NOTE ON SOME PROPERTIES OF DECUSSATE FOLIAGE LEAVES WHICH ARE CONNECTED WITH SPACE-FILLING IN THE BUD.

by

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During the bud stage foliage leaves of successive developmental stages continue to be closely packed and notwithstanding the different growth rates of the different leaves the space-filling usually does not give rise to serious difficulties.

Of course this is only possible in such cases where the growth processes are in due harmony. For decussate leaves as for other leaf arrangements this harmony may be reached in a great number of ways, as there are many kinds of efficient space-filling.

When we consider the simplest case of simple, entire and flat leaf blades we may, for example, get a satisfactory packing for decussate leaves when every blade is curved towards the adaxial side, or folded towards the same side by a rectangular fold along its midrib; our schematic Fig. 1. A may serve to illustrate this

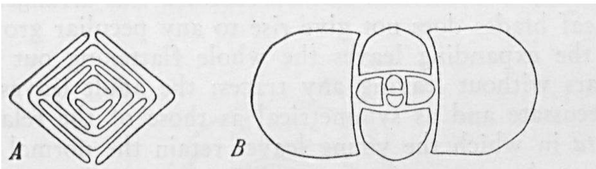

Fig. 1. Theoretical diagram of two possible ways of aestivation of decussate foliage leaves with a satisfactory space-filling.

case. Similarly for fleshy and thick leaves our Fig. 1 B may give another solution of the problem.

It will be clear however that flat and plane leaf blades, at least when they are not very narrow, are not easily packed without any folding; our schematic Fig. 2 A may serve as an illustration. In such a case a great improvement may however be reached by a flattening out of the whole bud in one of the two diagonal planes between the four leaf orthostichies, cf. Fig. 2 B. If the flattening out becomes somewhat more advanced than in that figure, a satisfactory space-filling may be easily reached.

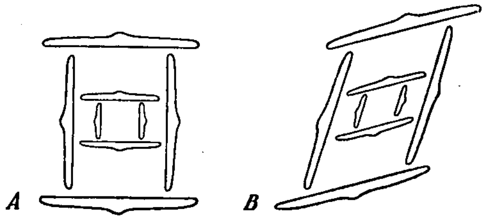

Fig. 2. Theoretical diagram of a possible way of aestivation of decussate foliage leaves with an unsatisfactory space-filling (A) and the same improved by a flattening out of the bud in a diagonal plane (B).

Such a condition may be readily observed in the young leaves of *Rochea coccinea* without any preparation, by simply looking at the apex of a growing shoot. A characteristic feature of such a case is that the two leaves of a pair are no longer right opposite each other; as viewed from the side every leaf juts out of the other [1]). In the successive pairs it is alternately to their right and to their left that both leaves of a pair are jutting out; in our Fig. 2 B the first and third pair jut out to their left, the second and fourth to their right.

In the above mentioned *Rochea coccinea* this arrangement of the young leaf blades does not give rise to any peculiar growth process and in the expanding leaves the whole flattening out of the bud disappears without leaving any traces; the adult leaves are accurately decussate and as symmetrical as those of the related *Rochea perfoliata* in which the young leaves retain the normal position of our Fig. 2 A.

There are however many decussate plants in which the leaves are induced by the same kind of packing in the bud condition to

[1]) This has already been observed as early as 1826 by Roeper (3, p. 465) who wrote: "Occurrunt quandoque folia opposita, juventute omnino plana et vernatione complanata, ita tamen, ut nervi medii non omnino invicem superpositi sunt, et ut portio quaedam marginis dextri vel sinistri utriusque folii ab altero non tegatur. Folia haec tunc, primis saltem vitae stadiis, foliis nodi praecedentis opposita esse videntur, neque alterna, sed videntur tantum, quia internodium cui insident aliquantulum torsum est, foliaque quasi resupinans."

certain peculiar growth processes leading to a more or less lasting structural property.

As such consequences to the leaf plastics I am able to mention here two quite different groups of cases, the one being the peculiar kind of contortion of decussate leaves, the other the curious shape of the falcate leaves of *Rochea falcata.*

1. Contortion of decussate leaf pairs is a phenomenon that is wide-spread amongst the Dicotyledons: W y d l e r mentions it (6, p. 126) for *Hydrangea, Hortensia, Lonicera Xylosteum, Evonymus latifolius, Stachys sylvatica, Salvia glutinosa* and innumerable other plants; R o h r b a c h describes it (4, p. 15) for the genus *Silene* and most other *Sileneae.*

In all these plants the successive pairs are alternately right and left contort, a condition which figures very well as a counterpart to the remarkable facts of the heterotropous corolla contortion.

We have to take this alternate contortion as a consequence of the above mentioned peculiar growth processes; all jutting out edges namely are induced to become induplicate and to overlap the narrower edge of the partner leaf.

The connection between this kind of contortion and the space-filling in the bud has never been pointed out in botanical literature; the only author as far as I know who ever tried to explain the decussate contortion, R o h r b a c h, unfortunately took his starting point from the first visible stages of foliar development, from the cell divisions in the vegetative cone, which had been described two years earlier by N. J. C. M ü l l e r (2).

Finding in M ü l l e r the observation that the two primordia of

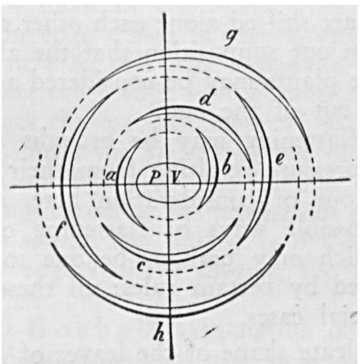

Fig. 3. Theoretical diagram of vegetative bud of Silene spp. from *Rohrbach* (3, p. 15).

a pair are not truly opposed, a fact which may be readily explained in the light of the derivation of decussate from spiral phyllotaxis (cf. S c h o u t e, 5), R o h r b a c h comes to the construction of a theoretical diagram, our fig. 3, which might have explained the origin of the contort aestivation if he had only been able to make clear that the supposed lateral shift of the leaves should not be present in both leaves of a pair but only in one of them, and that, moreover, in four successive pairs the shift should be as follows: in the first pair in the second leaf to the left, in the second in the second leaf to the right, in the third in the first leaf to the left, in the fourth in the first leaf to the right.

Being himself unable to find a reason for such a curious distribution, R o h r b a c h refrains from a definite explanation. His diagram may however serve us, irrespective of its wrong lateral shifts, to demonstrate its analogy with our Fig. 2 B. In both figures we have a diagonal plane (the "SW" and the "NE" corner) where all leaf edges overlap, and a perpendicular diagonal plane where all leaf edges are overlapped.

Moreover R o h r b a c h might have been aware that his starting point, the positions of the youngest leaf primordia, was wrongly chosen, when he had considered the observations by W y d l e r, who wrote about this leaf contortion: "Die Drehung ist durchaus ein secundäres Moment; die Blattpaare liegen anfänglich aufeinander, wenn grösser werdend, verschieben sie sich entweder sämmtlich in einer, oder wechselnd nach zwei entgegengesetzten Richtungen, bis endlich vor der völligen Entfaltung die Verschiebung in Drehung übergeht" (6, p. 126).

Precisely this observation, that the leaf blades originally are opposed, afterwards are shifted along each other and finally become contort, may confirm our supposition that the alternate contortion of so many decussate plants may be considered as due to the above described flattening out of the bud.

Whether such a flattening may be brought about by external pressure or by the pressure resulting from their own growth processes may be left out of consideration here, as also the choice between the two possible ways of flattening out along the two diagonal planes, which may perhaps be due to chance or which still may be governed by certain rules: all these points should be investigated for special cases.

2. The peculiar falcate shape of the leaves of *Rochea falcata* has been described and figured by G o e b e l (1, p. 202), from whom Fig. 4 is copied here.

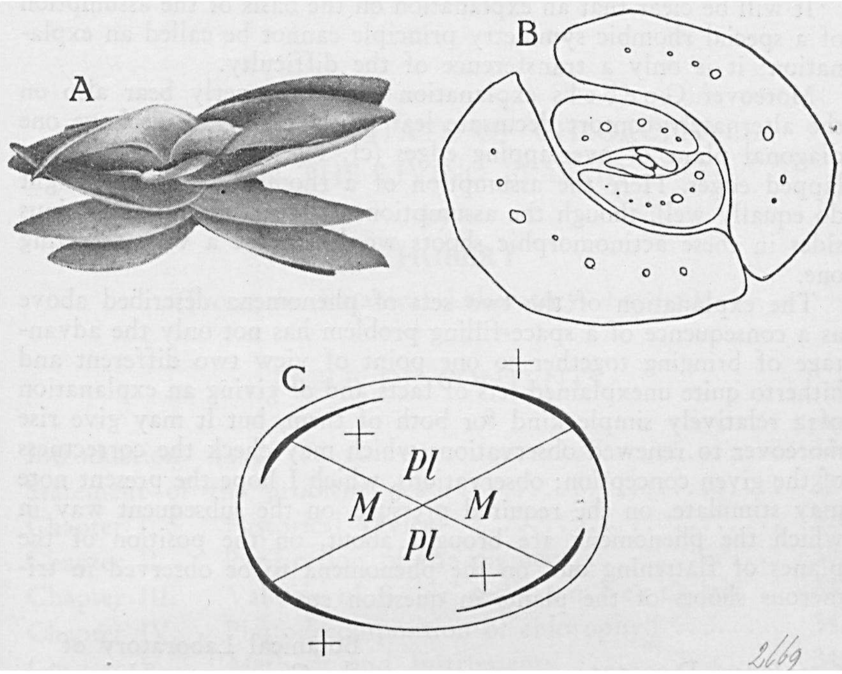

Fig. 4. *Rochea falcata,* after Goebel (1, p. 203). A: Apex of shoot from above; B: transverse section through terminal bud of young plant; C: diagram of distribution of shoot symmetry; Pl and M: plus and minus sides of stem; + : furthered side of leaf edges.

In 4 A we see a shoot of the plant from above. The falcate leaves have one thin edge which is turned upwards and therefore is perfectly visible in 4 A; this edge is convex and faces the broad side of the shoot; the other edge is thick and concave, it is turned downwards and faces the macrodiametrical plane of the shoot.

Fig. 4 B clearly shows the flattening out of the bud in exactly the same way as in our Fig. 2 B. The response of the plant is here however not an induplication of the jutting out edges, but a thickening of them; in the second leaf pair of 4 B this is especially clear. And as the thicker edge remains shorter, the falcate leaf form is brought about.

Fig. 4 C presents Goebel's explanation of the case by a supposed "bilateral" development of the stem apex with two plus sides Pl and two minus sides M. The plus sides produce the furthered thick edges, the minus sides the repressed thin edges.

It will be clear that an explanation on the basis of the assumption of a special rhombic symmetry principle cannot be called an explanation; it is only a transference of the difficulty.

Moreover G o e b e l's explanation should properly bear also on the alternately contort decussate leaf pairs: there too we have one diagonal plane of overlapping edges (cf. Fig. 3) and one of overlapped edges. Here the assumption of a rhombic symmetry might do equally well, though the assumption of two plus and two minus sides in these actinomorphic shoots would not be a very tempting one.

The explanation of the two sets of phenomena described above as a consequence of a space-filling problem has not only the advantage of bringing together to one point of view two different and hitherto quite unexplained sets of facts and of giving an explanation of a relatively simple kind for both of them, but it may give rise moreover to renewed observations which may check the correctness of the given conception; observations, which I hope the present note may stimulate, on the required pressure, on the subsequent way in which the phenomena are brought about, on the position of the planes of flattening out, on the phenomena to be observed in trimerous shoots of the plants in question etc.

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