PHENOMENA OF CORRELATION IN THE GROWTH OF LEAVES

by

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The leaves of one plant can be extremely variable in their shape, size, anatomy, etc. notwithstanding the fact that they may be considered as genotypically identical; it is true that the suggestions of HUBER (14d) admit the possibility of in induced hereditary difference between the extreme lowest and highest leaves of one and the same tree, but as long as this highly interesting view point has not been proved, we are entitled to stick to the classical conception expressed above. Indeed, the leaves of one individual, esp. in trees, offer the finest specimens of widely diverging modifications; it may suffice to recall to mind the sun and shade leaves (survey of literature in 9 g), the leaves of water shoots (7,12), those at the lower and the upper end of a branch (5, 24, 25), those on young and on older individuals (31); also in herbaceous plants the differences between the leaves can be of the same order; their plasticity, moreover, seems to be even greater (9 g).

The causes of these modifications are manifold and can be internal or external. Among the former I mention the age of the plant (3 bis, ter, 26 bis), the water supply, the provision with food materials, with hormones for the leaf veins (2) and with those for the mesophyll (4), the suction power, the reserve or synthesis of food materials in other parts of the plant (which can enable an etiolated leaf to reach the full grown size; see 1, 15, 18, 20b, 30, 36). The external factors, natural or experimental, which have been investigated more or less thoroughly, are in the first place the intensity of the light and the degree of humidity of the air (9 g); further the amount of salts in the surrounding medium (9 g), the climate in different seasons (6), a mechanical load (13) and the opposite, viz. the supporting of the branches (7); a positive hydrostatic pressure (27b), a mechanical tension (33), partly severing of the petiole (9 g, Ch. IV, § 1; 32), inducing the leaf to root in the soil (16, 19, 21, 22, 39), the removal of a part of one leaf (11, 20a), and finally the removal, with exception of a few, of the leaves of a branch or of a young plant.

The last mentioned method of interfering with growth can be applied in two ways: removal of all the buds of a branch save one (EWART, 8, *Tilia* NORDHAUSEN, 25, *Fagus*) or removal of one leaf, the plumule and the axillary buds of a seedling (16, 18, 26, 28, 37, 38); the result being that the remaining leaves develop appreciably larger than the control specimens.

During the spring and the summer of 1943 I made similar experiments, esp. with branches of trees, in order to see if the phenomenon just mentioned and up till now observed in only a small number of species presents a general rule, and if so, whether this abnormal enlargement of the leaf is due to cell stretching or to cell division, or to both. In March and April branches of 70—100 cm were cut and kept in water in a hothouse; somewhat later, just before the leaves unfolded, experiments were made with branches, 1—2 m long, which remained on the trees. Generally I removed all buds but one; it is indifferent whether this is the terminal or a lateral one. I stated that when two buds were left the effect on the whole was small, at the utmost about half of that with only one bud left. On branches which bear a great number of buds I sometimes left four or five of them; in these cases the result was nil. Sometimes I cut away the greater part of the only remaining bud as it developed, leaving only two or three leaves; these never showed a stronger growth than on intact shoots. Therefore I generally stuck to the very simple treatment of removing all buds but one. Dormant buds were taken away as soon as they developed. As controls served branches which were approximately of the same habitus as the test ones and especially those which grew at the same side and at the same height on the tree.

Some species gave no results at all; this is not very remarkable as my material was taken rather at random. Sometimes branches from 1 to 2 m bear dozens of buds, sometimes only a few (*Aesculus*); especially the latter ones proved unsuccesful; they presented only a small minority, however, as compared with the other species used, and will not be further discussed here. Some species responded readily to the treatment in the hothouse, but on the trees they showed no difference between test and control branches; (in one case, viz. *Acer saccharum*, the opposite occurred); amongst these was e.g. *Fagus*, a species which in NORDHAUSEN's experiments showed a strong correlative response. It is also remarkable that the branches of *Fagus asplenifolia*, cut from the south side of the tree, reacted much better to the defoliation than those of the north side, and that those of *Fagus pendula* remained smaller on the north side than those on the south side. There is also a divergence between the results of EWART with *Tilia europaea* and mine with *T. platyphyl-*

TABLE 1. Length of the shoots (in mm), number of leaves per shoot, surface of the leaf blades (in mm²).

Species	Length of the shoots in mm			
	branches cut off		br. on the tree	
	control	test	control	test
Acer pseudo-Platanus	8	40	100	95
Acer saccharum	no diff.		no diff.	
Carpinus Betulus incisa				
entire	28	100	100	315
incised	70	110	85	400
Crataegus monogyna	10	35–70	no diff.	
Fagus silvatica asplenifolia				
south side	3	75	no diff.	
north side	—	—	—	—
Fagus silvatica pendula				
south side	3	275	no diff.	
north side	—	—	—	—
Ginkgo biloba	2	85	100–300	300
Hedera Helix	not exam.		no diff.	
Platanus acerifolia	10–20	55–100	250	440
stipules				
Populus nigra italica	9	10	230	630
Quercus Robur	80	85	160	180
Robinia Pseudo-Acacia	2	25	120	260
Salix alba	16	38	no diff.	
Sorbus intermedia	not exam.		115	165
Syringa vulgaris	35	80	no diff.	
Taxus cuspidata nana	15–25	45	no diff.	
Tilia platyphyllos	5	80	no diff.	
Tilia platyphyllos laciniata	16	50	100	315
Tilia tomentosa	50	85	220	310
Ulmus glabra cornuta	10	35–70	140	300

los, although these species are probably identical. These and other questions must remain for the moment unsolved.

In the hothouse the test branches budded earlier, they developed longer shoots with more and larger leaf blades than the controls. Figure 1 gives an example which is typical for most cases. In table 1 are recorded the main measurements of the shoots and the leaves. The differences between test and control leaves, as they appear from the figure and from table 1, are considerable, but they do not mean much because on cut branches the leaves never reach their full growth; even on the test branches they grew at the utmost to the size of a normally developed lamina. Sooner or later their

TABLE 1. Length of the shoots (in mm), number of leaves per shoot, surface of the leaf blades (in mm^2).

Number of leaves per shoot [1])				Surface of the leaf blades in mm^2			
br. cut off		br. on the tree		branches cut off		br. on the tree	
control	test	control	test	control	test	control	test
4	6	no	diff.	2050	6200	17500	42500
no	diff.	no	diff.	no	diff.	13250	28800
5	8	5–10	17	920	1720	1900	4400
7	10	12	29 [2])	—	—	1000	1450
6	8	no	diff.	320	1270	no	diff.
4	12 [2])	no	diff.	800	2100	no	diff.
—	—	—	—	920	1250	no	diff.
4	9	no	diff.	2740	4200	no	diff.
—	—	—	—	1900	3200	no	diff.
4	8	no	diff.	285	980	3900	5825
not	exam.	no	diff.	not	exam.	4140	7625
3	4	8	10	3535	12570	20500	37300
—	—	—	—	—	—	±120	±450
4	8	21–24	25–31	320	650	2400	3500
8–11	10–12	no	diff.	295	2160	6030	13950
3	3	7–10	8–13	600	1230	8560	17950
6–7	7–9	no	diff.	355	860	no	diff.
not	exam.	8	12	not	exam.	5000	920
3–4	6–9	no	diff.	270	640	no	diff.
—	—	—	—	±25	±45	no	diff.
4	5	no	diff.	2150	3275	no	diff.
3	4–5	5–6	8	300	1020	±3500	±8100
4	5	7	9	2775	4600	14350	32500
3	5	5–8	10	350	960	7850	14250

development stops, although the lower ends of the branches were cut afresh every day or every other day. The phenomenon of correlative growth, therefore, can only be studied to its full extent on the tree.

The branches treated on the trees presented a striking difference in their behaviour when compared with those in the hothouse. They budded later than the control specimens and their leaves

1) Leaves on the test branches which have only partly unfolded are no counted; on the control branches there is no gradual transition between this year's unfolded leaves and next year's terminal bud.

2) With a number of axillary shoots.

TABLE 2. Anatomical details of the leaves.

Species	Branches cut off						
	av. diam. upp. epid. cells in micra		av. diam. lower epid. cells in micra		stom. per unit surf.		density of veins in control as comp. with test
	contr.	test	contr.	test	contr.	test	
Acer pseudo-Platanus	25	30	15	17	58	46	equal
Acer saccharum	results negative						
Carpinus bet.inc.(ent.)	120	140	75	85	16	15	equal
Crataegus monogyna	—	—	40	62	16	12	equal
Fagus silv. asplen.	no appreciable differences						denser
Fagus silv. pendula	40	50	26	38	23	14	equal
Ginkgo biloba	47	60	25	30	36	21	denser
Hedera Helix	not examined						
Platanus acerifolia	75	60	40	30	22	33	equal
Populus nigra italica	27	40	—	—	21	16	denser
Quercus robur	22	36	17	20	114	75	denser
Robiniapseudo-Acacia	16	17	15	15	no diff.		equal
Salix alba	43	46	—	—	6	4½	equal
Sorbus intermedia	not examined						
Syringa vulgaris	32	45	—	—	43	33	equal
Taxus cuspidata nana	40	60	55	85	24	16	
Tilia platyphyllos	28	40	25	32	—	—	equal
Tilia platyphyllos lac.	40	40	30	30	15	17	equal
Tilia tomentosa	27	43	—	—	—	—	denser
Ulmus glabra cornuta	31	35	—	—	—	—	denser

remained smaller; in the end of May or in the beginning of June, however, they made up for the arrears and within a few weeks they showed a positive response to the removal of the buds. The shoots which developed from the remaining bud were recognizable by the following characteristics when compared with the check shoots:

1. they are longer;
2. their growth lasts till much later in season and in many cases it does not stop even in August; comp. (5);
3. when the young leaves contain anthocyane, they keep it during a much longer period; this was esp. striking in *Acer saccharum*, its test branches thereby being noticeable at a large distance (comp. 7); (test leaves in cut branches of *Fagus silvatica atropunicea* were red, control leaves nearly green; test and control branches on the tree, however, showed the same intensely red colour; this holds true for shade as well as for sun leaves).

TABLE 2. Anatomical details of the leaves.

Branches on the tree						
av. diam. upp. epid. cells in micra		av. diam. lower epid. cells in micra		stom. per unit surf.		density of veins in control as comp. with test
contr.	test	contr.	test	contr.	test	
		no appreciable differences				
		no appreciable differences				
		no appreciable differences				
		results negative				
		results negative				
		results negative				
~100	70	46	62	10	7½	denser
		no appreciable differences				
		no appreciable differences				
		no appreciable differences				
		no appreciable differences				
		no appreciable differences				
		results negative				
		no appreciable differences				
		results negative				
		results negative				
		results negative				
		no appreciable differences				
		no appreciable differences				
		no appreciable differences				

4. species which possess stipules keep them for a much longer period; see table 1, *Platanus;*
   all these characteristics can be summarized by saying that the test shoots remain longer in the juvenile stage;
5. they develop a larger number of leaves; it is not easy to count them because the growth of the shoots hardly comes to a standstill; very young leaves are not included in the numbers in the table; in the control branches there is a clear division between the outgrown leaves and the terminal bud of the next year; it remains to be examined what will appear to be the influence of the long lasting growth of the test shoots on the shoots of 1944;
6. the leaves are larger.

Furthermore, these shoots often make the impression of being tn weak health; leaves are sometimes wrinkled and they are easily iorn; they are more apt to be attacked by lice and other insects.

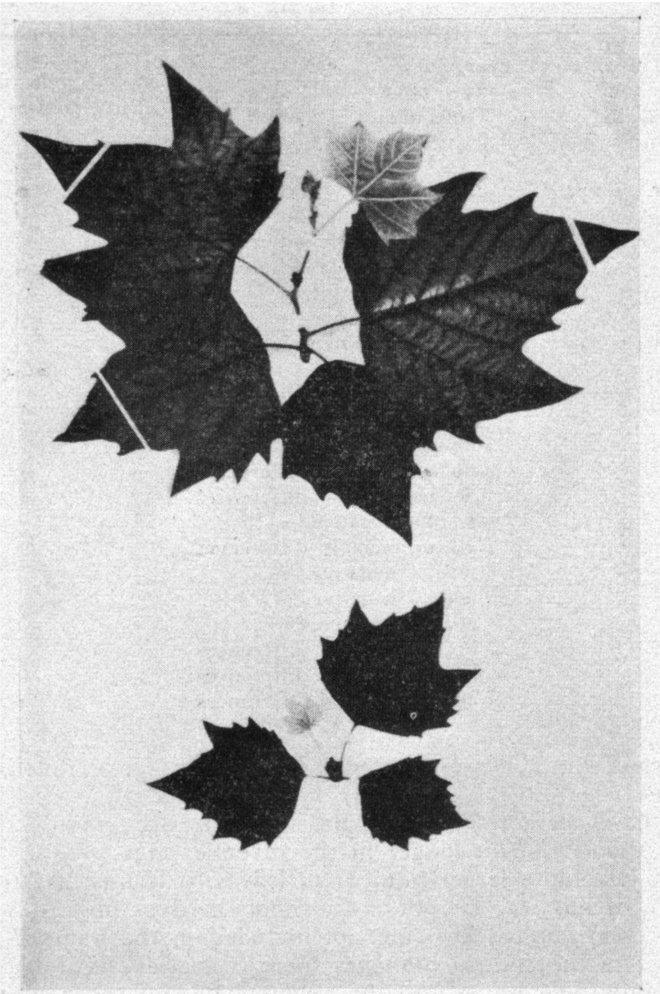

Fig. 1. *Platanus acerifolia;* branches cut off; above: shoot on defoliated branch; below: control shoot; Leyden, 30 April 1943.

Not all of these several characteristics presented themselves equally clear in all cases, but on the whole most of them were sufficiently distinct to show the effect of the removal of the buds in a convincing way. Photographs of my material can not be given save figure 1, but I think that the data in table 1 speak for themselves;

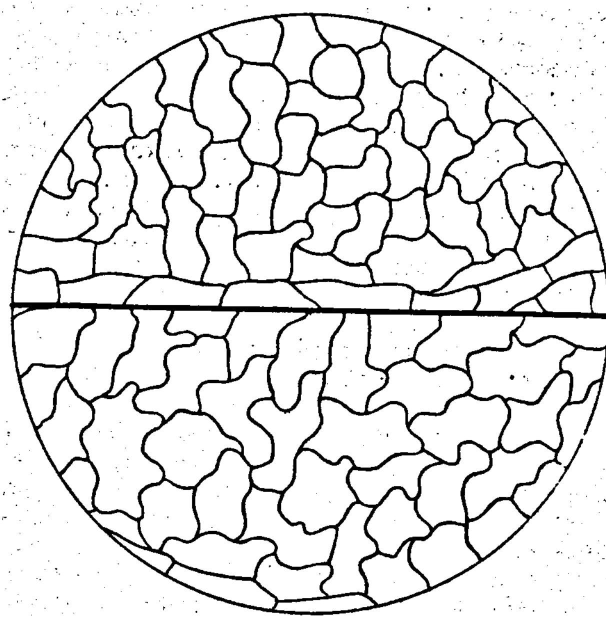

Fig. 2. *Platanus acerifolia;* branches cut off; cells of the upper epiderm, 220 ×; left: of control leaf, surface 3535 mm²; right: of test leaf, surface 12570 mm²; Leyden, 30 April 1943.

moreover, my herbary remains at the disposal of everyone interested. It may be emphasized that I always compared the best developed test leaves and shoots with the largest ones which I could find on the control branches; the dimensions of the latter, therefore, are invariably well above the average. The data of the table illustrate well the enormous difference in development between the leaves in the hothouse and those in the open air and explain why I attach little importance to the former ones.

When we compare the anatomy of the test and the control leaves, we see that on the whole they are of the same type. For practical reasons the treated branches and the controls were chosen among the lower ones, therefore I had generally to deal with shade leaves. (It would be extremely interesting to repeat this experiment with sun branches in the tops of the trees; I am anxious to know the botanic garden equipped for this sort of work). Although the test leaves attained considerably larger dimensions and sometimes were a little thicker, they nevertheless present the shade type too (density of the veins, number of stomata per unit surface, thickness of the cuticle, development of palisades, etc.). This is true for the specimens in the hothouse as well as for those in the open air, but these groups differ in one important point: in the hothouse the test leaves achieved their stronger growth mainly by cellstretching (exc. *Platanus*, *Robinia*, *Tilia*), on the trees by cell division (exc. *Ginkgo*). In table 2 some data are recorded which corroborate this assertion. It goes without saying that in those cases where the cell stretching is considerable the density of the veins and the number of stomata per unit surface are lessened; but this does not mean that the leaf presents a more distinct shade character.

Figure 2 presents the upper epidermal cells of *Platanus acerifolia* in the hothouse; it could serve equally well to illustrate the relative dimensions of the cells on the tree. It is clear that the cells on the right are distinctly smaller than those on the left. The surfaces of the test and control lamina were respectively 12570 and 3535mm^2 and therefore it is superfluous to argue the evidence that the strong expansion of the test leaf can have been attained otherwise than by cell division.

Figure 3 presents the upper epidermal cells in *Hedera Helix*, on the right those of the test leaf (7625 mm^2), on the left of the control (4135 mm^2); also here it goes without saying that cell division can have been the only means of reaching the greater surface. It will be noticed that in these preparations there are a number of cells which obviously have divided only recently. This is the only example among the species examined showing a phenomenon which one would expect to see rather frequently. In my former experiments with water plants (9 a-f) I noticed several times the remarkable fact that so very few indications were visible of a cell division which nevertheless undeniably takes place. We may conclude, however, that in species such as *Platanus*, *Hedera*, a.o. the process of cell division continues till a late stage of maturity of the leaf and that apparently the number of cells which will form the lamina is by no means fixed in the bud stage (comp. below).

I made experiments with a small number of herbaceous plants. Their tops and axillary buds were removed in order to see if the leaves grew larger than in the controls. EWART stated that removal

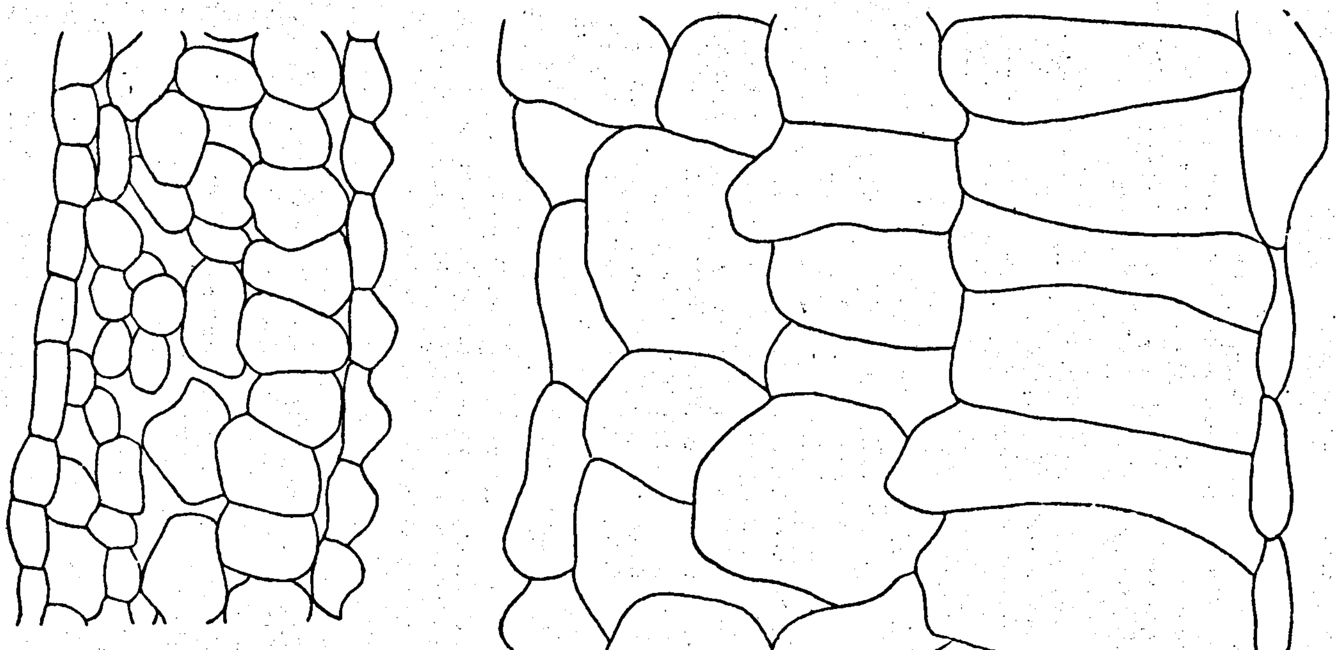

Fig. 3. *Hedera Helix;* branches on the tree; cells of the upper epiderm, 220 ×; left: of control leaf, surface 4135 mm^2; right: of test leaf, surface 7625 mm^2; Leyden, 13 July 1943.

of the buds during summer had no influence on the size of the adult leaves of trees, but most of the herbaceous plants which I chose responded very distinctly to this treatment as will be seen from table 3 where a few of my results are recorded. Species which gave doubtful results will not be discussed here.

TABLE 3. Size of leaf blades in herbaceous plants after removal of tops and axillary buds; in mm^2.

	control	test
Aster Novi Belgii f. Climax	2250	3750
Coleus hybridus	4350	6050
Plectranthus fruticosus	5900	9250
Solanum tuberosum f. Bevelander . .	1775	2875
„ „ „ Eigenheimer .	875	1420

The shoots of *Solanum* can be best compared with those of the trees, because they were young ones, sprouting from tubers which had been deprived of all buds but one. On the other hand, they achieved the extra growth consequent of the treatment in the same way as the species with adult leaves, viz. by cell stretching only. This stretching took place in all directions, the leaves thereby not only becoming larger, but also much thicker. Figure 4 presents cross sections of *Coleus* which are representative for the results with the herbaceous plants. The thickness of the test leaf is 165 against 85 in the control, but it is clear that this does not imply that is has the character of a sun leaf. When leaves are induced to root in the soil, expansion also takes place by means of cell stretching but it seems that in this case the lamina assumes more or less the aspect of the sun leaf; see 21, 22, 29 page 67.

"The facts first mentioned" (viz. the growth of the test leaves by means of cell division) "hardly agree with the usually accepted idea that the total number of leaf-cells is determined at an early date, and that the subsequent expansion of the leaf merely involves an increase in their size, for the large dimensions shown by the leaves on the shoot defoliated in spring were attained owing to a longer continuance of growth, and to a larger production of cells during expansion". With these words EWART (l.c. page 81) summarizes his results with defoliated branches of *Tilia europaea*. I could use the same words for describing the great majority of facts which I found, esp. in the branches which remained attached to the trees.

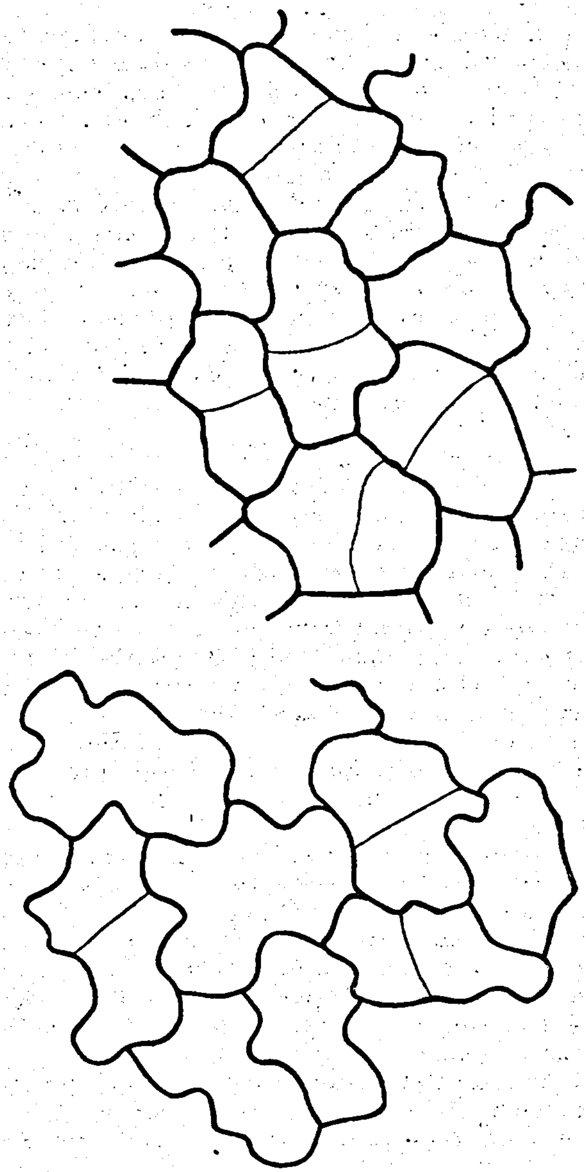

Fig. 4. *Coleus hybridus;* cross sections through adult leaves, 220 ×; above on plant derived of top and axillary buds, surface 6035 mm², thickness 165 μ: below: control, surface 4350 mm², thickness 85 μ; Leyden, 4 June 1943.

In my experiments with water plants I have repeatedly observed that an intense cell division can take place during growth processes which are generally ascribed to cell stretching. This not only hold true for the petioles, but also for the leaf blades. So e.g. I stated that the first floating leaves of *Limnanthemum nymphaeoides* expand in a few days to more than the 40-fold of their initial surface and that their cells at the end have the same dimensions as at the start (10). The capacity of cell division in this species is strongly developed; we see now that this is true in many more plants; species such as *Platanus* are worth while being examined farther in this respect. *Potamogeton natans* forms leaves which vary in size from 1 to 12 according to circumstances, and again the surface of the largest ones is due to cell division; the same holds true for *Aponogeton distachyus*; (full particulars about these species will be published later, 9 h).

These facts are not as isolated as many will be inclined to think. Other authors have come to similar results by using similar or other methods on other plant species. I think it of sufficient interest to quote a few instances here; see also 23 and 35.

DANIEL (7) defoliated the branches of a large number of species; his results tally with mine; his conclusions are rather vaguely expressed, but we can deduce from them that with a few exceptions (*Salix caprea*) the larger dimensions of the leaves are due to multiplication of the cells. VON PAPEN (26) deprived seedlings of their plumule and one primary leaf and examined the development of the remaining one (with primary leaves are meant those following on the cotyledons). In *Phaseolus vulgaris* this leaf reached a surface about 50% greater than the controls; (some years earlier VYVYAN, 37, found the same). „Vergleichen wir die Epidermiszellen solcher künstlich grössergezogenen Primärblätter mit denen normal wachsender Pflanzen, so ist festzustellen, dass sie im entwickelten Zustand alle gleich gross sind". (l.c., page 194). HÄRDTL (13a) in a similar experiment with *Phaseolus vulgaris* obtained identical results as far as the size of the lamina is concerned, but his measurements of the cells led to an opposite conclusion (l.c., page 660): „Die Veränderungen im Bau bewegten sich im Rahmen des Gegebenen, d.h. Verkleinerungen und Vergrösserungen wurden von der Pflanze an den vorhandenen Zellen ausgeführt, worin sich eine Bestätigung früherer Ergebnisse ergibt". The discordance between the results of VON PAPEN and HÄRDTL can for the moment only be explained by assuming that they used different varieties. In my experiments with two varieties of potato shoots (9 g) something similar occurred; and it should not be forgotten that the dimensions of cells are apt to vary considerably with circumstances.

VON PAPEN found that in *Cucurbita Pepo* a conformable experiment yielded an enlargement of more than 100%. „Vergleicht man die Zellgrössen normaler ausgewachsener Spreiten met denen der behandelten Pflanzen, so lässt sich feststellen, dass alle ausgewachsene Primärblätter unabhängig von ihrer Grösse fast gleich grosse Epidermiszellen aufweisen. Das starke Wachstum über die Normalgrösse der Primärblätter hinaus ist also in erster Linie auf Zellteilungen zurückzuführen". (l.c., page 197). This, however, is not a strict rule; cell division can be supplemented by stretching. In the case of *Sicyos angulata*, e.g., he states: „Die Zahlen besagen dass das Primärblatt von Sicyos seine Fläche um 60 bis 170% überwachsen kann, die einzelne Epidermiszelle vergrössert sich gleichmässig um etwa 70%". (l.c., page 200).

WAGNER (38) and KANZLER (16) deprived very young seedlings of one of their cotyledons with the consequence that the remaining one attained abnormally large dimensions which were due to cell stretching; see also 17. ROHRER (28) found in similar experiments that this holds true for the upper epidermis, but that in other tissues cell division can continue for a longer time; (l.c., page 417): „Der durch die Operation hervorgerufene Reiz hat die Zellteilung bei der oberen Epidermis vielleicht früher sistiert". In artificially grown dwarf leaves, on the other hand, he found a small number of large cells; (l.c., page 424): „Demnach müssen bei den Zwergblättern nicht nur relativ (zur Blattgrösse), sondern auch absolut weniger Zellteilungen stattgefunden haben. Sie müssen früher beendet gewesen sein als beim normalen Blatt, wo sie noch eine Zeitlang neben der Streckung einhergehen".

AVERY (2) in his fundamental researches on tobacco leaves corroborates the view that the duration of cell division can be different in different tissues. "Cell division ceases first in the epidermal layers, as indicated by their greater size in the mature leaf, next in the region which becomes spongy mesophyll, and last in the palisade. A few cells of the spongy mesophyll continue division after all others have stopped, and give rise to new provascular strands during intercalary growth of the lamina. The external factors which influence a continuation of cell division are numerous" (unfortunately he does not indicate them)", but in the material examined, epidermal cells were no longer dividing, even in the basal and central regions of leaves from 6 to 7 centimeters long (1/5 to 1/6 final size). The degree of maturity of all cells, however, is dependent upon their distance from the tip and their distance from the margin" (2 b. page 569).

In this experiment I concentrated my attention chiefly on the epidermal cells, because they are easiest to measure. Whenever I examined the layers of the mesophyll I could only state that their development was in accordance with the other tissues. If AVERY's observations on tobacco are generally true my results would be the more valid because they are derived from the tissue least disposed to cell division.

That there are really several external factors which influence a continuation of cell division appears also from the following examples. PEARSALL and HANBY (27b) have obtained an abnormally strong expansion of leaf blades in a number of species with palmate leaves by applying a slight hydrostatic pressure. "The leaves were originally of the same size (before treatment), but, after treatment those from increased pressure were much the larger. Since the cells are somewhat smaller in the larger leaves, much more cell division must therefore have taken place under increased pressure". (l.c., page 91). They were "originally tempted to consider cell elongation as the more likely, but the evidence available points definitely to cell division as the underlying cause"; see also 27a.

BATALIN (3) in studying the effect of light and darkness comes to the following conclusion: „Aus diesen Beobachtungen geht ein wichtiges Gesetz hervor, welches — ich weiss nicht warum — von Niemanden bis jetzt aufgestellt wurde, nämlich: die Zahl der Zellen im normalen Blatt ist eine grössere, als in den etiolirten, und die Grösse der Blätter ist proportional der Zahl der Zellen, welche sie enthalten". (Obviously in BATALIN's time the measurement of the cells was neglected as it has been since). „Diese Folgerung gibt die Möglichkeit, folgenden Schluss zu ziehen. Das Blatt wächst so viel, wie es neue Zellen erzeugt und das Wachsthum des Blattes, überhaupt angenommen, hängt nicht von der Vergrösserung der Länge einzelner Zellen ab" (l.c., page 674).

SKUTCH (34) put young banana trees in an oblique position and saw that they erect themselves owing to a renewal of growth in the bases of the leaves; (l.c., page 83): "The cortex becomes very much thicker on the lower than on the upper side. This is brought about by the enlargement and division of the large, thin-walled, starchladen mature cells of the ground parenchyma on this side".

For the present we must conclude that the expansion of the lamina is achieved by means of cell division and of cell stretching; the part which each of them takes in this growth process can vary according to the species, according to the different parts of a leaf (base, top, margin), according to the different tissues (epiderm-mesophyll; upper or lower epiderm), according to the many possible external conditions.

Up till now I could only investigate the morphological and anatomical sides of the problem; the physiological aspects will certainly prove very interesting, but they demand much more time than I had at my disposal; they involve the whole problem of transport in plants. When an experiment yields results, that is, when the remaining bud develops leaves much larger than the normal ones, it is clear that these leaves profit from the supply of water and food materials which were intended for the whole branch. Does it mean that their suction power has become greater? and in the opposite case, is this suction power of one bud insufficient to attract the current to the branch? These and other questions should certainly be dealt with; comp. 14, a—c.

Should the enlargement of the leaves on defoliated branches be ascribed to the abnormally great supply of water or rather to that of food substances? The results with the cut branches point to the former, those with the branches on the trees to the latter solution. VYVYAN obtained an abnormally large primary leaf in seedlings of *Phaseolus vulgaris* when the plumule and the opposite leaf were removed; when, however, the cotyledons were cut away as well, the remaining primary leaf grew very slowly and there was no question of surpassing the normal dimensions. This indicates that food materials are necessary for the achievement of the extra growth. It is a pity therefore that VYVYAN did not measure the cells of his test material.

The results of PEARSALL and HANBY, as well as the suggestions which they derive from them, point in the same direction; (l.c., page 92): "in whatever manner the nutrient solutions reach the dividing cells, it is clear that to do so they must pass through the cell walls. Diffusion through the cell walls would be most rapid if these were saturated with water under pressure; it would slow down and cease as the water content of the walls decreased. These considerations suggest that positive hydrostatic pressures are necessary in order that the meristematic tissues may be irrigated with water, and hence that dissolved materials may reach the dividing cells".

Further there is the action of hormones to be reckoned with. In my experiments the test leaves always unfolded harmoniously; the hormones for the veins and those for the leaf parenchyma are obviously equally well distributed notwithstanding the abnormally large dimensions. AVERY (2) and BONNER, HAAGEN SMIT & WENT (4) studied the auxins in leaves of seedlings and in circumstances widely different from those in my experiments; the same holds true for the results of KISSER and POPP (17). Therefore I will not go far into this side of the question; the following quotation from AVERY (2 c, page 328) indicates sufficiently the character of the problems which are awaiting their solution."At the base" (of the young tobacco leaves) "cell volume is increasing only 0.3 to 0.4 times as rapidly as the volume of the leaf as a whole, which corroborates the above evidence for cell division. New cells, therefore, are being added in the direction of polarized growth. It is difficult to interpret the data. The hormone may be promoting cell division. It may on the contrary be promoting cell enlargement, and the cells after reaching a certain size, divide and thus maintain a favorable nuclear-cytoplasmic ratio. In either case, there seems to be a definite relation of the auxin to polarized growth".

Summary.

In a number of trees branches were derived of all buds save one. The main characteristics which distinguished the shoots developed from the remaining bud, when compared with the control shoots, are the following:

(1) they are longer; (2) their development stops much later in season; (3) they develop a greater number of leaves; (4) the leaves are considerably larger.

Branches which were cut from the trees showed more or less the same phenomena, but the leaves in most cases did not reach their full size.

The abnormally large dimensions of the test leaves were attained by cell division (with one exception) when the branches were left on the trees; on cut off branches most species examined achieved the correlative enlargement by cell stretching.

Leaves of a number of herbaceous plants also attained abnormally large dimensions, when the top and the axillary buds were removed; in these species the enlargement was due to cell stretching.

It is pointed out that the capacity of cell division in leaf blades is more widely spread than is generally accepted. The expansion of leaves can be achieved by cell multiplication and by cell stretching. The part which each of them take in this growth process can vary according to the species, according to the different parts of a leaf, according to the different tissues, according to the many possible external conditions.

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