The Formation of Red Wood in Conifers.

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With Plate XV.

THE formation of red wood on the under sides of the branches of Conifers, which was studied in detail by Hartig, has been variously explained as being due to gravitational stimuli, to variations of pressure and tension, and to differences of illumination on the upper and under sides[1].

The latter explanation has in part been adopted by Sonntag[2], who has recently investigated and compared the mechanical properties of the red and white wood of Conifers.

It is not easy to see what direct effect differences of illumination on the two sides can exert upon the cambium of old stems covered with thick opaque layers of bark.

The only possible action in such cases would be due to the fact that the exposed upper side might be slightly warmer during the day time than the shaded under side.

In the case of *Pinus*, owing to the height of the branches above the ground, the effect of nightly radiation on the relative temperature of the upper and under sides is negligible; and in that of *Cupressus*, since mainly lower branches of compact trees are used, the under side would be more exposed and subject to greater radiation and cooling during the night. Hence, the only possible effective differences of temperature are those produced during the day time.

Sonntag lays main stress upon the influence of pressure, which he considers to be primarily responsible for the production of red wood, the

[1] Cf. Pfeffer's Physiology, Eng. Trans., Vol. ii, p. 108; Vol. iii, p. 416.
[2] Sonntag, Jahrb. f. wiss. Bot. Bd. xxxix, p. 71.

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latter appearing, according to him, on the side of an erect tree subjected to compression by the action of the wind.

Even here, however, although the tree may still remain upright, every time it is bent to one side by the wind it is subjected to geotropic action, and a geotropic stimulus, if frequently and rapidly repeated, will produce a geotropic curvature in a root, however short the individual periods of exposure may be.

To investigate these points more fully, a series of experiments were begun upon the main axes and lateral branches of plants of *Cupressus nutkaensis*, *C. Lawsoniana*, *Pinus contorta*, and *P. Cembra*, in May, 1905.

The stems were forcibly bent into circular or elliptical forms and fastened in such a fashion that the geotropic and pressure effects were not equally distributed, the former influencing the horizontal portions, whereas the compression was restricted to the inner surface of the ring.

The stems were sawn off and examined in November and December, and the distribution of the red wood is shown by the dark line on the appended figures.

The specimens represented by Figs. 3 and 4 were shaded from above, whereas the others were exposed to normal illumination; and it will at once be seen, by comparing the figures, that they give absolutely no evidence of the existence of the 'heliotropic' action which Sonntag postulates.

It is also evident that it is almost solely the action of gravity, and not that of pressure, which has in these specimens determined the formation of the red wood, for this appears mainly on the under sides, whether they are subjected to compression or tension.

The change from one side to the other is especially well shown in Fig. 1, but can be traced in the others also, the side of the erect portion on which the thin connecting layer of red wood develops being probably determined by the loop being slightly inclined to one side.

It will be noticed that in all cases there is a tendency for the formation of red wood to spread into the vertical regions, where it fades away.

This is, however, the result of the gravitational stimulus spreading from the upper and under surface, where it is directly perceived, to the neighbouring vertical portions, and in this way preventing the weakening effect of an abrupt transition from one type of wood to the other.

The formation of red wood begins first on the under surfaces and then spreads laterally, so that in the outermost vertical or nearly vertical regions to which it extends only a thin superficial layer of the year's annual ring consists of the red tracheides, the inner part being white wood.

Thus, on the under side of the uppermost point of the curvature of a branch the red tracheides averaged thirty-two deep, towards the side of the curved region the number fell to fifteen, and in the upper part of the vertical region to less than eight.

Hence this last region only received the gravitational stimulus from the horizontal region when three-fourths of the year's growth of wood had taken place.

A few peculiarities will be noted in the figures. Thus in the basal part of Fig. 3 the red wood appears on the upper inner surface of the main axis, on the side of the lower part, and on the inside of the upper part of the vertical segment. The lower part, however, formed but little wood and was very strongly compressed.

Hence it is possible that very strong pressure applied to a feebly active cambium may overcome the gravitational influences normally responsible for this special morphogenic response.

In Fig. 5 red wood appears on both upper and under surfaces of a few lateral branches, although both the gravitational and the pressure stimuli act alike on the under surface. Possibly this is the result of the diffuse spreading of the gravitational stimulus from above and below the branch; and in any case it is worthy of note that a slight deviation from the perpendicular is sufficient to produce a perceptible response, while the maximum possible morphogenic stimulus appears to be exercised by a comparatively small angle of deviation, beyond which but little further increase occurs.

In brief, therefore, it may be stated that, as far as these observations go, they show that the formation of red wood is a morphogenic response to a gravitational stimulus which is able to spread longitudinally from the region where it is directly perceived, and which may under special circumstances be modified or suppressed by very strong pressure stimuli.

NOTES ON FIGURES IN PLATE XV.

Illustrating Messrs. Ewart and Mason-Jones's paper on Red Wood in Conifers.

Fig. 1. Main axis of *Cupressus Lawsoniana.* Red wood very thick at under surface of top of curve, change from one side to the other well shown; the dotted line indicates here, as in all other figures, the distribution of the red wood on the back face of the stem.

As shown in the figure, the straight part of the stem grew slightly out of the perpendicular, also with a slight tilt away from the plane of the paper.

Fig. 2. Lateral branch of *Cupressus nutkaensis.* The upper branch and the thin twigs shown were dead.

This was a very good specimen, inasmuch as gravitational stimulation was practically at its maximum.

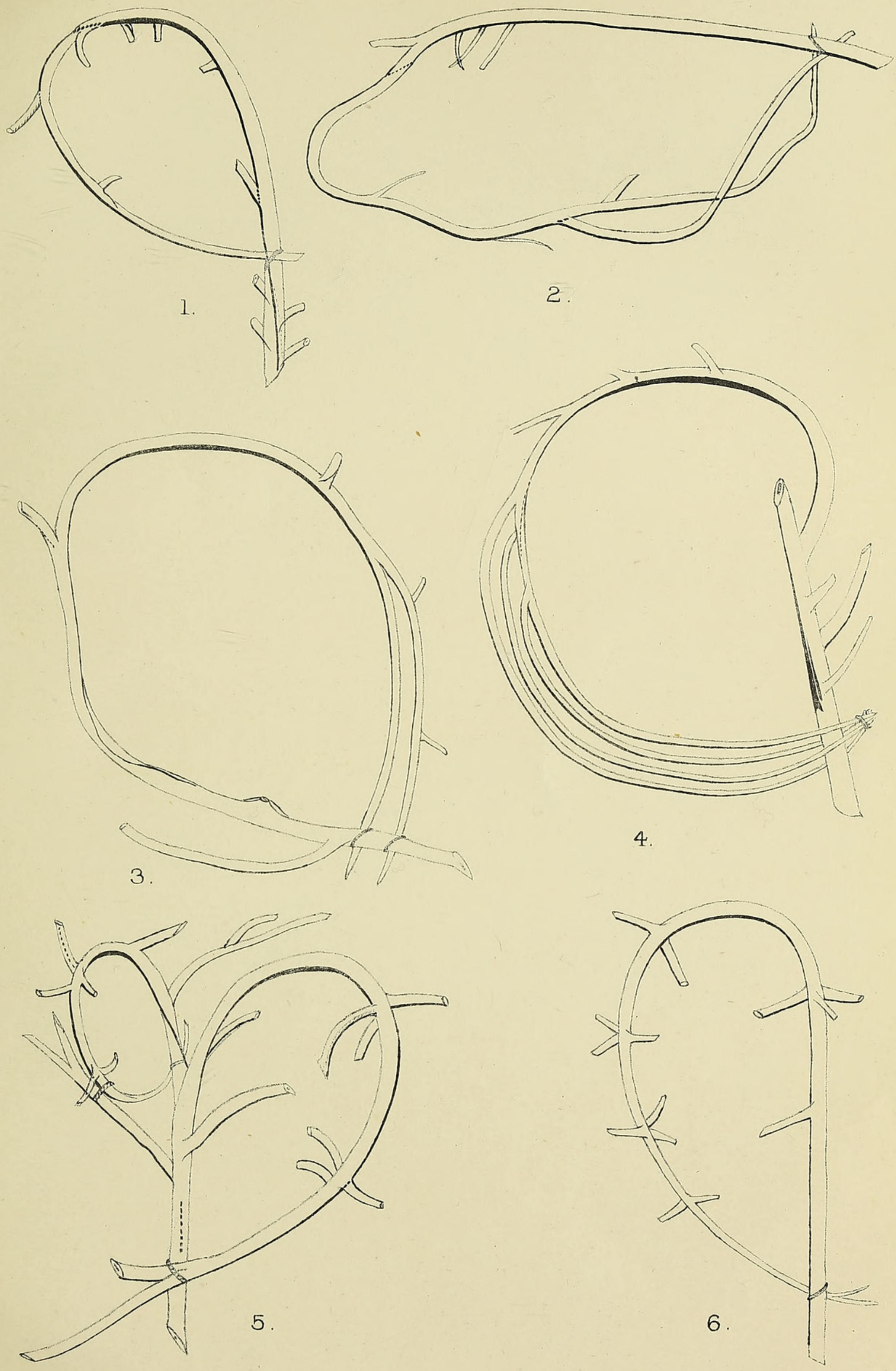
The entire absence of red wood from the region of greatest compression is well shown.

Fig. 3. Lateral branch of *Cupressus nutkaensis* shaded from above; peculiarities in distribution of red wood are mentioned in the text.

Fig. 4. Lateral branch of the same tree as Fig. 3 and under similar conditions of shade.

Fig. 5. Main axis and top branches of *Pinus contorta.* Peculiarities of distribution of red wood are given in the text; the main branches were bent and grew in planes practically at right angles to one another.

Fig. 6. Main stem of *Pinus Cembra.* In this specimen the pigment in the red tracheides is not as strong as in those of the other specimens used, so the stem had to be continually wetted with tap water in order to bring out the colour differentiation of the red and white woods.



Huth, lith. et imp.

EWART AND MASON-JONES,—RED WOOD IN CONIFERS.