticlinal length of the longest cell observed was 130 μ, and the 3-layered water tissue at this point was 176 μ thick, while the total thickness of the lamina was 416 μ. The degree of enlargement and the turgor attained by the expansion cells are increased by light, although an enlargement normally sufficient to unroll the lamina is independent of light.

When the experiment was terminated, and the dark-houses, which were equipped with handles and could be lifted by four men, were removed from over the plants, the leaves turned green in inverse order of their age; the youngest in about 24 hours. In the leaves which had been longest in darkness, chlorophyll was produced first along the principal and stronger subordinate veins; only later in the intermediate regions. At the apex of the first leaf which had emerged in the dark-house, these veins alone turned green. These observations seem to indicate that which is confirmed by microscopical examination, that the tissues along the upper side of the principal veins are the last to lose their embryonic character, since their peculiar function demands their maturation at a later period than the rest of the leaf.

Effect of premature unrolling

The preceding experiment suggested that the compression to which these cells are normally subjected, by their position on the concave surface of the rolled leaf, is responsible in the first place for their normal enlargement, and hence for the production of their ribs. A lamina which was just appearing above the false stem of a young sucker, and which had not yet become ribbed, was freed by cutting away all the leaf sheaths covering it. The left side was carefully unrolled, then rerolled around the midrib and right side as tightly as possible, but with the upper instead of the lower surface facing outward. It was then bound by cord in this position and supported to relieve the strain on the still immature petiole. The left side of leaves treated in this manner never became ribbed, but the upper surface remained smooth as in immature leaves, even after being bound for 3 weeks. The right side, which was allowed to remain rolled in the normal direction, became strongly ribbed, as in the bound leaves already described.

Rerolling the leaves with the ventral surface convex places the cells of the upper water tissue in an unnatural position, and it was desirable to determine the effect of merely flattening out the lamina. This experiment was attended by considerable practical difficulty. The framework which supports the lamina must hold it perfectly flat, and yet permit it to slip upward as the sheath of the leaf elongates. The leaf used must be of exactly the right age, for if too young it will be unable to withstand the exposure to which it is subjected by premature unrolling, and if too old, will already have begun to become ribbed. Finally these requirements were met by constructing a framework consisting of two parallel series of bars of split bamboo. A lamina about 1 m. long, which had emerged for one-quarter to one-half its length, from a young sucker, was chosen. It was freed of the surrounding leaf sheaths, the left side unrolled, the framework slipped over it and set into the ground beside the plant. During the first few days, or until the tissues had become green, it was shaded by tying cut banana leaves to the outside of the frame. The left side of these leaves became at most very slightly ribbed, always much less than in normal leaves. In small restricted areas, which had not been held perfectly flat in the frame, the ribs were much stronger, and in some places the expansion cells were even somewhat hypertrophied, showing that a slight concavity of the upper surface is sufficient to cause ribbing.

Leaves which were prematurely unrolled and did not become normally ribbed, usually hung more or less limp from their midribs instead of being spread out horizontally in the morning and evening, and on wet days. The ribs are necessary for the mechanical support of the broad flat lamina, and the expansion cells, in addition to the function of unrolling the lamina, must create the framework for its support.

Effect of rerolling mature leaves

Two mature leaves, the youngest completely unfolded leaf, and the one next below this on a young sucker, were loosely rolled into the position of vernation and held by binding with cord. After 9 days they were unrolled and examined. The younger leaf had been affected by this treatment much more than the older. The water tissue above and beside the principal veins of the former was strongly hypertrophied, and the leaf much more conspicuously ribbed than normal. When the water tissue was three layers thick only the inner two layers were hypertrophied; when two layers thick, only the inner. The hyaline cells on the upper side of the pulvinar bands, particularly on the right side, which was the more strongly inrolled, were also considerably hypertrophied. The older leaf showed the same symptoms in a reduced degree.

Development of pulvinar band

At night, in the early morning and late afternoon, and continuously on wet days the two sides of the lamina stand out in a plane on either side of the midrib. In the middle of bright sunny days they bend beneath the midrib, and eventually, if the day is dry the dorsal surfaces of the two sides are brought into contact. Since the stomata are situated principally on the lower side of the lamina, and are thereby brought into a more protected position, and moreover because by the assumption of the profile position the absorption of sunlight is greatly decreased, the water loss must be considerably diminished, although at present no actual measurements on this point are available. When a leaf has been torn into strips by the wind, the individual strips behave as though the lamina were still intact. If the sky suddenly becomes overclouded or there is an unexpected shower during the middle of a day which was at first sunny, recovery of the horizontal position by the lamina halves is rapid.

That the halves of the lamina do not passively sink down as the result of wilting may easily be demonstrated by holding such a leaf in an inverted position, when the lamina halves will not droop down but remain folded upward. Their movements are determined by changes in the turgor of the pulvinar bands which border the midrib on each side, and the flexure is sharply localized in these bands. It therefore becomes of interest to examine their structure. Their width is about 5 mm. in large leaves, and in thickness they taper from about 1.8 mm. next the midrib to 1.2 next the lamina half. Fig. 7 represents a portion of the cross-section of a pulvinar band of a leaf of medium size, which was just appearing from the false stem. It shows the condition found in the mature leaf tolerably well, except in the form of the cells lying immediately below the upper and above the lower epidermis. The change which occurs in the cells of the upper water tissue during the process of expansion has already been described. The central portion of the organ is characterized by the absence of lacunae (although small spaces between the rounded cells are numerous), the many vascular bundles, and the conspicuous sheaths of fibers which accompany them. Toward the lower surface bast bundles are numerous, surrounded by exceedingly thick sheaths of fibers, and still lower in the cross-section strands of fibers alone are found. Above the lower epidermis two layers of collenchymatously thickened cells occur. It is the behavior of these cells, and those immediately above them, which is of particular interest.

When the leaf first expands, the great turgor engendered in the upper water tissue of the pulvinar bands causes the halves of the lamina to become reflexed below the midrib (fig. 1). After a few days the lamina becomes flattened out again. This is brought about by the gradual enlargement of those cells on the lower side of the pulvinar band which lie between the hypodermal layer and the lowest of the bast bundles. Their elongation does not begin until the leaf has expanded, and is completed in about 10–12 days. The process of elongation was studied by removing with a sharp scalpel little rectangular pieces from the apex, middle, and base of each pulvinar band of a single leaf at intervals of 4 days. The leaf was so large that the loss of these small pieces of tissue did not seem to affect it, and successive samples in each region were spaced a few centimeters apart, so as to avoid wound reactions. The thickness of the tissue formed by these elongating cells, and the length (anticlinal) of the longest cell in each region, were measured by a micrometer scale, and the results of one series of measurements are recorded in table I. In the mature leaf the tissue is composed of enormously elongated, irregularly prismatic cells, with clear contents and containing few chloroplasts (fig. 8).

Very young leaves do not respond to changes of atmospheric conditions by rising and sinking. The diurnal movements do not become

TABLE I

DEVELOPMENT OF PRISMATIC CELLS OF PULVINAR BAND; TOTAL THICKNESS OF PRISMATIC TISSUE IN MICRONS

Position	March 1*	March 5	March 9	March 13	March 25
Left side					
Apex	64	224	272	336	384
Middle	96	304	400	544	512
Base	96	320	416	528	496
Right side					
Apex	80	272	304	400	448
Middle	96	368	400	512	512
Base	96	384	400	400	496
	Length of longest cell in three sections				
Left side					
Apex	26	122	130	204	204
Middle	26	115	207	229	233
Base	30	144	267	241	215
Right side					
Apex	30	155	163	222	233
Middle	26	144	192	241	218
Base	26	144	174	167	207

* On March 1 the base of the lamina had just become free from the false stem; the cells on the lower side of the pulvinar band were not in the least elongated, but appeared as in fig. 7.

pronounced until after development of the prismatic cells. The movements seem to be the result of variations in turgor of the two antagonistic layers, the upper water tissue and the lower prismatic tissue. In a segment of a cut leaf the latter loses water more rapidly, and the lamina halves bend downward beside the midrib. Placed in water, the prismatic cells rapidly regain their turgor, and the lamina halves are again spread in a plane.

The conditions necessary for development of the prismatic cells are pressure and light. The pressure is normally supplied by the antagonistic action of the upper water tissue, which, by its strong development when the leaf first expands, bends the pulvinar band downward and throws the cells on its lower side into a state of compression. In the experiments in which unrolling of the leaf was prevented by binding, the cells on the lower side of the pulvinar band did not become prismatic. When the left side of the lamina was unrolled and then rerolled in the reverse direction, development of prismatic cells on this side was very irregular, because in bending the leaf back the flexure generally occurred in the lamina itself rather than in the thicker pulvinar band, and the lower surface of the latter only occasionally became concave. On the right side in these experiments no prismatic cells were formed. When the time of unrolling of the lamina was delayed a week or two by binding, and the water tissue on the upper side of the pulvinar band was greatly hypertrophied, the lamina halves became strongly reflexed after the cord was removed, but gradually bent upward as the prismatic cells developed. Leaves which expanded in darkness never developed prismatic cells so long as they were left in the dark-house. Since, as a result of the slighter enlargement and turgidity of the cells of the upper water tissue of the pulvinar band, the leaves which unfold in darkness never become so strongly reflexed along the midrib as leaves which emerge in the light, there was a possibility that failure of development of the prismatic cells was a result of insufficient compression of the lower side of the pulvinar band. Leaves were bound as they emerged in the darkness and the unfurling delayed a week or more, which resulted in a slight hypertrophy of the upper water tissue, and when unbound the lamina halves became more strongly reflexed. Even under these circumstances there was no development of prismatic cells in darkness. The appropriate cells retain their capacity to elongate, however, and even after their development has been delayed 20 days by darkness, when returned to the light they enlarge and become prismatic.

In all of the species which I have been able to examine, including *Musa textilis*, *M. tomentosa*, *M. malaccensis*, *M. sanguinea*, *M. rosacea*, and many varieties of *M. sapientum*, the pulvinar band with its prismatic cells is well developed, and the lamina halves fold downward as the leaf loses water. Although there is great development of fibers, undoubtedly made necessary by the strategical position of the organ, in the pulvinar bands of all of these species they are in general weakly or not at all lignified. The same strand of fibers is usually strongly lignified on both sides of the pulvinar band, that is, in the midrib and the lamina half, but in the band itself it is either not lignified or its lignin reaction is much weaker than in the adjacent regions. The failure of lignification is typical of pulvini, and is of advantage to an organ which must bend repeatedly. I have already described (5) a peculiarity of the cuticle over the pulvinar band of *M. sapientum* which seems associated with the motility of this organ.

The genus *Musa* is the only member of the Scitamineae known to the writer the leaves of which fold downward in dry weather. In all others (including the species described later) the leaves fold upward, exposing the lower surface, in which the stomata are principally situated. In these species there are no distinct pulvinar bands, and the bundles of fibers are continuously lignified as they pass from the midrib to the lamina halves. Like the majority of monocotyledonous leaves, these reverse the movements of unfolding as they dry (3). GOEBEL (2) points out that the movements of plant organs must be considered primarily in relation to their development, external and internal symmetry, and mode of unfolding. An organ performs movements because its structure is asymmetrical (whether or not the lack of symmetry is externally evident), and opposite sides are differently affected by various external or internal changes. The movement may be performed first as the organ expands, and subsequent movements of the mature organ may be merely reversals and repetitions of the act of unfolding. Since the movements of plants are determined by structural peculiarities which frequently originate in response to needs or conditions unrelated to these movements, they may or may not happen to prove useful, but are not of necessity useful. This certainly is true of the movements of many monocotyledonous leaves in dry weather. The leaf tends to return to the position it occupied in vernation, because the expansion cells, which by their turgor spread out the lamina halves and hold them so, lose their turgor and permit the antagonistic forces of the tissues on the opposite side of the leaf to reverse the process of unfolding. Far from being of advantage to the plant, these movements appear just the reverse, for the stomata are thereby more exposed. But because of development of the prismatic tissue of the pulvinar bands, movements of the lamina in dry weather are not mere reversals of the act of expansion, and appear to be advantageous to the plant. Like the sleep movements of the leaves of *Tropaeolum majus*, which bend outward at night although the upper surface is directed inward in the immature leaf, they are exactly opposite to the movements of unfolding. The prismatic cells of the pulvinar band appear to be a late acquisition in the phylogeny of *Musa*, since its nearest relatives, *Ravenala* and *Heliconia*, lack them; they are certainly a late development in the ontogeny, and originate only under special conditions of pressure and light.

Unfolding of leaves in other genera of Scitamineae

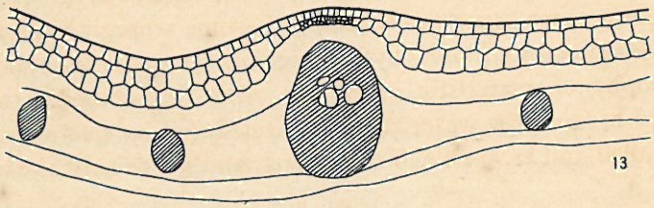
Musaceae

Heliconia bihai L.—The long, slender leaves of this plant emerge very gradually from the short false stem, and the apex has usually spread out long before the base has escaped from between the sheaths of the older leaves. The upper water tissue is everywhere (except close to the midrib) but a single layer in thickness. Unrolling of the lamina halves and formation of transverse ribs proceed almost exactly as in *Musa*. The prevention of unrolling by binding with cord caused the water tissue above and immediately adjacent to the principal veins to become enormously swollen, forming thick welts running across the lamina half. Single cells reached 432 μ in anticlinal length, about 3–4 times the normal depth. The thickness of the hypertrophied water tissue often exceeded that of the remainder of the leaf, and at one place, where the total cross-section was 560 μ, it occupied 352 μ. The water tissue above many of the stronger subordinate veins was hypertrophied, and in places where the upper surface was particularly concave (the lamina does not form a perfect helix in vernation) the hypertrophy extended completely across the interval between the principal veins.

In dry weather the leaf folds upward, exposing the stomata, as do those of all other species of *Heliconia* with which I am familiar.

Zingiberaceae

Alpinia exaltata (L.) R. & S.—The aerial shoots of this species, attaining 5 m. in height, consist of a slender stem everywhere surrounded by many thicknesses of the long overlapping sheaths, and are continued upward into a false stem composed of these sheaths alone. When a new lamina emerges it is practically full-grown. If such a leaf is unrolled, it is found to be perfectly flat and without



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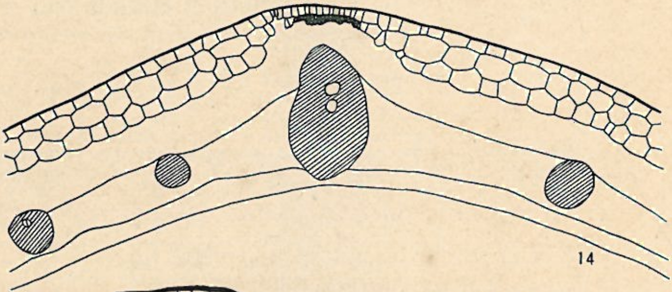

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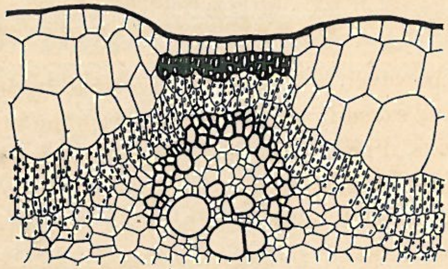

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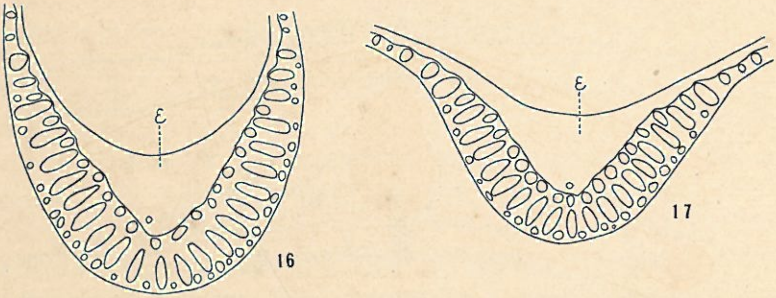
FIGS. 13–15.—*Alpinia exaltata:* Fig. 13, cross-section through principal vein of leaf just beginning to emerge; only water tissue and epidermis shown in detail; camera lucida ×50; fig. 14, same, from fully expanded leaf; ×50; fig. 15, cross-section through upper portion of principal vein of leaf bound 14 days; ×112.

ribs, but it feels slightly rough if the finger is drawn across it transversely to the veins, which project slightly above the surface (fig. 13). Even the strongest veins do not occupy the entire interval between the upper and lower water tissues, as in *Musa*, but the palisade tissue is continuous across them. The two-layered upper water tissue is interrupted above the stronger veins by a group of small cells, the walls of which become thickened even before the leaf appears at the top of the false stem. For this reason the process of unrolling differs from that in *Musa* and *Heliconia*. The cells of the water tissue on either side of the principal veins are the chief expansion cells, and by their enlargement cause the lamina to become strongly ribbed (fig. 14). Prevention of unrolling by binding does not cause the enormous hypertrophy characteristic of all the other Scitamineae studied, probably because the water cells are interrupted by cells which are thick walled and incapable of elongating, and hence hold the others



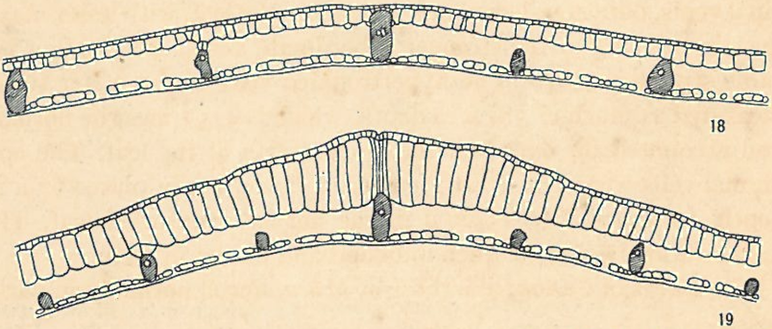
FIGS. 16, 17.—*Alpinia exaltata:* fig. 16, cross-section through midrib of leaf before expansion; fig. 17, same, from expanded leaf; *e*, expansion cells; ×5.

back. There is, however, a definite though small hypertrophy of the upper water tissue extending completely across the interval between the principal veins. Fig. 15 shows the region above a principal vein of a leaf which had been bound for 2 weeks. The water tissue bulges up above the mechanical tissue on either side, but appears to be held in check by the attachment of the epidermis to the latter. The outer side of the bound lamina exhibits other symptoms of the high turgidity of its expansion cells, such as splitting of the tissue and rolling backward of the margin, and feels smoother and more turgid than the normal leaf.

Fig. 16 shows how the clear transparent expansion cells occupy the entire central portion of the cross-section of the midrib, while the vascular bundles are all crowded to the lower side. At the proper time the former increase in size and turgidity, spread the midrib, and flatten out the lamina halves (fig. 17). On drying, the lamina halves fold together again, as a result of the loss of turgidity by these strategically situated cells. The stomata, situated chiefly in the lower surface of the leaf, are thereby exposed.

CANNACEAE

Canna sp.—The *Canna* chosen for study is a species with small red flowers commonly cultivated about the province of Bocas del Toro, Panama, and often found growing spontaneously. It is apparently undescribed, and in the unsatisfactory state of the taxonomy of the genus it appears undesirable to make a new species of it without a revision of the group. The leaves of *Canna* species show great uni-



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FIGS. 18, 19.—*Canna* sp.: fig. 18, cross-section through principal vein of normally expanded leaf, showing water tissue; fig. 19, same, from leaf bound 7 days; ×25.

formity in structure, however, so specific identity is not important for the present purpose.

Canna is the only genus of the Scitamineae studied by Löv, or about which there is any published account of the mode of unrolling of the lamina. Löv recognized that the water tissue furnishes the principal expansion cells, but failed to notice the greater enlargement of those above and adjacent to the principal veins, which results in the formation of the ribs so essential to the mechanical support of the lamina throughout the order. The epidermis plays an inconsiderable part in the act of unrolling. Löv also gives some interesting observations on the substitution of other tissues in the act of unrolling when the water tissue is destroyed. By scratching the upper surface with a sharp knife, it is possible to injure the water tissue without destroying the epidermis. In this case the latter cells become much deeper than normal, and the leaf continues to unfurl. When the epidermis and water tissue are both destroyed by touching with a glowing needle, an abnormal growth of the palisade cells takes place, particularly in the neighborhood of the large veins, where periclinal divisions of the cells occur. The leaf manages to unroll.

The leaf which is just beginning to emerge is unribbed. Formation of the weak ribs is accomplished without the cells of the single layered water tissue becoming much larger above and adjacent to the principal veins than midway between them (fig. 18). Prevention of unrolling by tying caused the great hypertrophy of the cells of the upper water tissue (fig. 19). It was most pronounced above the principal veins, but extended completely across the leaf, with lesser maxima above many of the stronger subordinate veins. The lamina became strongly ribbed. The hypertrophied cells of the water tissue measured as much as 384 μ in depth, which is 4–5 times the normal, and accounted for over half the cross-section of the leaf. The epidermal cells were also greatly enlarged, becoming in places 67 μ in depth, as opposed to 15–26 μ in the normally unfurled leaf. The leaves curled backward when unbound and placed in water.

The leaves of *Canna*, like those of *Musa*, unroll normally in darkness.

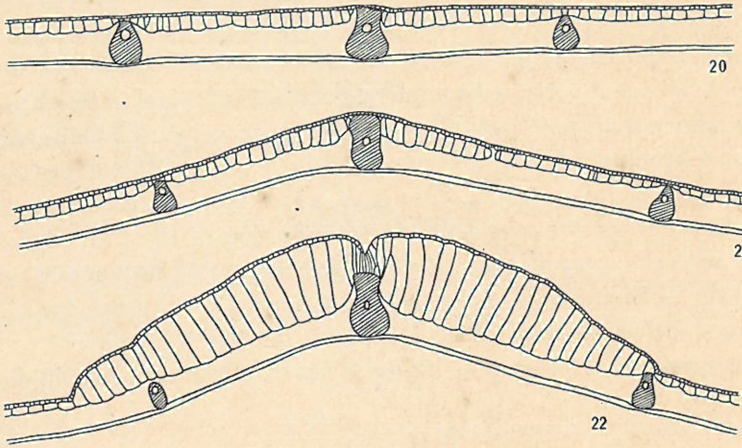
MARANTACEAE

Calathea magnifica Morton & Skutch.[4]—The leaves of this newly described species are ovate-oblong and very large, reaching 114 cm. long by 58 cm. broad. At the time the lamina appears above the short false stem, and even after the apex has begun to turn green, the upper surface is perfectly smooth, without the ribs so conspicuous in the mature leaf (fig. 20). The fibers on the upper side of the vascular bundles are thin walled, while those on the lower side are already conspicuously thickened. The water tissue is single layered everywhere except in the immediate vicinity of the midrib. It is usually not continuous above the principal veins; the fibers on their upper side are either in direct contact with the epidermis or separated from it by a few small scattered cells which appear to belong to the water tissue. In unfurling, the cells on either side of the principal

[4] Jour. Wash. Acad. Sci. 20: 372. 1930.

veins enlarge considerably, with the result that the leaf becomes ribbed (fig. 21).

Prevention of unrolling by binding the leaf causes great hypertrophy of the cells of the water tissue in the neighborhood of the principal veins. The region of hypertrophy is laterally sharply delimited from the surrounding water tissue (fig. 22). Single cells 464 μ in depth were observed, 2.5–3.7 times the depth found in normal leaves. Where it was thickest, the water tissue accounted for two-



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FIGS. 20–22.—*Calathea magnifica:* fig. 20, cross-section through principal vein of leaf before expansion, showing water tissue; fig. 21, same, through normally expanded leaf; fig. 22, same, through leaf bound 8 days; $\times 23$.

thirds to three-fourths the entire cross-section of the lamina. There was generally a deep furrow in the cushion of tissue above the center of the vein, except in the rare cases where the water tissue was continuous above it. This occurred because the epidermal cells, here in contact with the fibers, were unable to elongate as rapidly as the cells of the water tissue, which for this reason bulged above them. The epidermal cells in this position did undergo an enormous elongation, becoming 44–78 μ in depth when normally they were 7–11 μ, but they appeared to have been passively stretched by the water tissue (fig. 22).

As in the other species described, not only must the two halves of the lamina unroll individually, but it is necessary that they bend outward along the sides of the midrib. This is accomplished by the great development of prismatic expansion cells, with clear cell contents, in these regions. The largest vascular bundles are situated near the upper side of the organ, and numerous smaller ones are scattered beneath (fig. 23). The expansion cells penetrate deeply between the largest bundles, and by their enlargement at the time of unfurling of the leaf bend back the lamina halves. In drying they lose their turgor, and the lamina halves bend upward. In the middle of sunny days it is striking to see the large leaves of these plants, which grow in dense stands in low open places, all folded together upward, exposing the white, wax encrusted lower surface, in which most of the stomata are situated.

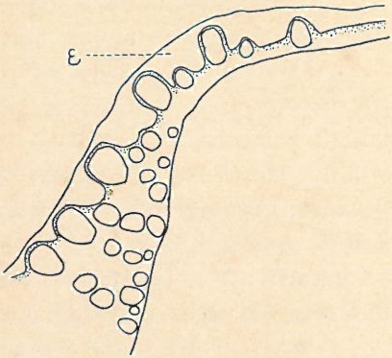

FIG. 23.—*Calathea magnifica:* cross-section through junction of midrib and lamina half; *e*, expansion cells; ×12.

Summary

1. An experimental study was made of the mechanics of the unrolling of the leaves of *Musa* and *Heliconia* (Musaceae), *Alpinia* (Zingiberaceae), *Canna* (Cannaceae), and *Calathea* (Marantaceae), representing each of the four families of the tropical order Scitamineae.

2. The large laminae of all the species studied are convolute in vernation. They are practically full-grown at the time they begin to emerge from the top of the false stem, which, to a greater or less degree, is characteristic of most of the genera of this order. At this time, if the lamina is unrolled, it is found to be smooth and flat, without the transverse ribs so characteristic of these plants.

3. Unrolling is effected by the timely enlargement of the cells of the upper water tissue above and immediately adjacent to the principal veins. The localized enlargement of these cells results in raising the principal veins above the general surface of the lamina, thus forming the ribs. In the coiled position of the leaf they are pushed inward, come to occupy a curvature of smaller radius, and are thus

(with the turgid cells which lie above them) brought into a state of compression. In this compressed state they force the lamina to unroll.

4. In *Musa* the fibers on the dorsal side of the veins are thick walled and become lignified somewhat before the portion of the leaf in which they lie begins to unroll. The fibers on the ventral side remain thin walled until the leaf has unfolded, and never become lignified.

5. Enlargement of the expansion cells proceeds inward from the outer margin of the lamina, and from the apex toward the base.

6. If the unrolling of the leaf is prevented by binding it with cord, the expansion cells in all species studied except *Alpinia* become greatly enlarged, and occupy over half the entire cross-section of the lamina. In *Alpinia* the hypertrophy is relatively slight, apparently because the water tissue is interrupted by thick walled cells which are not able to stretch. Only in *Canna* does the hypertrophy extend completely across the lamina half; in most cases it is strictly limited to the region of the principal and the stronger subordinate veins.

7. Leaves of *Musa* and *Canna* were found to unroll in complete absence of light. In darkness, however, the hypertrophy of the water cells of bound leaves is much less than of those in the light.

8. If the lamina of *Musa* is prematurely unrolled and held in a plane, the expansion cells fail to enlarge. They enlarge only when in a state of compression.

9. The ribs are essential to impart rigidity to the lamina halves, which are otherwise without lateral support.

10. In addition to the unrolling of each side of the lamina, a special arrangement is necessary to bend it outward from the midrib. This is effected by great development of expansion cells along the edges of the midrib (*Musa*, *Heliconia*, *Calathea*), or in the center of the midrib (*Alpinia*).

11. In most members of the Scitamineae, when the leaf suffers great water loss and the expansion cells lose their turgidity, the process of unfolding is in part reversed. Each side of the lamina bends upward along the midrib, exposing the stomata, which are situated principally in the lower surface. This non-adaptive movement is a necessary result of the structure and method of unfolding of the leaf.

12. In *Musa* the sides of the lamina fold downward in dry weather. This is a result of the formation of a rather massive tissue of prismatic cells in a strip along either side of the midrib, which thus becomes a pulvinar band. The rising and falling of the lamina halves are brought about by differential changes in the turgor of two antagonistic tissues, the expansion cells on the upper side and the prismatic cells on the lower.

13. The prismatic cells begin to develop only after complete expansion of the leaf, when stimulated by the compression to which they are subjected after the expansion cells on the upper side of the pulvinar band bend it downward. Hence they do not develop in leaves which are prevented from unfolding by binding. They develop only in the light.

In conclusion, I wish to express gratitude to Professor DUNCAN S. JOHNSON for his continued interest in the course of my tropical studies; to Dr. JOHN R. JOHNSTON, Director of Agricultural Research of the United Fruit Company of Boston, for allowing me the use of the Company's research stations in Central America, and for many other courtesies extended to me by the Company; and to Mr. JOSEPH H. PERMAR, Director of the station at Almirante, Panama, where the present study was completed, for his unfailing cooperation in my work.

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LITERATURE CITED

1. DUVAL-JOUVE, M. J., Histotaxie des Feuilles de Graminées. Ann. Sci. Nat. Bot. VI^e Ser. **1**:294–371. 1875.
2. GOEBEL, KARL, Die Entfaltungsbewegungen der Pflanzen. pp. vii+483. Jena. 1920.
3. LÖV, LEOKADIA, Zur Kenntnis der Entfaltungszellen monokotyler Blätter. Flora **20**:283–343. 1926 (contains a full list of previous works on the subject).
4. RUDOLPH, KARL, Zur Kenntnis der Entfaltungseinrichtungen an Palmenblättern. Ber. Deutsch. Bot. Ges. **29**:39–47. 1911.
5. SKUTCH, A. F., Anatomy of leaf of banana. BOT. GAZ. **84**:337–391. 1927.
6. ———, On the development and morphology of the leaf of the banana. Amer. Jour. Bot. (In Press.)
7. TSCHIRCH, A., Beiträge zu der Anatomie und dem Einrollungsmechanismus einiger Grasblätter. Jahrb. Wiss. Bot **13**:544–567. 1882.