ON THE PHYLLOTAXIS OF THE ULMUS SEEDLING

by

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§ 1. Introduction.

Though the foliage leaves of the adult elm tree are always distichous, it is well known that the main axis of the seedling has quite another leaf arrangement, being usually decussate.

The descriptions in literature of this decussate region and of its transition to the distichous arrangement are more or less contradictory and in any case insufficient. Thus a renewed investigation was needed and in 1932 I was so fortunate as to receive good material from Dr CHRISTINE J. BUISMAN, whose premature death since has been such a loss to the Netherlands' botany. This year moreover I got new material from her successor Dr JOH.a C. WENT, to whom I would here tender my best thanks.

The material consisted of 10 specimens of *Ulmus foliacea*, collected in August of their first year (WENT), 25 specimens of *U. campestris* and 25 of *U. americana*, collected in their first winter (BUISMAN), and 34 specimens of *U. hollandica* in their second summer (WENT).

§ 2. Literature.

The first description is probably that by DUTROCHET (2, p. 227), who wrote that the main axis of the seedling begins with a decussate region, and that a sudden transition to distichy takes place, either in the course of the first year, or at the beginning of the second year.

The change is described as so sudden, that one cannot observe how it is brought about, but DUTROCHET supposes that it is due to a discontinuation of two opposed orthostiches and by a separation of the members of the leaf pairs of the two remaining orthostichies.

As we shall see this description in the main is correct, wanting only some amplification and a small correction.

A similar description is given by WYDLER who writes (8, p. 199): "Die Keimpfl. trägt anfangs opponirt decussirte Blätter, auf welche dann zweizeilige folgen. Alles das erinnert an d. ähnlichen Verhältnisse bei den distichophyllen Papilionaceen" (i.e. all foliage leaves being placed in two orthostichies at right angles to the cotyledons).

A wholly different description is given by DELPINO (1, p. 140), who finds that the main axis "presenta la fillotassi quincunciale curviseriata". Yet this description in a certain sense also remains true, as in some seedlings the decussate region is followed by a spiral part, sometimes with a 2/5 phyllotaxis.

On more than one occasion GOEBEL touches on the topic (3, p. 84, 4, p. 254, 5, p. 343). GOEBEL describes the usual transition from decussation to distichy and points out that at the transitional zone one or two rudimentary scale-like leaves are often to be observed.

This brings GOEBEL to the view that the transition is due to an abortion of two of the orthostichies, the rudimentary phyllomes being partly aborted leaves. The idea is further elaborated by the assumption that the vanishing orthostichies are not opposed, but that, as in the case of *Elatostema*, the upper leaf rows abort, the lower leaves being well developed and shifted from their adjoining positions at the under side to the right and left flanks.

In support the fact is adduced that the inequilaterality of the leaves, for which *Ulmus* is known, is absent in the decussate region and makes its appearance in the distichous part, the former obviously being radial, the latter dorsiventral.

The individual seedlings are found by GOEBEL to vary much in the details of the transition; on the whole however he believes that the described type is the general one, complicated only by numerous twists of the internodes.

TROLL, quoting GOEBEL's description and accepting his views, yet remarks (7, p. 406) that the possibility is not excluded that the transition takes place in the same way as in *Phaseolus*, by simple junction phenomena without any abortion, in the way as intimated already by the comparison made by WYDLER.

§ 3. Observations.

All my specimens confirmed the well known fact, reported for instance by WYDLER (8, p. 199), that the terminal bud of all annual shoots aborts at the end of the season; the main shoot in this respect makes no exception.

And as all lateral shoots invariably are laterally distichous, it follows that any elm seedling from its second year onward only bears distichous leaves.

When therefore DUTROCHET ascribes the transition to distichy to a discontinuation of two opposed orthostichies, this may be correct for such cases where it takes place in the main axis itself, during the first year, but for those in which the first distichous leaves are formed in the second year it is wrong, as no real transition takes place in such specimens.

For a more detailed description the four lots of specimens will be dealt with separately.

1. *Ulmus foliacea.*

Ten of the five specimens were decussate throughout, whereas the other five exhibited a transition to distichy in the main axis, all after three leaf pairs.

According to GOEBEL's view we might have expected that the decussate regions should all be radial, the distichous regions dorsiventral, that the rudimentary scale leaves should be present in those orthostichies which are about to vanish and that the persisting orthostichies should be free of them.

The facts however proved to be different. The decussate region, it is true, was radial throughout, but the distichous region was of the same symmetry, all leaves of the main axis expanding their laminas in the same way, the upper side facing the shoot apex, and all leaves being equilateral.

Scale-like leaves were observed in two of the throughout decussate specimens, each having one scale in the fourth leaf

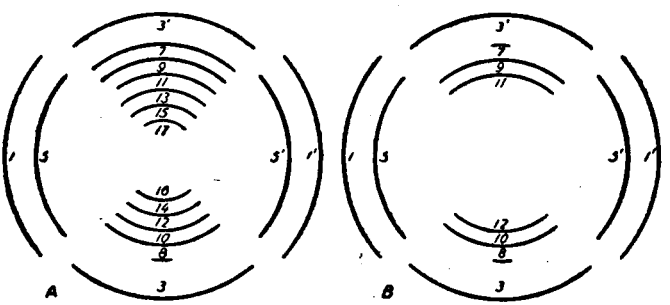

Fig. 1. *Ulmus foliacea,* diagrams of seedlings as observed in August of their first year. Leaves with same number (1 and 1' etc) at same level, 7 to highest at different levels. Rudimentary scale-leaves represented by very short arcs.

pair; in the five specimens with a transition to distichy, leaf number 8 was a scale in four cases, leaves 7 and 8 in one case.

Fig. 1 gives diagrams of two of these latter cases, 1 A with only one scale, 1 B with two of them. We see that in these specimens the scales were present in those orthostichies which are continued higher up, and the same was the case in the other specimens.

2. *Ulmus campestris.*

Nineteen of the investigated specimens were wholly decussate, bearing from 7—14 leaf pairs. In the other six specimens 3—5 leaf pairs were followed by 10—17 distichous leaves, the two orthostichies being the continuation of two opposed orthostichies of the decussate region.

3. *Ulmus americana.*

Here five specimens had a region of scattered leaves, while 20 were wholly decussate. The scattered region this time was distichous in only one single specimen, the four others having a clear spiral with a divergence of about 160° to 150°, extending over 4—12 leaves. The first of these spirally placed leaves fell right between the two leaves of the highest pair.

The transition between the decussate and the spiral part was gradual in two of the specimens; in the first of them the third leaf pair had a distinct difference in level and a distinct convergence, so as to indicate a dextrorse spiral. The same spiral was continued in leaves 7—16. In the other specimen it was the fifth pair that had the same level difference and convergence, indicating a sinistrorse spiral, continued in the leaves 11—20. In these scattered leaves the pairs 11—12, 13—14 and 15—16 were still recognizable by the incomplete though increasing separation of their members; 17—20 were regularly spiral.

4. *Ulmus hollandica.*

The material being already at an advanced stage, five specimens through corrosion of the surface were no longer to be analysed with sufficient certainty. The remaining 29 could be divided into three groups.

In the first group of 13 specimens the phyllotaxis was throughout decussate, and from 4 to 16 leaf pairs were formed.

In the second group of 13 specimens the main shoot had formed a scattered leaf region, after a basal region with from 3 to 6 decussate leaf pairs; though the transition was often accompanied by some irregularities, on the whole the first two

scattered leaves were placed in two opposed orthostichies of the decussate region.

In most cases the scattered region was decidedly distichous, notwithstanding the irregularities to which the orthostichies were often subject.

In some cases however it was clear that the divergence was less than 180°, as the deviations of the two „orthostichies" were clearly expressed and continued to be in the same direction; in these cases the divergence was about 160° or 150°, or in two cases even 144°. As an instance fig. 2 may be given, a

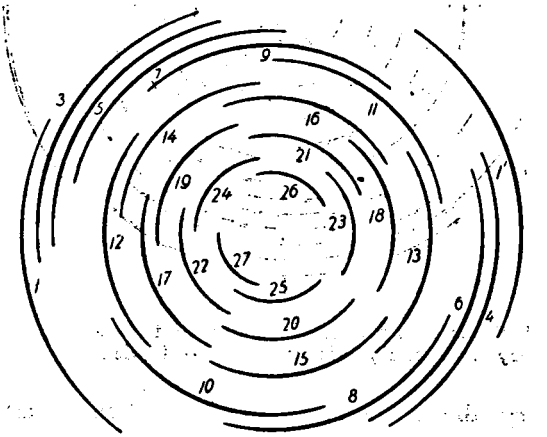

Fig. 2. *Ulmus hollandica*, diagram of completed first annual shoot. Leaves 3—6 nearly distichous, 7—27 in a dextrorse spiral.

diagram of a specimen in which leaves 3—6 were nearly distichous, but 7—27 clearly spiral, the divergence from leaf 15 onward being about $^2/_5$.

The last group of 3 specimens was remarkable for the fact that, a short decussate region having been succeeded by scattered leaves, the decussation was again restored in the apical region.

Fig. 3 gives a diagram of such a specimen, in which the leaves 3—15 being irregularly distichous, one converging and nine regular decussate leaf pairs followed.

§ 4. Discussion.

The facts related above prove clearly that we cannot accept

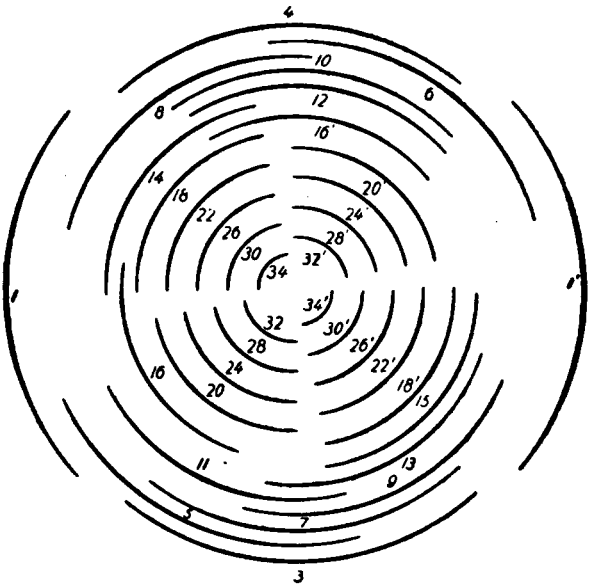

Fig. 3. ***Ulmus hollandica,*** **diagram of completed first annual shoot. Leaves 3—15 very irregularly distichous, 16—34' decussate.**

GOEBEL's theory about the origin of the distichous arrangement in *Ulmus*.

In the first place we have the fact that in those seedlings where the decussation of the main axis merges into distichy, the two discontinued orthostichies are opposed, not adjoining.

In the second place the two orthostichies are simply discontinued, not aborted. GOEBEL's assumption of abortion would imply that in any distichous elm shoot two rows of leaves should have been induced at the dorsal side, and that all leaves of these rows should be subject to abortion. For such an assumption no morphological or teratological facts are to be adduced.

The production of scale leaves, taken by GOEBEL to be a proof of the supposed abortion, in my material was only found to take place in the orthostichies which were continued; it was observed in wholly decussate specimens too. Evidently the phenomenon is not related to phyllotaxis; perhaps it may be connected with the temporary close of the embryonic development in the seed.

In the third place the relation between the transition in phyllotaxis and the change in symmetry, postulated by GOEBEL, was not to be observed in my material, the distichous or spiral parts of the main axis being as radial as the decussate region.

So we may drop GOEBEL's conception altogether, the more as it is perfectly superfluous. A transition from decussation to a spiral arrangement is of the most common occurrence in Dicotyledons, and a transition of decussation to distichy is not without examples, as already remarked by WYDLER and by TROLL.

Such a transition may be wholly explained on the basis of the conception that the dimerous whorls in the decussate region are binding whorls, as are all other dimerous leaf whorls of decussate Dicotyledons (compare SCHOUTE, 6, p. 678). For in that case a discontinuation of the binding is of very common occurrence.

In the case of *Ulmus* the supposition that the whorls are binding whorls is almost raised to certainty by the gradual transitions observed in *U. americana,* where the whorls still being recognizable the spiral character is yet at the same time evident.

From these premises the phyllotaxis of *Ulmus* may be described as follows.

All foliage leaves are arranged in systems of the main series. In the basal region of the main axis of the seedling the divergence is about 135° and by the influence of binding factors a decussate arrangement is brought about.

In the higher regions of the main axis the same conditions may be continued, until the apex dies back at the end of the first year.

In part of the specimens however the binding is discontinued earlier and the spiral comes to light; its divergence then increases to values between 144° and 180°.

In lateral axes the divergence is always more or less in the vicinity of 180°, and as these lateral shoots at the same time are dorsiventral, the two leaf rows being placed laterally, all minor deviations from pure distichy may be eliminated under the influence of the dorsiventrality factors.

§ 5. Summary.

1. GOEBEL's conception that the distichy of the foliage leaves of the elm tree is due to the abortion of the two upper leaf rows of the dorsiventral shoot, is not supported by the facts.

2. The main axis of the seedling in the investigated specimens was found to be orthotropic and radially symmetrical throughout; all laterals, the pseudoterminal sympodial branches included, are dorsiventral.

3. All foliage leaves are arranged in phyllotactical systems of the main series.

4. In the basal region of the main axis the divergence is about 135°, increasing in some specimens in the higher region even up to 180°. In the regions where the divergence is not increased, binding whorls are formed in a decussate arrangement.

5. In all lateral branches the divergence is about 180°. A fixed spatial relation is established between the dorsiventrality factors and the two leaf rows, ensuring a regular distichy.

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