On the twisting of the leaves on their bases on the horizontal shoots of the flat-leaved Spruces (PICEA § OMORICA) as contrasted with the same phenomenon in the flat-leaved Silver Firs (ABIES), the flat-leaved Hemlock Firs (TSUGA), and the Douglas Fir (PSEUDOTSUGA).

BY

A. D. RICHARDSON.

With Zincographs 1—10.

In the flat-leaved spruces, in which the stomatic leaf-surface is morphologically the upper one, and which constitute Willkomm's section *Omorica* of the genus *Picea*, the twisting of the leaves on their bases on the horizontal (plagiotropous) shoots, in order to direct their stomatic surfaces downwards, differs from that which obtains in flat-leaved silver and hemlock firs, and in the Douglas fir, in all of which the stomatic leaf-surface is morphologically the under one, in being reversed in direction, and, as a result of this reversion in direction, in the order of succession in which the leaves twist on their bases from the position in the median plane of the shoot at which no twisting takes place to that at which the maximum is reached being also reversed.

In a flat-leaved spruce, a leaf arising in the median plane upon the upper side of a horizontal shoot does not twist on its base, but bends forward and becomes nearly parallel in direction with the shoot, so that its stomatic (upper) surface is directed downwards. A leaf arising in the median plane upon the under side of a horizontal shoot, on the other hand, twists on its base through 180 degrees in order to direct its stomatic (upper)

[Notes, R.B.G. Edin., No. 1, 1900.]

surface downwards, and, by a swing movement at its base, which is independent of the twisting movement, it moves upwards so that it usually lies in a more or less horizontal plane; and it also moves outwards to a position nearly at a right angle to the direction of the shoot. In the leaves arising from the shoot on either side of the median plane, more or less twisting takes place at the base of each, according to its position on the axis, in order to direct its stomatic (upper) surface downwards, the amount through which each twists (assuming the direction of the shoot to be quite horizontal, and the median plane of the leaf after twisting to be truly vertical) being equal to the angular divergence of its point of insertion from that of a leaf inserted in the median plane in which no twisting takes place—in other words, the twisting commences in the leaves adjacent to those in the median plane upon the upper side of the shoot and increases as successive leaves are passed through from above downwards. By a swing movement at the base, the leaves lying on either side of the median plane move upwards or downwards, according to their positions on the axis, so that they arrange themselves in a series of superposed more or less horizontal planes lying between those of the uppermost and undermost leaves of the shoot; and they also move outwards into positions more or less divergent in direction from that of the axis, according to their positions thereon, the divergence increasing as successive leaves are passed through from above downwards from a few degrees in those adjacent to the leaves in the median plane upon the upper side of the shoot to nearly a right angle in those adjacent to the leaves in the median plane upon the under side of it.

In flat-leaved silver firs, and in the Douglas fir, on the other hand, in which the stomatic leaf-surface is morphologically the under one, a leaf arising in the median plane upon the upper side of a horizontal shoot twists on its base through 180 degrees in order to direct its stomatic (under) surface downwards, while a leaf arising in the median plane upon the under side of a horizontal shoot does not twist, but moves upwards by a swing movement at its base, so that it usually lies in a more or less horizontal plane; and it also moves outwards into a position nearly at a right angle to the direction of the shoot. As is the

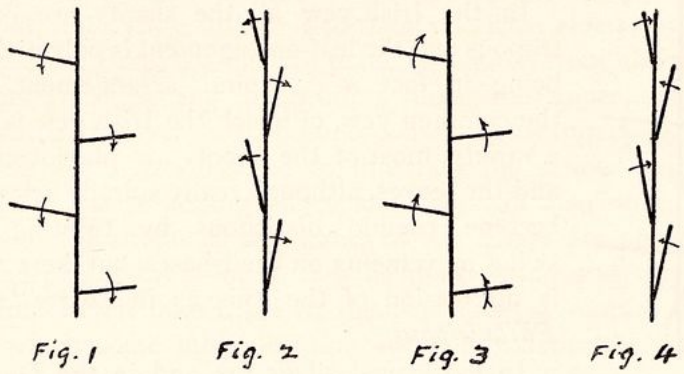
case in the flat-leaved spruces, the leaves arising from the shoot on either side of the median plane twist more or less on their bases according to their positions on the axis, the amount through which each twists being equal to the angular divergence of its point of insertion from that of a leaf inserted in the median plane in which no twisting takes place; but, contrary to what takes place in the case of the spruces, the twisting here commences in the leaves adjacent to those in the median plane upon the under side of the shoot and increases as successive leaves are passed through in an upward direction. These leaves also move upwards or downwards, according to their positions on the axis, by a swing movement at the base, into more or less horizontal positions, as in the case of the leaves corresponding with them in position on the horizontal shoots of the flat-leaved spruces, and they also move outwards into positions more or less divergent in direction from that of the shoot; but this movement, unlike that which occurs in similarly situated leaves in the flat-leaved spruces, varies in different species of flat-leaved silver firs. In species such as *Abies grandis* and *A. Lowiana* all the leaves on the horizontal shoots move outwards into positions nearly at right angles to the direction of the axis, so that a "pectinate" arrangement is produced; but in other species such as *A. amabilis* and *A. Nordmanniana* the leaves on the upper sides of the horizontal shoots assume a disposition having a somewhat superficial resemblance to that of the leaves of the flat-leaved spruces, inasmuch as the uppermost leaves, in addition to twisting on their bases, often bend forward, so that they lie almost parallel in direction with the shoot, while those adjacent to them on either side move outwards into positions more or less divergent in direction from that of the axis, the divergence increasing as successive leaves are passed through in a downward direction to, in some instances, nearly a right angle in those adjacent to the leaves in the median plane upon the under side of it.[1]

[1] These species are taken as representing perhaps the two extremes of leaf-arrangement in the flat-leaved silver firs—*A. grandis*, Lindl., and *A. Lowiana*, Murray, on the one hand being very pronouncedly "pectinate," while *A. amabilis*, Forbes, and *A. Nordmanniana*, Spach, are more or less what may be termed "spruce-like." Between these extremes lie a number of species which are more or less intermediate, such as *A. pectinata*, DC., *A. balsamea*, Mill., *A. sibirica*, Ledeb., *A. Veitchii*, Lindl., and others.

In some flat-leaved hemlock firs, such as *Tsuga Sieboldii*, the arrangement of the leaves on the horizontal shoots is essentially the same as that which obtains in flat-leaved silver firs and in the Douglas fir; but in such species as *Tsuga canadensis* and *Ts. Mertensiana*, and one or two others, a slight divergence occurs. In the leaves inserted in the median plane upon the upper side of the shoot, which are generally smaller than the others, no twisting on the base takes place. These leaves behave in precisely the same way as do those in a corresponding position on the horizontal shoots of the flat-leaved spruces, but with this difference, that whereas in the spruces the stomata, being on the upper side of the leaf, become directed downwards when it bends forward in the direction of the apex of the shoot, in these hemlock firs, owing to their being on the under side of the leaf, they become directed upwards.

In the flat-leaved spruces, then, in consequence of the stomata being located on the upper leaf-surface, the arrangement of the leaves on the horizontal shoots is quite distinct from that in flat-leaved silver and hemlock firs, and in the Douglas fir. In these latter the mode of twisting of the leaves on their bases is identical with that observable in a plagiotropous shoot of such a plant as the common yew, or in fact of any broad-leaved plant such as *Diervilla* or *Philadelphus*—that is to say, the direction, as seen from above, in which the leaves twist on their bases on a horizontal shoot, when they come to occupy positions nearly at right angles to its axis, is away from the apex of the shoot, or when nearly parallel with it the direction of twisting is away from the median plane on the upper side of the shoot. In Figs. 1 and 2 horizontal shoots of this sort are represented diagrammatically as seen from above. The centre line represents the axis, the lateral lines the leaves, and the curved arrows show the direction in which the leaves twist on their bases. Fig. 1 illustrates the arrangement of the leaves on the horizontal shoots in such flat-leaved silver firs as *A. grandis* and *A. Lowiana*, and also the arrangement on the under side of the shoot in such flat-leaved species as *A. amabilis* and *A. Nordmanniana*, while Fig. 2 illustrates the arrangement on the upper side of the shoot in species such as the last named. In the case of a flat-leaved spruce, on the other hand, the direction in which the leaves

twist is, when viewed from above, either towards the apex of the shoot, as represented in Fig. 3, which illustrates the



Figs. 1 and 2. Directions of twisting and movement in silver fir.
Figs. 3 and 4. Directions of twisting and movement in spruce.

arrangement of the leaves on the under side of the shoot, or towards the median plane on the upper side of the shoot, as represented in Fig. 4, which illustrates the arrangement on the upper side of the shoot.

In plagiotropous shoots in which the stomatic leaf-surface is morphologically the under one, and where the leaf-arrangement is normally not a truly distichous but a polystichous one, a pseudo-distichous arrangement is frequently brought about either by twisting and other movements of the leaves on their bases, or by torsion of the axis itself. In *Diervilla* and *Philadelphus* the leaves are opposite and decussate on the orthotropous shoots, but they all lie in one horizontal plane on the plagiotropous shoots, with their stomatic surfaces directed downwards. In these cases the pseudo-distichous arrangement on the plagiotropous shoots is brought about by torsion of the axis alternately to right and left between the nodes, so as to bring all the points of insertion of the leaves into nearly the same plane, and at the same time each leaf twists at its base through 90 degrees and brings its surface into a horizontal position, so that they all lie in the same horizontal plane. This arrangement is illustrated diagrammatically in Fig. 5, which represents a plagiotropous shoot of this sort as viewed from above.

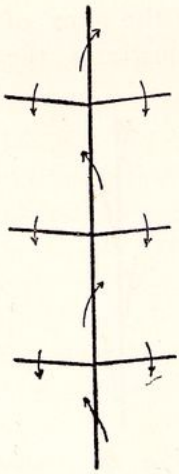


Fig. 5

Direction of twisting of shoot and leaves in *Diervilla*.

The curved arrows on the central axis indicate the direction in which it twists in each successive internode.

In the Irish yew all the shoots are orthotropous and the leaf-arrangement is polystichous, being in fact a $\frac{5}{13}$ spiral arrangement. In the common yew, of which the Irish yew is only a variety, most of the shoots are plagiotropous, and the leaves, although really spirally arranged, become pseudo-distichous by twisting and swing movements on their bases, but here there is no torsion of the axis as in *Diervilla* and *Philadelphus*.

In flat-leaved silver firs, and in the Douglas fir, there is a pseudo-distichous arrangement of the leaves on the horizontal shoots which, as before mentioned, is identical with that which occurs in common yew. In such species as *Abies grandis* asnd *A. Lowiana* this pseudo-distichous arrangement of the leaves is brought about independently of the twisting of the leaves on their bases by the way in which they move outwards on either side of the shoot into positions nearly at right angles to the direction of its axis. In species like *A. amabilis* and *A. Nordmanniana* the pseudo-distichous arrangement is often masked by the upper leaves assuming directions parallel with, or only slightly divergent from, that of the axis. But, as the direction in which the leaves twist on their bases on the upper side of the shoot is away from the median plane, as viewed from above, their stomatic (under) surfaces turn outwards from each other in opposite directions, to either side of the shoot, so that there is a parting or shedding of the leaves along the median plane on the upper side; and as there is also a parting or shedding of the leaves by the swing movement already referred to along the median plane on the under side of the shoot, a pseudo-distichous arrangement is the result. The resemblance between the arrangement on the upper sides of the horizontal shoots here and that of the flat-leaved spruces is therefore entirely superficial. In a flat-leaved spruce, on the other hand,

a pseudo-distichous arrangement is impossible. The leaves in the median plane upon the upper side of a horizontal shoot do not twist on their bases, nor do they move to either side of the shoot, while those adjacent to them on either side twist towards, not away from, the median plane, as viewed from above, so that there is no parting or shedding along the upper side of the shoot, and therefore no pseudo-distichous arrangement.[1]

Figures 6-10 will serve to illustrate the various points dealt with in the preceding pages, and they will also serve to show how the positions of the tissues of the leaves are affected from a morphological point of view by the twisting and other movements which take place at the leaf base, a matter in regard to which some misconception seems to exist in the descriptive accounts of some of the flat-leaved species of *Picea*.

Fig. 6 represents diagrammatically on a ground plan the positions assumed by the leaves in an erect (orthotropous) shoot of a flat-leaved silver or hemlock fir, or of the Douglas fir, while Fig. 8 represents the same thing in a flat-leaved spruce. In the figures the axis of the shoot occupies the centre, and the leaves are arranged in a circle surrounding it, the spiral arrangement being disregarded in order not to introduce complications. The number of leaves (twelve) fixed upon is purely arbitrary, the even number being adopted in order to avoid fractions of a degree. The leaves are numbered consecutively, and the angular divergence from zero (leaf 1) is indicated on the outside of each leaf. The various tissue-groups of the leaf are indicated thus: —X = xylem; P = phloem; R.C. = resin-canals; S.S. = stomatic surface.

A glance at Figs. 6 and 8 will show that they differ in one particular only—namely, the position of the stomatic surface of the leaf. In Fig. 6 it is in the normal position on the phloem-side of the leaf, but in Fig. 8 it is on the xylem-side and faces the axis of the shoot.

[1] The arrangement of the leaves on the horizontal shoots of spruces (flat-leaved and other) is frequently incorrectly described as pseudo-distichous. Dr. Engelmann, in Watson's Flora of California, II. p. 121, describes the leaves of *Picea* as "spirally arranged all round the branchlets or (by a twist of the base) somewhat 2-ranked," and other authorities variously refer to them as being "2-ranked," "2-rowed," or "pseudo-distichous."

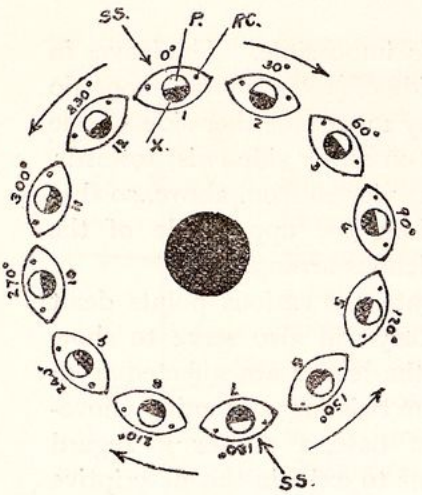


FIG. 6

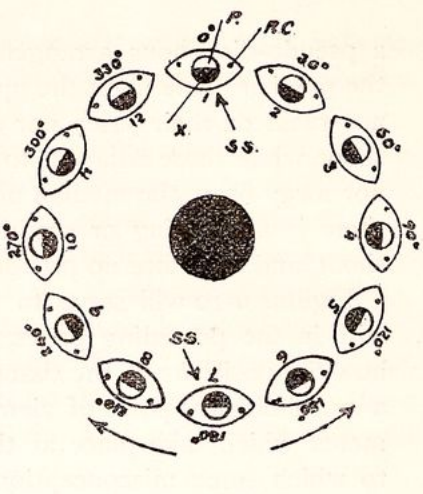


FIG. 8

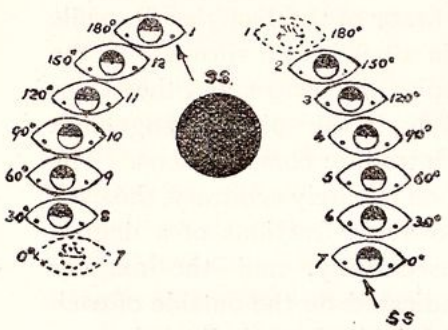


FIG. 7

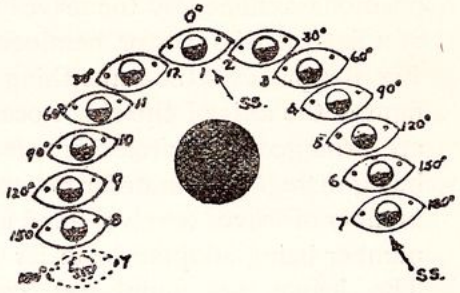


FIG. 9

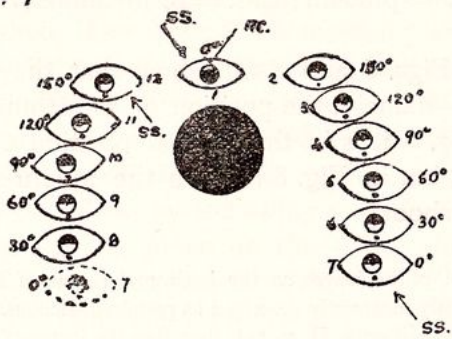


FIG. 10

Figs. 6 and 7. Arrangements in flat-leaved silver fir, *Tsuga Sieboldi*, and Douglas fir.
Figs. 8 and 9. Arrangements in flat-leaved spruce.
Fig. 10. Arrangement in *Tsuga canadensis*, *Ts. Mertensiana*, and others.

Fig. 7 represents the positions assumed by the leaves in flat-leaved silver firs, in some hemlock firs, and in the Douglas fir when such a shoot as that represented in Fig. 6 becomes horizontal. The leaves corresponding to those in Fig. 6 are indicated by corresponding numbers, and the degree-numbers indicate the angles through which the leaves twist on their bases, as well as their angular divergences from the leaf in which no twisting takes place.

In Fig. 7, leaf 7, which is in the median plane upon the under side of the shoot, is the one in which no twisting takes place, but, by the swing movement on its base already referred to, it moves upwards and outwards to the position indicated in the figure. As, however, its point of insertion is in the median plane of the axis, it may move either to the right or to the left. In leaf 1, which is in the median plane upon the upper side of the shoot, on the other hand, the maximum amount of twisting at the base takes place, and owing to its being in the median plane of the shoot, it may, like leaf 7, move either to the right or to the left. In those lying between 1 and 7, on either side of the median plane of the shoot, the amount of twisting which each undergoes is equal to the angular divergence of its point of insertion from that in which no twisting takes place, as indicated in the figure. For example, the points of insertion of leaves 4 and 10 are each divergent 90 degrees from that of leaf 1, and this is equal to the angle through which each twists in order to bring its median plane into a vertical position.

The curved arrows above and beneath Fig. 6 indicate the direction in which the leaves shed away from the median plane of the axis, on the upper side by twisting, and on the under side by a swing movement at the base, when a shoot such as this becomes horizontal as in Fig. 7.

Figure 9 represents the positions assumed by the leaves in a flat-leaved spruce when a shoot such as that represented in Fig. 8 becomes horizontal, and the leaf-numbers and degree-numbers have the same significance as those in Fig. 7. Leaf 1 in Fig. 9 is that in which no twisting takes place, and it retains precisely the same position in relation to the axis as does the corresponding leaf in Fig. 8. In leaf 7, on the other hand, the maximum amount of twisting on the base takes place, and in addition

to this twisting there is the swing movement at the base, by which the leaf moves upwards and outwards into the position indicated in the figure ; and, as the point of insertion of this leaf is in the median plane upon the under side of the shoot, it may move either to the right or to the left. In the leaves lying between 1 and 7, on either side of the median plane of the shoot, the same rule as to twisting obtains as that which governs the twisting in Fig. 7, but here the order of succession in which the leaves twist is reversed in direction as compared with that illustrated in Fig. 7.

The curved arrows beneath Fig. 8 indicate the direction in which the leaves shed away from the median plane of the axis when a shoot such as this becomes horizontal as in Fig. 9 ; but the shedding of the leaves along the median plane on the under side of the shoot is not here due to a swing movement at the base only, as in Fig. 7, but to a combination of both a twisting and a swing movement. Both these movements, in fact, culminate in the leaves in the median plane on the under side of the shoot in a flat-leaved spruce ; whereas in a flat-leaved silver, in some hemlock firs, or in the Douglas fir, the twisting movement culminates in the leaves in the median plane on the upper side of the shoot, while the swing movement culminates in those in the median plane on the under side.

Fig. 10 represents, in the same way as in Figs. 7 and 9, the positions assumed by the leaves on a horizontal shoot of a hemlock fir such as *Tsuga canadensis*, or *T. Mertensiana*, as described on p. 16. The leaves inserted in the median plane upon the upper side of the shoot show no twisting at the base, but, bending forward in the direction of the apex of the shoot, they occupy positions similar to that of leaf 1 in Fig. 10, in which the stomatic (under) surface is directed upwards, whereas in all the other leaves of the shoot it is directed downwards as in the flat-leaved silver firs, and in the Douglas fir.[1]

[1] In a paper entitled a "Review of some Points in the Comparative Morphology, Anatomy, and Life-History of the Coniferæ," published in the "Journal of the Linnean Society, Botany, Vol. xxvii, Dr. Masters refers to the leaf-arrangement in these plants as follows (p. 247) :—"Another instance of variation in the arrangement of "leaves is often seen in *Abies Nordmanniana*, *A. Pichta*, *A. amabilis*, as also in "*Tsuga canadensis*, &c. The leaves on the lateral and more or less horizontally "spreading branches, though polystichous, in reality arrange themselves in three rows,

The effect of this twisting of the leaves on their bases on the horizontal shoots of the firs and spruces referred to results in but a slight deviation from the normal condition of the internal leaf-structure, and this only in the flat-leaved spruces. In the flat-leaved silver and hemlock firs, and in the Douglas fir, there is no departure from the normal condition, and the arrangement of the internal tissues of the leaf is precisely the same both in leaves of the leader shoots (where no twisting takes place) and in leaves of the horizontal shoots; but in the flat-leaved spruces, owing to the stomata being located on the morphologically upper leaf-surface, and to the consequent inversion of the leaves on the horizontal shoots as compared with those on the leader (erect) shoots, or with those on both the erect and horizontal shoots of a flat-leaved silver fir, or the Douglas fir, the positions of the various leaf-tissues are completely reversed, so that the phloem is towards the non-stomatic, actually upper (but really morphologically under) side, and the xylem towards the stomatic under (but really morphologically upper) side, while the resin-canals occupy their normal positions on the phloem side of the leaf. The only anatomical change which results from this abnormal (inverted) position of the leaves on the horizontal shoots of these flat-leaved spruces is the formation of palisade cells in the non-stomatic upper (but really morphologically under) side of the leaf in two or three of the species; and no doubt it is the abnormal position of these cells on the same side of the leaf as the resin-canals (which always belong to the under side of the leaf[1]) that has led to the little

"one on either side of the branch (in which case the leaves are nearly at a right "angle to the branch), and one in the median plane of the upper surface (in which "case the leaves are appressed along the branch parallel to its main axis). The "median leaves are usually smaller than the lateral ones."

It is quite true, as Dr. Masters says, that in hemlock firs like *Tsuga canadensis* the leaves are really arranged in three groups, but such a description is incorrect when applied to any of the flat-leaved silver firs, as has been shown in this paper.

[1] In connection with this it may be pointed out here that the figures of the transverse sections of the leaves of *Picea Alcockiana* and *P. Glehnii* of the "Gardeners' Chronicle" (Vol. xiii, N.S., pp. 212 and 301) and of the "Journal of the Linnean Society" (Botany, Vol. xviii, pp. 509 and 513) are, judging from the positions of these resin-canals, evidently inverted, as is also apparently that of *P. Breweriana* of the "Gardeners' Chronicle" (Vol. xxv, N.S., p. 497). In the two first-mentioned species no twisting takes place at the bases of the leaves on the horizontal shoots, so

confusion which exists in the descriptive accounts of some of these species.

In conclusion, it may be pointed out that in the silver firs (*Abies*) and in the hemlock firs (*Tsuga*) species occur in which the leaves are not distinctly flattened, and where, as in the true spruces (*Picea* § *Eupicea*), the stomata are more or less evenly distributed over the four faces of the leaf. This occurs in such species as *Abies Pinsapo*, *A. nobilis*, *A. magnifica*, and others, amongst silver firs, and in *Tsuga Hookeriana* of gardens amongst hemlock firs. In such cases there is, of course, as in the case of spruces, no pseudo-distichous arrangement.

that the resin-canals are always in the actually, as well as the morphologically, under part of the leaf. About *P. Breweriana*, a species of which I have not seen specimens, I am unable to express an opinion as to whether the leaves twist on the horizontal shoots or not. Beissner ("Handbuch der Nadelholzkunde," p. 350) places it amongst the true spruces (*Eupicea* of Willkomm), in which no twisting of the leaf base occurs; but Professor Sargent says ("Silva of North America," Vol. xii, p. 52) "it most resembles in leaf structure and in the form of its cone-scales the flat-leaved *P. Omorica* of the Balkan Peninsula." Judging from the figures alone (both of the "Gardeners' Chronicle" and of the "Silva") it would appear that the stomata are confined to one leaf-surface only, and, from the position in which the canals are shown, no doubt this is the upper one, as in the other flat-leaved species. I therefore incline to Professor Sargent's opinion that it is more closely allied to the flat-leaved species than to the true spruces.