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# The significance of compression wood in restoration of the leader in *Pinus silvestris* L. damaged by moose (*Alces alces*)

## I. Distribution and function of compression wood in the stems

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## INTRODUCTION

Compression wood formation is one of the interesting problems in the growth of trees and shrubs, closely connected with the morphogenetic maintainance of the genetically determined forms of trees in spite of damages and disturbances of the environment (Sinnott 1951, 1952, 1960). The replacement of a destroyed leader by one of the lateral branches is of great significance in the competition with the environment and survival in spite of damages in the population of the species of trees or shrubs.

The branch movements involved in the replacement of the leader, brought about through the compression wood have been described many times for different species by various authors: Mer (1887) described it for *Abies alba* and *Picea excelsa*; Hartig (1901) and Peterson (1914) for *Picea excelsa*; Jaccard (1924—1927) for *Pinus nigra*, Onaka (1935) for *Pinus thunbergii*, Münch (1938) for *Picea excelsa* and *Pinus peuce*, Hartmann (1942) for *Abies alba*, *Picea excelsa* and *Pinus silvestris*; Sinnott (1952) for *Pinus strobus*, and Szczerbiński and Szymański (1958) described the process of leader replacement for *Pinus silvestris* in Polish forests. It is interesting to note that Schmidt (1940) reported that the pattern of leader replacement differs somewhat from one ecotype to another of *Pinus silvestris*; this is understandable when taking into account the wide range of occurrence of this species on the Eurasian continent.

In spite of extensive research on the problem of leader replacement in the *Pinus* genus, the author is of the opinion that it is worth studying a few pines from a forest where the trees have been continuously damaged for several thousand years by an animal such as moose (*Alces alces*) strongly selecting the trees in the forests. The investigation might throw more light on the problem of survival of Pinus in an unpropitious environment.

## MATERIALS

The pine trees for study were collected near Helsinki in the Experimental Forest of the Forest Research Institute of Finland in Helsinki. The author is of the opinion that these pines are for a few reasons the most suitable objects for such a type of investigation, i.e., a study of reaction wood formation in natural forest conditions and the biological function of such wood in the process of regeneration of pine.

Scots pine is one of the species with a very wide range of occurrence on the Eurasian continent from the Arctic Circle to Spain, the Middle East and the Far East. Such a wide range causes high ecological and genetic variability (Sokołowski, 1931; Tyszkiewicz, 1949; Fabijanowski, 1961; Staszkiewicz, 1961), The pine came to Finland a few thousand years ago after the last glaciation and succeeded in forming during such a short time distinct ecological types and forms (Staszkiewicz, 1961; Molski, 1962) notwithstanding some similarities to the pine growing at present on the Polish Lowland (Staszkiewicz, 1961).

Tyszkiewicz (1949) and Fabijanowski (1961) list several features characteristic for the pine growing in the northern part of Europe; the most important of which from the point of view of regeneration are:

- high resistance to frost injury;
- adaptability to a shorter vegetation period, that is the tree starts growth later in spring and ends it earlier in autumn;
- smaller yearly growth rings;
- root system more extensive in relation to stem than in pines of the same species from other provenances;
- tree trunks very straight, very seldom subject to deformation by various factors;
- branches shorter, smaller and not very dense, therefore crowns small, cone-shaped.

The pines for study were collected in a natural forest among peat-bogs and had grown naturally from local seeds by natural regeneration. The forest represented a typical primeval pine forest. It is worth noting that to this day planted forests in Finland are very rare. In such naturally regenerating forests, selection among seedlings is very strong indeed.

In Finland one of the most common factors in tree selection is the moose (*Alces alces*). This animal is very destructive in forests, especially among pines, almost every young tree is at least partially gnawed off, especially among pine trees up to ten years old. Damages vary, often only lateral branches are eaten, but about 25 per cent of trees is damaged so severely that they are not able to regenerate and die (Kangas, 1949; Yli-Vakkuri, 1956).

The most common damages of the pine tree are the gnawing off of one or two youngest yearly growths of the leader. Pines gnawed once, twice or thrice, regenerate the leader very easily and form a normal tree, but those which have their leaders damaged several times during the first 10 years, or so, of growth, die. The time of regeneration varies depending on the severity of the damage. The process of regeneration has been described by the author in another publication (Molski, 1970).

The pines in Finland seem to be very resistant to damage by moose (*Alces alces*) and regenerate very easily, what cannot be said of pines growing in Poland even in such areas as the Rajgród peat-bogs, where moose has been a native resident for thousands of years. It seemed justified to choose the pines for a study of the function of reaction wood in natural regeneration of the leader in Finland.

For anatomical study three pines were selected from the young pine forest about 50 kilometres distant from Helsinki. The forest belongs to the MT type (*Myrtillus* Type, Kujala, 1952), it is the most common type of forest in Southern Finland. All the pines grew seperately without any other trees close to them during all the time of their growth, since no stumps were noticed around them. The leader of one of the studied pines had never been damaged and was very straight. Two other trees were gnawed a few times and were a little bit curved in some height growths (see Fig. 7), marking the places of restored leader from the lateral branches. All the trees looked prosperous, green and healthy.

The ungnawed pine was used as control in the studies. It was an eleven-year-old tree, but only nine height growths were used in the investigation, since the two lowest ones were very short, and had such big nodal swellings due to branch whorls, that they had to be excluded from investigation. Those deformed growths had tree rings which could not be compared with others. Five-centimetre long sections of the main stems were collected from all the investigated pines at a few centimetres above the whorls of branches in order to avoid any deformation due to nodal swellings, marking the cardinal directions (North, South, West and East). The sections were deposited in a mixture of ethyl alcohol, water and glycerol in order to soften the wood.

## METHOD

Cross sections of all the pieces of main stems of the investigated pines were cut with a microtome, and the sections mounted on slides were investigated under the microscope. Tracheids in all growth rings were counted in the four cardinal directions under magnification $\times 100$. The tracheids were separated into early, late and compression wood in every cardinal direction.

The observations were done with a Reichert microscope using ocular $\times 10$ with a micrometric scale and objectives $\times 10$, $A = .25$; $\times 20$, $A = .40$; and $\times 45$, $A = .65$.

One of the basic problems was to establish clear cut differences between compression-wood cells and normal cells, and the late tracheids from the early ones among the normal cells of wood. The distinction between normal and compression wood was not so difficult, since the compression-wood tracheids have a specific shape with big intercellular spaces, and they are very round on the cross-section. This shape of the cells on cross-section served as criterion for classification of the tracheids into compression and normal woods.

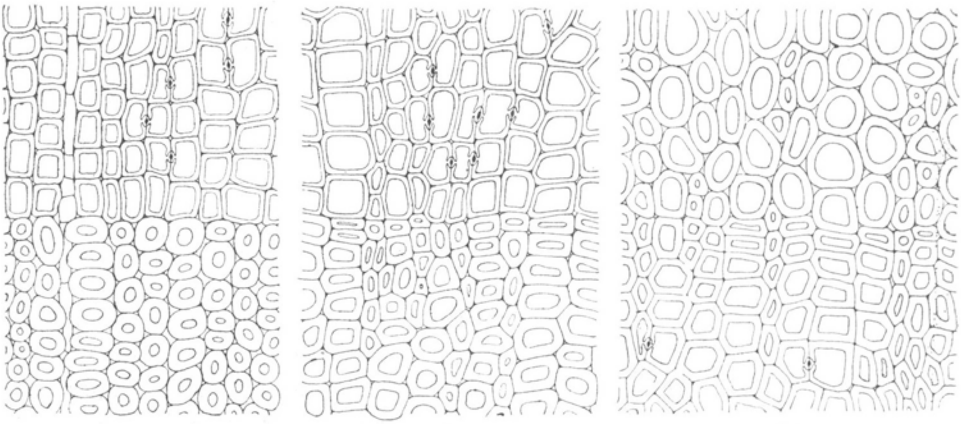


Fig. 1. The figures represent four main types of wood in the conifers (early and late normal, as well as early and late compression wood) seen on the growth ring borders.

*A*. Early normal wood is seen in the upper part, and in the lower part of the drawings late compression wood produced in summer or autumn with very thick cell walls and relatively small, as for compression wood, intercellular spaces.

*B*. Early and late normal wood.

*C*. Compression wood (seen in the upper part of the picture) produced in spring with relatively thin cell walls, as for compression wood, and with very big intercellular spaces; and the normal late wood, seen down in the picture. Tracheids of the early normal wood produced in the next year after the compression wood was produced, are often a little bit smaller with thicker cell walls, and the normal late wood, produced one year before the early compression wood was going to be produced are a little bit larger with thinner cell walls, as compared with tracheids of the normal wood not adjacent to the compression wood (compare *A*, *B*, and *C*). Drawings are made after the photographs of the pine wood.

The compression-wood cells have a strong golden colour due to heavy lignification and this is an additional feature helping in differentiation.

Compression wood might also be divided into early and late. Compression tracheids formed in spring are bigger and with thinner cell walls than those formed in summer or autumn. However, in classification all the compression wood was treated without distinction into early and late; such a division needs further studies to establish reliable differentiating features, and this problem was not included in the investigation. The differences between all the kinds of wood are presented in Fig. 1 a, b, and c.

The distinction between late and early tracheids of normal wood was more difficult. The normal growth ring has very clear differences at the peripheries, but between typical late and early wood there is a narrower or wider transition zone. Usually the early-wood are bigger than the late wood tracheids, but the difference is not so clear, therefore practically it cannot be used in classification.

Much larger differences are noted in the thickness of the cell walls. Cell walls of the early wood are usually about 4 microns, and the late ones about 8 microns thick, so in the course of measurement the early-wood cell walls were covered by about 2 units of the ocular scale, and for the late ones about 4—5 units were necessary (with $\times 10$ ocular and objective $\times 45$). The differences were very clear and easy to use in classification in the course of measurement.

Therefore the cell wall thickness was the main feature used in differentiation of the tracheids into early and late wood. Proceeding from the late to the early wood, transition zone tracheids were classified according to the marked differences in cell wall thickness. All the tracheids with cell walls about 7 microns thick or more (three and half units of the ocular scale) were considered as late ones, and all 6 microns thick or less (three or less units of the ocular scale) as the early ones. Usually, with much larger cell wall thickness, lignification accompanied the late wood, therefore the colour of the cell wall was helpful in classification to some extent, but the main criterion was the cell wall thickness. In doubtful cases, such as the first-year tree rings, or tree rings with normal and compression wood, the border cells were measured and averages were established, and the averages were the guiding figures in the classification into late and early wood. For the cells which were very untypical, not only cell wall thickness, but also lignification and diameter of the cell were used too.

Such classification proved to be in agreement with the macroscopic differentiation in use of tree rings in pine into early and late wood.

By the procedure described it was possible to obtain a full picture of the appearance of the compression wood in the course of growth of the investigated trees in all four cardinal directions.

All the results were compiled in tables for each of the cardinal directions separately, in order to visualize clearly the differences. The results of counting are presented in this publication in form of diagrams.

## RESULTS

Control pine: The control pine was eleven years old and eight yearly longitudinal growths were studied. Only once compression wood appeared in the spring 1959 growth ring, in the second internode from the apical meristem. In this growth ring the proportion between the early and late wood was opposite than in all other growth rings; if every normal growth ring had about one third of late wood and two thirds of early wood, here there was about one third of early wood and two thirds of late wood. Compression wood appeared only in this growth ring and only in the West quarter.

Anatomical observations of this growth ring showed that the tree had been damaged by frost during the 1958/59 winter, this is, however, a doubtful cause of compression wood formation. It is possible also, that the young leader was bent during the winter by birds, or snow, and compression wood formation was the response to the bending in order to restore the shoot to upright direction of growth. The growth ring with compression wood had 23 layers of compression wood followed by 31 layers of early wood and 110 layers of late wood in the West quarter (see Fig. 2 a and b).

In spite of the appearance of compression wood in one of the growth rings of the control pine, this tree may by used as a representative of a normal heal-

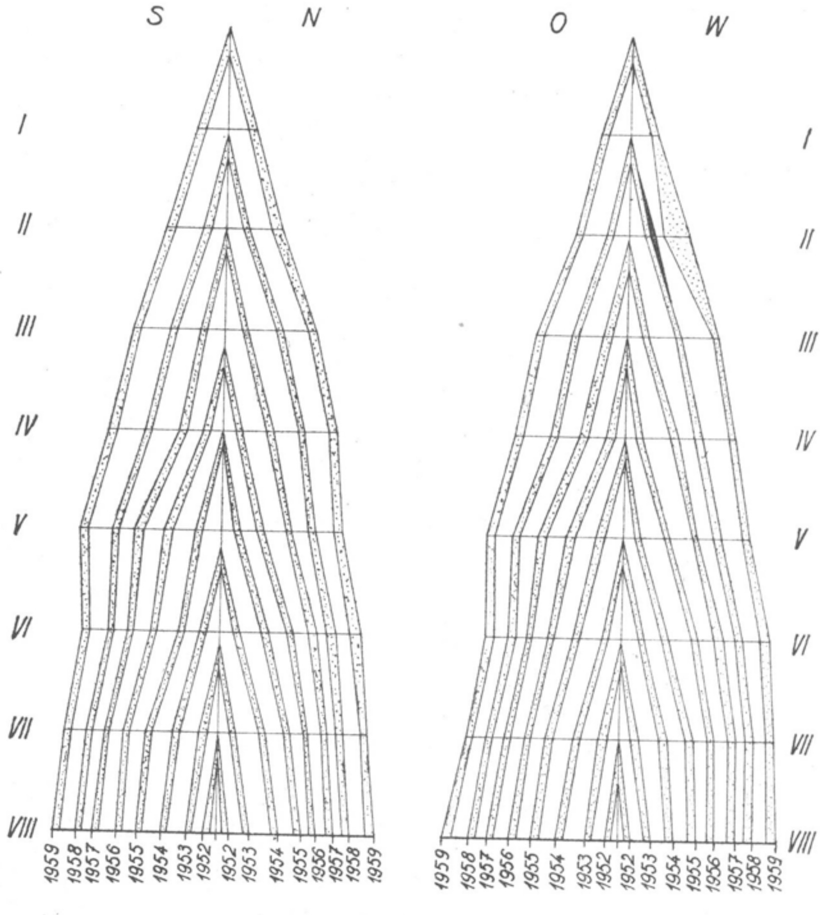


*Fig.* 2*a*

Fig. 2 *a* and *b*. Diagrams representing in longitudinal (2 *a*) and cross sections (2 *b*) the relationship between early and late wood layers in the control pine in all internodes.

Internodes marked with the Roman numerals from the highest one (Ist) produced in 1959, to the lowest one among the investigated (VIIIth) produced in 1952, in all four quarters (N-north, O-east, S-south, and W-west). The black area represents compression wood, the dotted one late wood and the white area (between the rings) represents early wood.

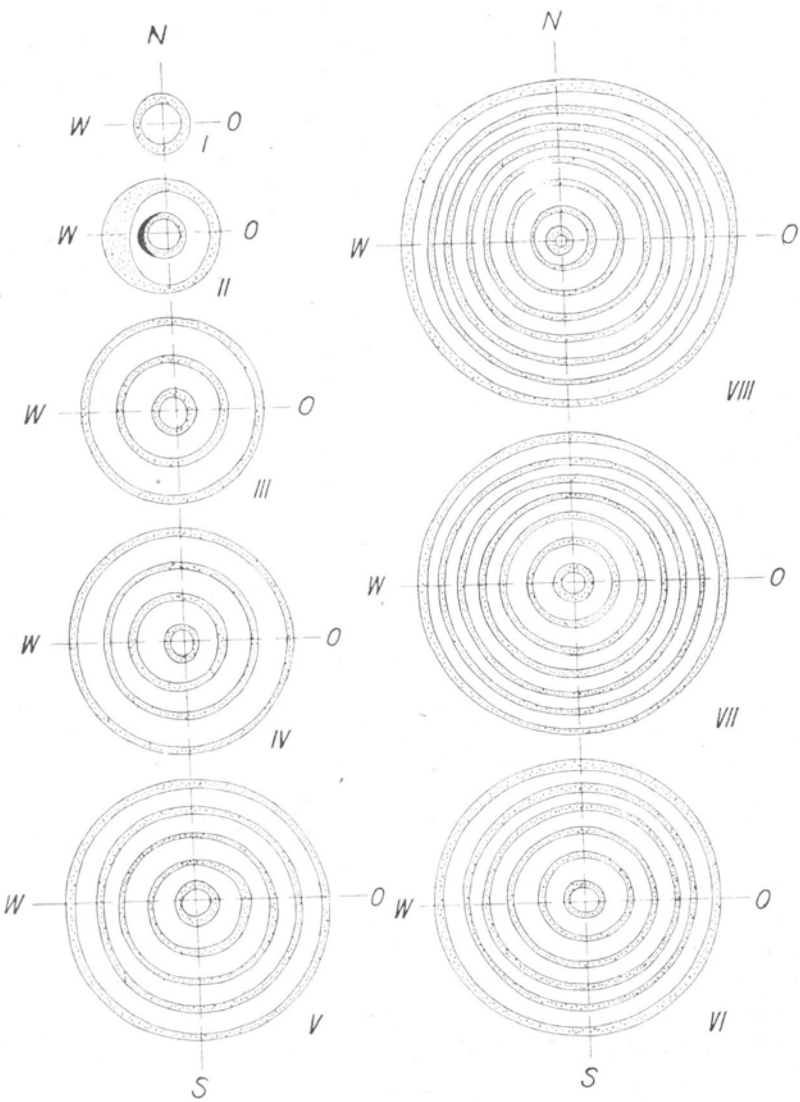


*Fig.* 2*b*

One millimetre represents 30 layers of wood cells in the respective quarters. It is interesting to note the different amount of the juvenile wood (or corewood) in the consecutive internodes: in the VIIIth, VIIth and VIth — there were four rings of corewood, and in the Vth — five rings, the IVth, IIIrd, IInd and Ist — consist only of the corewood. Compression wood was only in the IInd internode, changing the relationship between early and late wood in this ring.

thy pine from the forests around Helsinki. Moreover, this single case of the compression wood was in one of the highest longitudinal yearly growths and in the latest growth ring, so it is possigle to neglect it in an analysis of the growth of the tree. However, the rest of 1959 growth rings, and even the three directions of the ring with compression wood in the whole tree are all without any distribances in the balance between early and late wood, and can be regarded as normal ones.

Damaged pine No. 1: The tree was 12 years old and nine yearly longitudinal growths were studied. The leader of this pine had been damaged three times: 1951/52, 1955/56, and 1957/58. The history of the tree growth from 1951 to 1959 traced back in this research is as follows (see Figs. 3 a and b, and 4):

1951: The three-year-old seedling grew more or less normally forming the IXth internode, the lowest among those studied. But in the winter 1951/52 the leader was damaged and the new one began to substitute it from a lateral branch in the spring of 1952.

1952: The restoration of the new leader from a lateral branch is connected with the formation of compression wood in all four directions, but only in one (IXth) internode. In the early spring in the South and West quarters, 5 and 6 layers of compression wood occurred, but soon they ceased to be produced and were followed by 33 layers of early and 30 of late wood in the West quarter, and 31 of early, and 31 of late wood layers in the South quarter. But in the East quarter after 20 layers of early wood 62 layers of compression wood appeared, followed by 15 layers of late wood; and in the North quarter after 34 layers of early wood only 21 layers of compression wood were formed followed by 31 layers of late wood. The internode therefore changed its direction of growth from the East and North towards the West and South, in spite of the action of compression wood in opposite directions at the beginning of the growth season.

1953: Compression wood was formed in all three internodes, (IXth, VIIIth, and even in the VIIth), formed actually in this growth season). In the IXth internode of this year compression wood was formed in two quarters: East and South, and in both places at the beginning of the growth season; in the East as 119 layers of compression wood followed by 69 layers of late wood, and in the South as 40 layers of compression wood followed by 78 layers of late wood. In both quarters there was no early wood.

In the VIIIth internode compression wood occurred in all four quarters. At the beginning of the growth season compression wood occurred in the East quarter as 64 layers followed by 60 layers of late wood only; therefore it was produced very late in the spring. But in all the remaining three quarters compression wood occurred after many layers of early wood had already been formed. In the West quarter of the VIIIth internode (therefore opposite to the East, where in both the IXth and VIIIth internodes very many layers of compression wood were formed in the spring) 98 layers of compression wood were formed after 40 layers of early wood. The situation was similar in the North quarter, where after 56 layers of early wood 48 layers of compression wood occurred. Both in the West and North compression wood ended the wood formation in this year. In the South quarter the situation of compression wood formation was different. Here, after 55 layers of early wood, 59 layers of compression wood occurred, followed by 26 layers of late wood; this was the largest growth quarter in this internode, with 140 layers of wood cells.

In the VIIth internode, which was formed this year, compression wood appeared in three quarters in the middle of the vegetation growth, that is after many layers of early wood were formed and followed by many layers of late wood. And in the North after 23 layers of early wood, 9 layers of compression wood occurred, followed by 49 layers of late wood; in the West 6 layers of compression wood, after 34 layers of early wood followed by 38 layers of late wood; and in the East 7 layers of compression wood. After 22 layers of early, and followed by 46 layers of late wood. Therefore there was a change in the direction of growth towards the South.

1954: As in the previous year, there was also a very active change in the growth of the lateral branch replacing the damaged leader, and compression wood occurred in all internodes this year which were studied (see Figs. 3 a and b, and 4). But now in almost all cases compression wood was formed in the opposite direction than in the former year in the respective internodes. If a year ago, in the IXth internode, compression wood was in the East and South quarters, now it was formed in the West and North quarters, in both cases in early spring: in the West as 63 layers of compression wood followed by 36 layers of early and 23 of late wood, and in the North as 50 layers of compression wood followed by 58 layers of late wood only. Here the question arises whether the rate of compression wood formation was different in both quarters, or if at the same time early and late wood can be formed in different quarters, since in the West there were more layers of compression wood followed by early and late wood (however in not so many layers) but in the North there were fewer layers of compression wood followed only by late wood.

In the VIIIth internode compression wood occurred mainly in the West quarter that is in the same one as in the former year, but in the beginning of the growth season, and in a much greater amount, there were 116 layers of compression wood followed by 89 layers of late wood; this was one of the biggest growth ring quarters having 205 layers of wood formed in one year. A similar situation was in the North quarter, where there were 80 layers of compression wood followed by 72 layers of late wood. In the South quarter there were 36 layers of compression wood followed by 74 layers of early and 33 of late wood.

In the VIIth internode compression wood mainly occurred in the South quarter as 100 layers of compression wood formed after 18 layers of early and 14 layers of late wood. In the North quarter there were only 13 layers of compression wood followed by 49 layers of early and 37 of late wood, similarly in the East there were only 4 layers of compression wood followed by 53 layers of early and 41 of late wood.

In the highest internode, that is formed in 1954, compression wood at first occurred in the South quarter after 15 layers of early wood, as 12 layers of compression

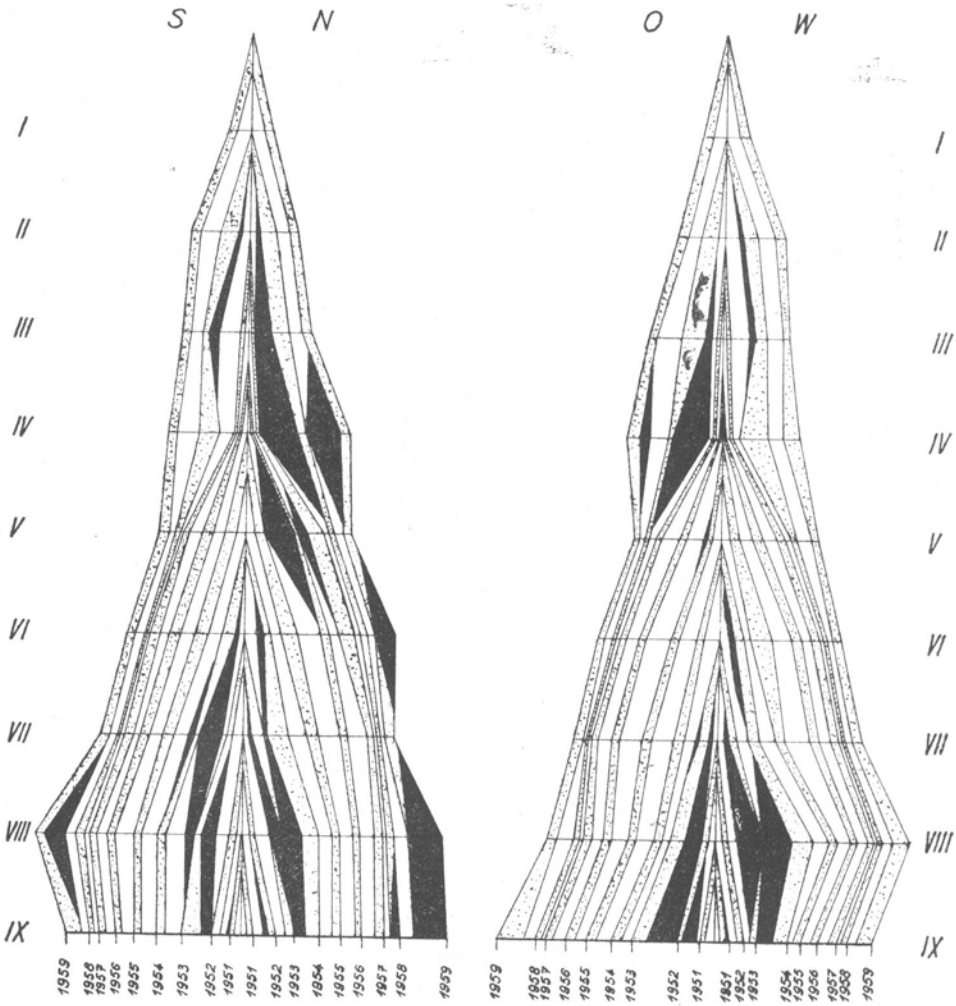


*Fig. 3a*

Fig. 3 *a* and *b*. Diagrams representing in longitudinal (3 *a*) and cross sections (3 *b*) the relationship between early and late wood layers in the damaged pine No. 1 in all internodes.

Internodes marked with the Roman numerals from the highest one (Ist) produced in 1959, to the lowest one among the investigated internodes, (IXth) produced in 1951, in all four quarters (N-north, O-east, S-south, and W-west). The black area represents compression wood; the dotted one late wood, and the white area between the rings represents early wood. One millimetre represents 30 layers of wood cells in the respective quarters. Three main patterns of compression wood formation are seen: (i) compression wood occurred only in one direction, as in the internodes IVth, Vth, and VIth; (ii) compression wood occurred in the opposite directions, as in the internodes IXth, VIIIth; and (iii) the spiral arrangement as in the IIIrd, and VIIIth internodes.

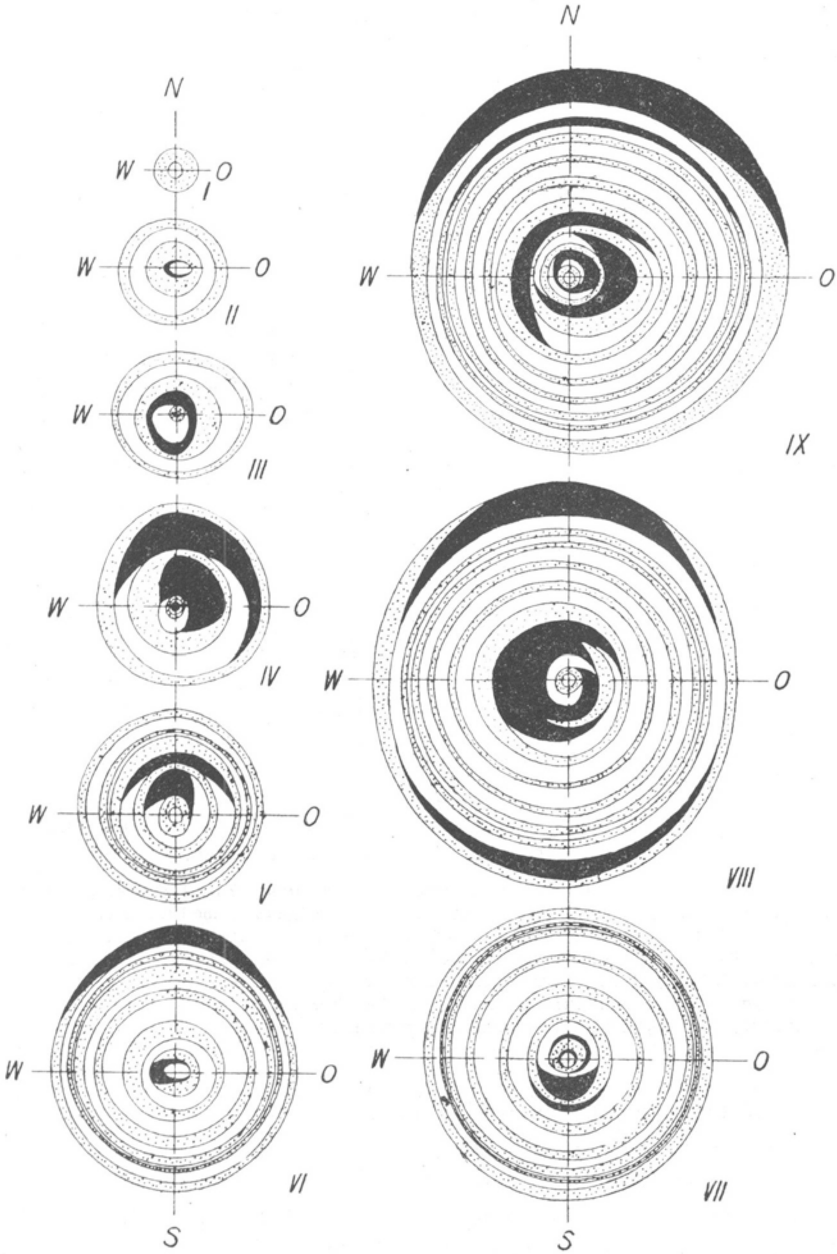


*Fig. 3b*

wood followed by 54 layers of late wood; a little later it occurred in the North and South after 44 layers of early wood in the South, and 51 layers of early wood in the North; in the West quarter 57 layers of compression wood ended the growth ring, but in the North after 23 layers of compression wood 28 layers of late wood occurred too.

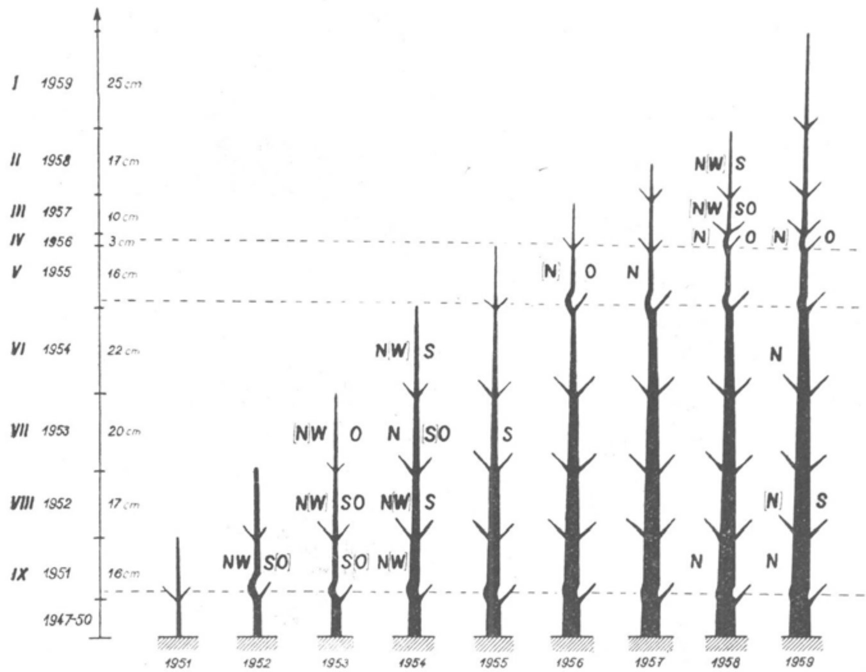


Fig. 4. Diagrams showing the appearance of compression wood in the stem of the damaged pine No. 1 during the successive years of growth.

The Roman numerals indicate the internodes of the investigated pine, from the Ist, highest one, produced in 1959, to the IXth, the lowest one among investigated, produced in 1951. The figures on the left side of the diagrams show yearly growth in height in centimetres and the year of the growth in height. Each drawing shows the actual appearance of compression wood in this particular year and internode in accordance with the quarters (N-north, S-south, W-west, and O-east). The quarter in which the compression wood is greatest is in brackets. Broken lines indicate the level of the gnawing on the main stem by moose (*Alces alces*). The tree has been gnawed three times, in 1950/51, 1954/55, and 1955/56. The curved stem shows restoration of the leader from a lateral branch.

Closer examination of compression wood shows that it occurred at different times in successive internodes and various quarters altering the direction of growth in relation to the actual position of the leader at different times of the growth season. The mechanism of this change is very sensitive indeed, not only in respect to the occurrence and extent in the growth ring quarters and directions, but also to the time and probably to the rate of normal and compression wood formation.

1955: Compression wood occurred only once and only in the South quarter of the VIIth internode as 23 layers of compression wood followed by 54 layers of early and 44 of late wood.

It seems that the leader of the tree was already quite straight in 1955, and all parts of the tree were more or less in balance owing to the very intensive action of the compression wood formed in the three previous years, as may be supposed in view of the amount of compression wood in the successive years 1952, 1953 and 1954. So, after three years of alteration of growth by compression wood, it seems that one of the lateral branches completely substituted the leader.

1956: In the winter 1955/56 the one year old leader was gnowed off, and one of the lateral branches produced 120 layers of compression wood at the beginning of the growth season (the North quarter of the Vth internode). The compression wood was followed by 14 layers of late wood only. Also in the same internode in the East quarter compression wood occurred, but only 3 layers in the beginning of the season followed by 76 layers of early and 29 layers of late wood. The great amount of compression wood, practically only in one quarter, shows a very intensive alteration of the growth of the branch definitely in one direction, from the North to the South.

1957: Compression wood occurred in the Vth internode and in the North quarter only. There were 33 layers of compression wood followed by 68 layers of late wood. The compression wood further altered the direction of growth in the some way as in 1956.

1958: In the winter 1957/58 the two highest internodes formed in 1956 and in 1957 were damaged, therefore the leader could be replaced only by a two-year-old lateral branch, and one such branch which finally took the place of the leader produced much compression wood. Just in the beginning of the vegetative growth in the IVth internode in the North quarter 158 layers of compression wood were formed, followed by 31 layers of late wood. In the East direction of the same internode after 21 layers of early wood 147 layers of compression wood occurred too, which were followed by 12 layers of late wood. This shows very strong restoration in the South-West direction. In the IIIrd internode compression wood occurred at first in the North quarter as 68 layers of wood followed by 31 layers of early and 35 layers of late wood. Later, it occurred in the East quarter after 19 layers of early wood, as 26 layers of compression wood followed by 100 layers of late wood. In the West quarter compression wood occurred as 12 layers after 84 layers of early wood and followed by 45 layers of late wood. In the South quarter compression wood occurred as 40 layers after 91 layers of early wood had been formed, and followed by 19 layers of late wood. In this internode compression wood occurred first in the North quarter, later moved to the East quarter, and much later also from the North to the West quarter, finally ending in the South quarter.

In the II nd internode compression wood occurred in three quarters in the middle of the season, more or less at the same time. In the West quarter after 32 layers of early wood as 12 layers of compression wood followed by 76 layers of late wood. In the North as 7 layers of compression wood after 27 layers of early wood and followed by 71 layers of late wood, and in the South as 4 layers of compression wood after 23 layers of early and followed by 83 layers of late wood.

It is obvious that the change of direction of growth was very strong, what changed

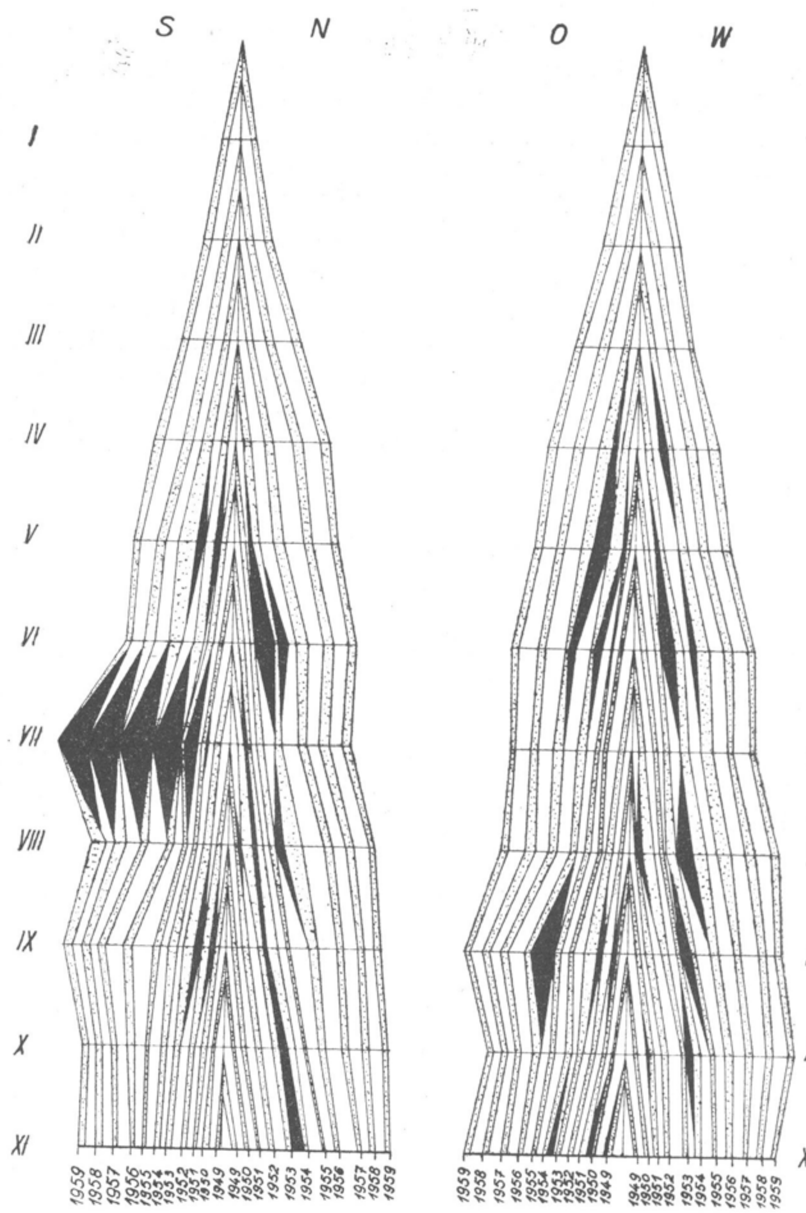


*Fig. 5a*

Fig. 5 *a* and *b*. Diagrams representing in longitudinal (5 *a*) and cross sections (5 *b*) the relationship between early and late wood layers in the damaged pine No. 2 in all internodes.

Internodes marked with the Roman numerals from the highest one — Ist produced in 1959, to the lowest one, among those investigated — XIth produced in 1949, in all four quarters (N-north, O-east, S-south, and W-west). The black area represents compression wood; the dotted one — late wood, and the white area between the rings represents early wood. One millimetre represents 30 layers of wood cells in the respective quarters. Three main patterns of compression wood formation are seen: (i) compression wood occurred only in one direction, as in the internode VIIth, VIth, Xth, and XIth; (ii) compression wood occurred in the opposite directions, as in the central rings of the VIIth internode, and in the IXth internode; and (iii) the spiral arrangement as in the IVth, Vth, and VIIth internodes.

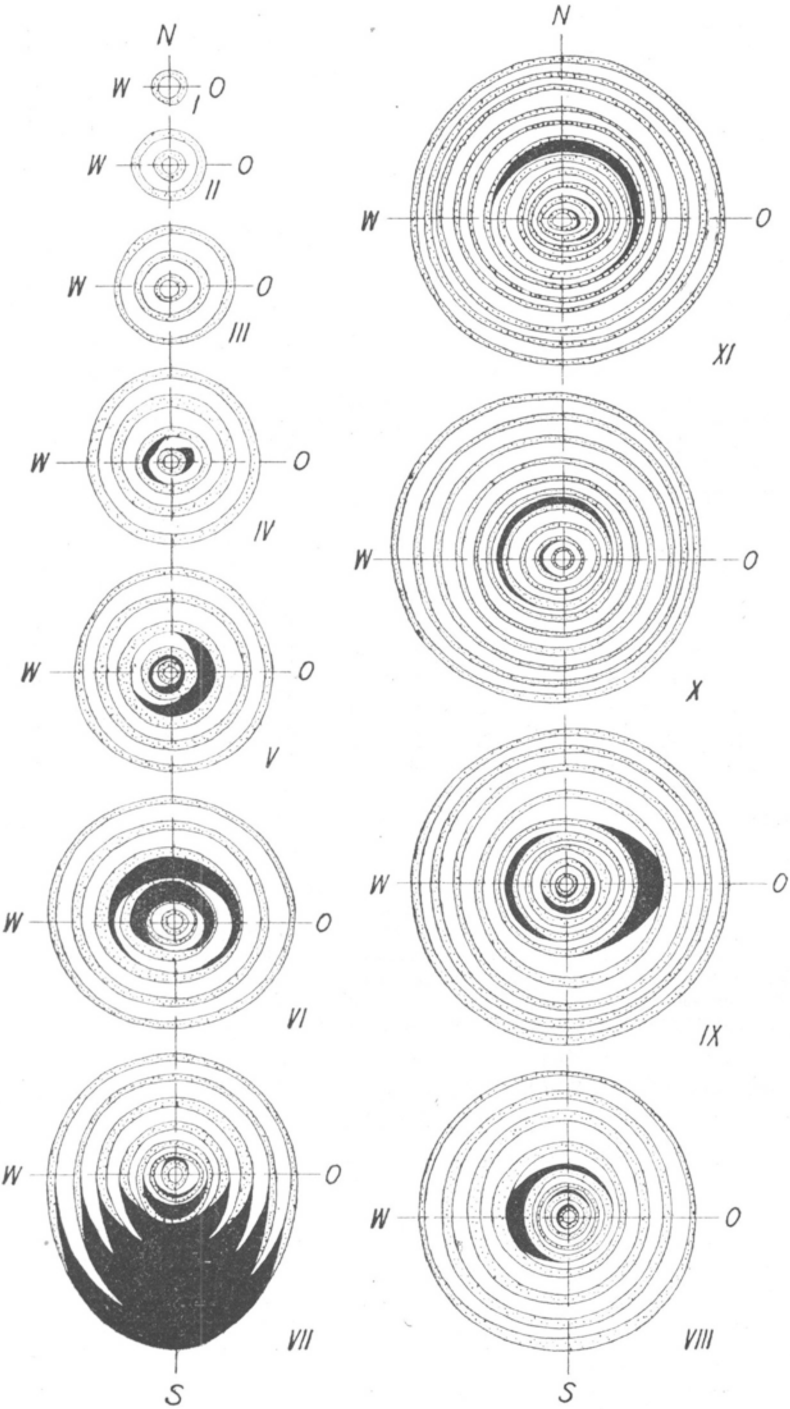


*Fig. 5b*

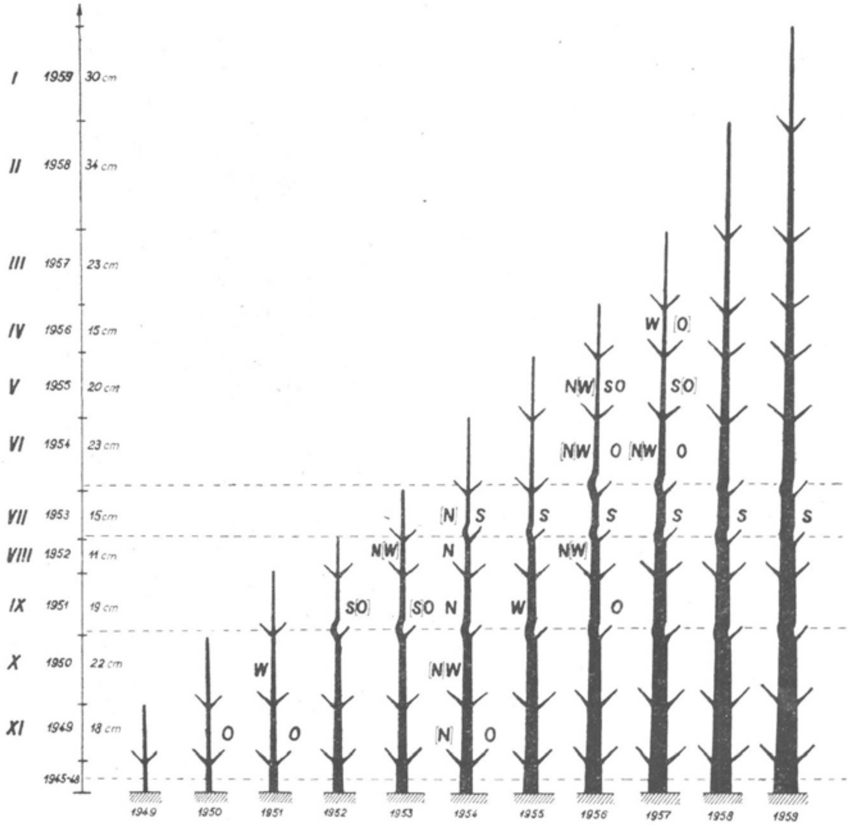


Fig. 6. Diagrams showing the appearance of compression wood in the stem of the damaged pine No. 2 during the successive years of growth.

The Roman numerals indicate the internodes of the investigated pine, from the Ist, highest one, produced in 1959, to the XIth, the lowest one among those investigated, produced in 1949; and the figures on the left side of the diagrams show yearly growth in height in centimetres and the year of the growth in height. Each drawing shows the actual appearance of compression wood in this particular year and internode in accordance with the quarters (N-north, S-south, W-west, and O-east). The quarter in which the amount of the compression wood is greatest is in brackets. Broken lines indicate the level of the gnawing on the main stem by moose (*Alces alces*). The tree has been gnawed four times, before 1949, in 1950/51, 1952/53 and 1953/54. The curved stem shows restoration of the leader from a lateral branch

the equilibrium of the whole tree, therefore at the end of the growth season compression wood occurred again in the IXth internode where it had not formed for 3 years. Here in the North quarter at the end of the growth season, after 25 layers of early wood had been formed, 41 layers of compression wood occurred.

1959: Compression wood was formed in four internodes mainly down in the tree in order as reinforcement of the curves probably due to an increase of the weight of the crown. At the beginning of the growth season compression wood appeared in the IVth internode as 140 layers in the North quarter followed by 41 layers of late wood. In the same internode it was also in the East quarter as 39 layers of compression wood after 82 layers of early wood had been formed and followed by 44 layers of late wood. The compression wood here was connected with the further alteration and reinforcement of this internode after it changed

Phot. B. Molski

Fig. 7. A photograph showing the curved leader of *Pinus silvestris* L. due to the gnawing of the main stem a few years ago, and the restoration of it from a lateral branch.

from a lateral branch to the leader position. Later, compression wood occurred in the VIIIth internode in the South quarter, after 45 layers of early wood had been formed as 81 layers of compression wood followed by 32 layers of late wood. But in the opposite North quarter of the same internode compression wood occurred at the end of the growth season, as 133 layers after 58 layers of early wood had been already formed. It seems probable that the compression wood in this internode was produced in the two opposite quarters at the same time (?).

In the VIth and IXth internodes compression wood was formed in the North direction only at the end of the growth season. In the IXth internode as 131 layers of compression wood after 54 layers of early wood had been formed, and in the VIth internode after 33 layers of early wood, as 75 layers of compression wood. All the compression wood in the lower internodes IXth, VIIIth and VIth, was connected with the reinforcement of the curved parts of the leader.

Damaged pine No. 2: The tree was 14 years old and eleven yearly longitidinal growths were studied. The leader of this pine had been damaged four times: before 1949, in 1951/52, 1953/54, and 1955/56. The history of the tree growth from 1949 to 1959 is as follows (see Figs. 5 a and b, and 6):

1949: The three-year-old seedling grew more or less normally forming the lowest (XIth) internode studied. There was no compression wood, but the proportion of late and early wood differed from normal. If in the West, East and North quarters of the XIth internode the ratio of late wood layers to early wood was 16:44, 17:46, and 15:43 respectively, in the South quarter there were 18 late wood layers and only 4 early wood layers.

1950: In the East quarter of the XIth internode 9 layers of compression wood appeared, but in the South and North quarters 22 and 19 late wood, to 32 and 28 early wood layers occurred, helping somehow to restore the position of the leader towards the West direction, where only 7 layers of late wood and 32 of early wood occurred. The new, Xth yearly longitudinal growth of the leader produced only 4, 4, 5, and 7 layers of late wood, and 43, 40, 42, and 37 layers of early wood.

1951: Now in the same XIth internode in the East quarter compression wood appears again, but in greater quantity than in 1950, 19 layers were produced in the early spring, followed by 29 layers of early and 4 layers of late wood in this quarter. In the same year, but much later, sometime in summer (after 43 layers of early wood) 3 layers of compression wood appeared in the opposite West quarter of the Xth internode indicating its restoration together with the newly formed IXth internode towards the East, which previously had deviated to the West by the compression wood formed in the spring 1951 in the lower XIth internode in the East quarter. After the formation of these 3 layers of compression wood, 19 layers of late wood were formed. All the compression wood produced in the XIth and Xth internodes was connected with the restoration to the vertical direction of the leader deviated by former damages.

1952: In the winter 1951/52 the highest yearly growth was gnawed and the restoration of the new leader started from a lateral branch of the highest whorl. Therefore in the IXth internode which in 1951 was a lateral branch, 12 layers of compression wood occurred in the early spring in the East quarter followed by 28 layers of early and 20 layers of late wood. Six layers of compression wood appeared also in the South quarter, but in midsummer, after 29 layers of early wood had been produced, the compression wood here was followed by 19 layers of late wood. It is worth noting that in 16 quarters (four internodes with four quarters each) the two quarters with compression wood had a medium size diameter increase, i.e. 60 and 54 layers of wood in their growth ring quarters, whereas four growth ring quarters without compression wood had more layers of wood in their growths (61, 59, and 55), and 10 of them had less (from 37 to 53 layers) than in the growth rings with compression wood. It proves that compression wood formation is not necessarily connected with the widest growth rings.

1953: Compression wood occurred in two internodes, IXth and VIIIth, mainly in the IXth internode, that is the same as in 1952, and in the same quarters: South and East. In the South quarter in the early spring 24 layers of compression wood were formed, followed by 18 layers of normal early and 32 layers of normal late wood; and in the East quarter 17 layers of compression wood followed by 22 layers of normal early and 35 of normal late wood.

In the upper VIIIth internode compression wood appeared in opposite directions than in the IXth, that is North and West, and in very few layers. In the West quarter there were only 6 layers of compression wood followed by 35 layers of early and 20 layers of late wood; and in the North quarter only 2 layers of compression wood followed by 23 layers of early and 31 of late wood.

Compression wood, therefore, formed in opposite directions in two internodes restored the leader to vertical position acting as a very sensitive mechanism. In all quarters where compression wood occurred (except the West quarter of the VIIIth internode) the proportion of late and early wood was opposite than in the normal growth rings without compression wood, more or less 2 layers of late wood to 1 layer of early wood.

1954: In the winter 1953/54 the highest yearly growth was gnawed off by moose, therefore the new leader was restored from a lateral branch.

In 1954 compression wood occurred in five different internodes: XIth, Xth, IXth, VIIIth, and VIIth. In the XIth internode it again was formed after a break of two years, since compression wood was formed in 1950 and 1951, it did not appear in 1952 and 1953, and in 1954 it was formed again. Compression wood grew in the North and East directions. Early in spring, after the start of vegetation growth, a few layers of normal early wood were formed (8 and 5 layers), but after that 55 layers of compression wood in the North, and 26 layers in the East quarters were formed; in both quarters compression wood was followed by 16 (East) and 14 (North) layers of late wood. It seems possible that formation of compression wood in this internode is due to the disturbed equilibrium of the tree in the upper parts of the crown; and the mechanical stress on the lower part caused formation of compression wood.

In the Xth internode compression wood occurred also in the North quarter (25 layers at the beginning of growth followed by 21 layers of early and 17 layers of late wood), and in the West quarter (24 layers of compression wood followed by 26 layers of early and 16 of late wood). Compression wood was formed first in this internode, and later in the lower, XIth internode. In the latter compression wood was formed in the North direction only, and in a very small amount, 7 layers only, followed by 20 layers of early and 26 of late wood. The same may be said of the VIIIth internode, where 10 layers of compression wood were formed at the beginning of the vegetation period, followed by 14 layers of early and 11 layers of late wood.

In the VIIth internode which was a lateral branch on its way to take place of the leader, the situation was different: at the beginning of the vegetative growth, where the branch was in lateral position, 8 layers of compression wood occurred in the North quarter followed by 21 layers of late wood only. But later in summer, in the same internode, after 28 layers of early wood had been already formed, 3 layers of compression wood appeared.

It is striking to note that compression wood is formed in all internodes in North direction, but it increases from the upper parts of the tree to the lower ones, that is from 8 layers in the VIIth internode, through 10, 7, 25, to 55 layers in the lowest internode, forcing the tree from the North to the South on its growth. Only in the VIIth internode (the highest one with reaction wood) and in the middle of vegetative growth, compression wood occurred in the South direction forcing the leader towards the North.

1955: The leader damaged a year before now replaced from a lateral branch, and therefore in the VIIth internode 58 layers of compression wood occurred. The compression wood, however, was formed after 11 layers of early wood had been already formed in this growth ring in the early spring, and was followed by 7 layers of late wood. It is worth noting that in all directions in this growth in the VIIth internode, there was much late wood as compared with the early one (almost one to one); a similar situation was also in the nearest (upper and lower) internodes. Compression wood occurred also in the IXth internode, at the beginning of the vegetative season, as 33 layers followed by 23 layers of early and 13 layers of late wood. This compression wood was connected probably with the restoration of the general equilibrium of the tree, since it occurred in this direction (in this internode) only once, and only in this growth ring (see Fig. 5, IX).

1956: In the winter 1955/56 the two top internodes were gnawed off and the tree in 1956 restored the leader from a lateral branch producing much compression wood. Also the entire equilibrium of the tree was disturbed, so compression wood was produced in five internodes (from IXth to Vth) in order to reinforce the straight position of the main stem.

In the IXth internode in the East direction 102 layers of compression wood were produced (see Fig. 5, IX) followed by 27 layers of normal late wood. The compression wood in this internode was formed in direction opposite as in the preceding year. In the VIIIth internode compression wood was produced in direction opposite to that in the lower IXth internode in the same growth ring, here it was in the West quarter as 63 layers followed by 61 layers of late wood, therefore here was almost the same number of wood layers (124), as in the lower internode (129), but the number of compression wood layers was much smaller, only 63, to 102 in the lower internode. The compression woods in both internodes acted in opposite directions leading to a straightening of the stem. In the VIIIth internode compression wood occurred also in the North quarter, but in the beginning of the growth ring as 21 layers followed by 49 layers of early wood and 37 layers of late wood. In the VIIth internode there was only compression wood — 117 layers.

In the VIth internode compression wood formed in three directions: in the North as 83 layers of compression wood followed by 10 layers of late wood, in the West quarter as 57 layers of compression wood followed by 35 layers of late wood; and in the East as 39 layers of compression wood formed after 34 layers of early wood and followed by 6 layers of late wood.

In the Vth internode compression wood appeared in all four quarters, but in the South and East it was formed at the beginning of the growth ring as 20 layers of compression wood followed by 14 layers of early and 32 of late wood in the South, and as 12 layers of compression wood followed only by 51 layers of late wood in the East. In the North and West compression wood was formed in the middle of the growth ring as 13 layers of compression wood, after 13 layers of early wood were already formed, and followed by 32 layers of late wood in the North quarter, and as 15 layers of compression wood, after 23 layers of early wood had formed, and followed by 26 layers of late wood in the West quarter.

In the IXth, VIIIth, VIIth, and VIth internodes compression wood acted as a straightening force counterbalancing one another in the consecutive internodes, leading finally to a straight stem, but in the Vth internode compression wood worked as a very sensitive mechanism acting in different parts of the growth season from different directions, starting from East and South, and moving later to the North and West. It depended probably on the actual position of this internode moved by the action of the compression wood in lower internodes.

1957: Compression wood occurred in four internodes starting from the VIIth to the IVth. In the VIIth internode in South direction, as in the previous year only 131 layers of compression wood were produced, but the first 49 had much thinner cell walls than the remaining 82 layers. In the upper internodes compression wood was mainly formed in opposite directions, moving up the stem, and in the VIth one compression wood was in the North quarter as 75 layers followed by 42 of late wood, and in the West quarter there were 32 layers of early wood followed by 17 layers of compression wood, and 58 of late wood; a similar situation was in the West quarter: 71 layers of early wood at the beginning of the growth ring followed by 27 layers of compression wood and only 10 layers of late wood.

In the Vth internode the distribution of compression wood was again more or less opposite to that in the lower internode, that is in the South and East. In the South quarter 24 layers of compression wood formed at the beginning of the growth ring, followed by 38 layers of early and 42 layers of late wood, and in the East — 73 layers of compression wood followed by only 42 layers of late wood.

In the upper IVth internode the compression wood grew in two opposite quarters West and East, but in the East it formed 32 layers at the beginning of the growth season, followed by 31 layers of early wood and 32 layers of late wood, and in the West, at the beginning of the growth season early wood was produced — 41 layers, later — compression wood as 20 layers followed by 25 layers of late wood. Therefore it seems that compression wood was produced only in one direction at any given time.

1958 and 1959: Compression wood was produced in the South quarter in the VIIth internode only, but in a very high amount, 138 layers in 1958 and 111 layers in 1959. It was due to a very big curving of this internode, which had to be supported.

It is interesting to note that field observations showed a regularity in pine damages by moose (*Alces alces*). When trees are young and short, usually only the highest growth is eaten, but when it is older and taller, two or sometimes even three highest longitudinal growths are damaged and the new leaders are reproduced from two or three-year-old lateral branches.

The rate of regeneration differed in the two pines with compression wood.

Pine II regenerated the damaged main stem much slower than pine I. In pine I the tree-ring with compression wood were much wider than in pine II. With age the rate of regeneration was faster; if for example, the first damage was regenerated in three or four years, the next ones were regenerated in as little as one or two years; probably owing to more leaves on the tree and therefore more intensive assimilation.

## CONCLUSIONS AND DISCUSSION

Very exact counting of all types of wood layers in the successive growth rings showed clearly how precise is the mechanism of action of compression wood in trees, and how sensitive and responsive to all influences of environment disturbing normal growth. However, it is possible to see its action when a very precise method of investigation is applied, since it is difficult to ascertain the appearance of compression wood in tree rings without microscopic investigations if there are only a few layers of it between many layers of normal wood. Any interpretation of compression wood appearance in a tree ring might be misleading without good knowledge of the whole situation and the copartnership of all the types of wood in this tree ring.

The investigation proved that compression wood appears only if the stem is already forming secondary growth and if there was a possibility to move the stem to a new position in space owing to changes in the environment or partial damage to the tree crown leaving an empty place in it, for example after damaged leader, for a lateral branch to change the direction of its growth and take the function of the leader. Owing to the ability of movement of the already formed stems of any tree in spite of damages by environment, the trees were able almost at any time of growth to regenerate damaged leaders and preserve the genetically established shape of growth and adjust it to the actual circumstances and possibilities formed by the changing environment.

Compression wood appeared in the investigated tree rings in the quantity required for changing the position of the stems or branches. Sometimes compression wood appeared only as a few layers (even two or three) and sometimes as a very wide zone up to two hundred layers. It occurred on a small or wide section of the tree ring around the interior of the stem. It usually started from a small section and grew taking finally the shape of a crescent which enfolded three sides. However, it never reached all the four quarters encircling completely the tree ring. Compression wood was never produced around the tree ring simultaneously, but its formation has been noted in the same year (in the same tree ring) in opposite quarters, but at different times (see Fig. 3, in 1959 in S-N quarters). This is contrary to the observations of Wałek-Czarnecka and Smoliński (1956), and Prażmo (1954) who pointed out that reaction wood appeared at various places and very often in all directions from the pith and also on the opposite sides in the same sections. They arrived at the conclusion that it is difficult to decide whether the reaction wood is located according to some definite rules or whether it appears accidentally. It seems however, that precise studies show formation of reaction wood only in one or at most three sides at a time, and never all around the tree ring.

The amount of compression wood produced in the tree ring depended on the thickness of the branch which had to be moved to a new position. If the branch was young, very few layers of compression wood were enough to move the branch, if it was thick (two or three years old), many layers had to be produced. But not only the thickness of the moving branch is important, but also the rate of movement. If the branch had to be moved to a new position in a short period of time (in cases of being the only branch left in this whorl after damage) then there also appeared more layers of compression wood as compared with those in branches moved slowly when a few layers of compression wood were formed, but throughout a few years, acting slowly but longer and reaching finally the same result; this happened when a few branches in one whorl were competing for the leadership. But if the stem was very thick, the quantity of reaction wood was large and its production extended over several years.

Compression wood acted very precisely not only by production of the appropriate amounts of it in any particular tree ring, but also in the consecutive longitudinal growths of the tree. If any particular lower internodes produced compression wood, for example in the northern quarter in order to set it upright from a curvature, and this moved the upper internodes to the South as the result of straightening of the lower part of the tree, then in the next upper internode the compression wood was produced a little later in time, in the opposite southern quarter, in order to move the upper part of the tree to the North. This way of compression wood production in opposite quarters followed all the consecutive internodes and finally, by this action the tree was set in upright position.

Such a system of compression wood production might follow downward from above, or from the lower part of the stem to the top — depending on the cause that provoked it. If the crown increased in weight on one side, and this was the cause of compression wood formation, it followed from the upper internodes down the tree. But if the tree was curved in the lower internodes owing to, for instance, regeneration of the leader from a lateral branch, the compression wood formation advanced from the lower internodes up the tree.

Compression wood may appear at different times of the vegetative season in any of the internodes. It may be produced very early in spring, so early that after several layers of compression wood normal early wood is produced too, or it may be produced very late in autumn, so late that before it several layers of the normal late wood are formed. If, for example, the crown of the tree owing to its growth in this vegetative season increased and this changed the equilibrium of the whole tree, the static forces in the lower parts of the stem could change so greatly that the inclination of the tree caused formation of compression wood late in summer or in autumn.

Sometimes cambium ceased for a few years to produce compression wood in any particular quarter, but when the crown of the tree grew upwards, the centre of gravity changed, and new forces acted on the lower part of the tree increasing its inclination, and then the cambium started production of compression wood again in the bent parts of the stem in order to straighten it or to prevent further inclination of the main stem.

The anatomical studies agree completely as regards the function of compression wood in leader restoration from a lateral branch after damage with the former observations made by Sinnott (1952), Hartmann (1942) and other authors whose papers were reviewed by Westing (1965, 1967), and Low (1964). All investigations done so far in the problems of compression wood indicate that it plays a very important role in the preservation of the characteristic shape of the species and helps to regenerate the damaged parts of the tree through their replacement by others. Szymański and Szczerbiński (1958) investigating the problem of replacement of the damaged leader by a lateral branch noted that the pine (*Pinus silvestris* L.) retains this ability for a very long time, it is, however, strongest in the period of intensive height growth of the main stem. Their observations agree completely with those of the present author that the process of leader replacement is very rapid and a lateral branch takes the leader position in two or three years so well that after this time it is difficult to distinguish the place of regeneration in the stem.

Reaction wood helps the tree to survive and produce offspring for a very long time in spite of such difficulties and disturbances as heavy snow, frost, large yields of fruit, animal damages, etc., which damage the leader of the tree or the leaders of main branches, and in this way the shape of the tree can be preserved very well. This might be of great importance in the first stages of surviving on the way to adaptation before the genetic mutation occurs. The work of Szafer (1959, 1963) on the problems of phylogenesis of trees might be considered here.

Szafer (1959) investigating the genealogy of Salix suggested a very interesting hypothesis as to the morphological transformation among the species of this genus from monopodial to sympodial growth. He described it as follows: "Taking into account the morphology of the main stem, the oldest (from the historical point of view) willows still existing, such as *Salix humboldtiana* of Madagascar, India and South America, have a monopodial growth, that is, their main stems end with a terminal bud which after some period of rest continues its growth to form the main stem. All modern willows have sympodial growth and their terminal buds die periodically. The range of sympodial growth of willows at the present time might be treated as a post-Tertiary Era adaptation. The creative stimulus which guides the evolutional trends in the genus *Salix* has been acting from the Cretaceous Period and still acts at the present time."

The morphological transformation among the species of *Salix* from monopodial to sympodial growth may have been the result of emergence of new mountain ranges and appears to have resulted from temperature decreases (Szafer 1959, 1963); the idea being that the tips of monopodially growing stems were destroyed systematically. Similar processes of adaptation apparently occur in the growth of trees at the present time, but they are very slow and fractional, and often difficult to observe; it is moreover very hard to give an exact account of their phylogenetic importance. Such adaptational processes of anatomical transformation from ontogenetic restoration, as in a regenerated stem, to the phylogenetic steady genetic adaptations may last thousands or even millions of years.

A good example of the regeneration of main stems is found in forests of Scandinavian countries where the young pines have been gnawed by moose (*Alces alces*) for several thousand years. The restoration of the main stems is usually so perfect that after a few years it may be quite impossible to recognise that such a pine had once lost the upper part of its leader. It is very interesting to compare the growth of three kinds of pines: *Pinus montana* Mill., *Pinus silvestris* L., and *Pinus silvestris* L. f. *montana* Molski 1962. *Pinus montana* Mill. which grows in the mountains above the timber line, forms a lot of compression wood owing to the difficult growing conditions. The formation of this compression wood enables trees to restore the growth of branches and stems after being bent downwards by snow in winter. But *Pinus silvestris* L. in view of its nature, cannot survive in an environment above the timber line even though it forms reaction wood. *Pinus silvestris* L. f. *montana* Mol. in Lapland is of the *Pinus silvestris* type, but this pine grows exactly as *Pinus montana* Mill., that is like a shrub and is able to survive in severe high mountain environment in Lapland, where normal *Pinus silvestris* L. cannot survive. In all these three pines compression wood plays a very important function in the regeneration of all types of leaders, both of the main stem and the branches after damage caused by the environment, but besides the ability of compression wood formation there has to be something else, viz. genetic adaptation. Nevertheless the ability of compression wood formation is a very old adaptation of conifers, since it is known to exist for a few hundred million years (Lämmermayer, 1901; Westing, 1965; Molski and Reymanówna, in print).

Reaction wood in this sort of transformation might play an important role in the early stages during such adaptations enabling the species to survive and produce offspring before a suitable genetic mutation occurs. Reaction wood might mediate in the transformation from monopodial to sympodial growth and also from high tree growth shape to shrub-like growth shape as well.

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## SUMMARY

Compression wood formation is closely connected with the movement of stems aiming at the maintenance of the genetically determined morphogenetic forms of trees and shrubs in spite of damages and disturbances of the environment. When a very precise method of investigation is applied, it is possible to see clearly how sensitive and responsive is the mechanism of action of this wood to all influences of environment disturbing the normal growth.

The investigation proved that compression wood appears if there is a possibility to move the stem to a new position in the crown owing to changes in the environment or partial damage

of the tree, and thus an empty space in the crown; for instance, after damage to the leader, for a lateral branch to change direction of its growth and take the function of the leader. Owing to the ability of movement of the already formed stems of the tree in spite of damages and disturbances, the trees are able to preserve the genetically established shape of the crown and adjust it to the actual circumstances formed by the changing environment.

Compression wood appears in tree rings in the quantity required for changing the position of the stems or branches. Sometimes compression wood appeared only as a few layers, and sometimes as a very wide zone up to two hundred layers. It occurs on a small or wide section of the tree ring around the interior of the stem. It usually starts from a small section and grows taking finally the shape of a crescent which enfolds three sides. However, it never reaches all the four quarters, encircling completely the tree ring. Compression wood is never produced around the tree ring at the same time, but it has been noted that the wood was formed in the same year (in the same tree ring) in opposite quarters, but at different times.

The amount of compression wood produced in the tree ring depends on the thickness of the branch which is moved to a new position. If the branch is young, very few layers of compression wood are sufficient to move it, if it is two or three years old, then many layers have to be produced, and when the stem is very thick, the quantity of reaction wood is large and its production extends over several years. But not only the thickness of the moving branch is important, but also the rate of movement. If the branch is moved to a new position in a short period of time, as in cases of being the only branch left in this whorl after damage, then there are more layers of compression wood as compared with that in branches moved slowly, as when a few branches in one whorl compete for the leadership, but in such cases compression wood is formed over a few years.

Compression wood acts very precisly not only by occurring in suitable amounts in any particular tree ring, but also in the consecutive longitudinal growths of the tree. For example, if any particular lower internode produced compression wood in the northern quarter in order to set it upright from a curvature, and this moved the upper internodes to the South by straightening of the lower part of the tree, then in the next upper internode compression wood was produced a little later in time, in the opposite southern quarter in order to move the upper part of the tree to the North. This way of compression wood formation in opposite quarters following the successive internodes sets the tree in upright position.

Compression wood may appear at various times of the vegetative season in any of the internodes. It may be produced very early in spring, so early that after several layers of compression wood normal early wood is produced too, or it may be produced very late in autumn, so late that before it several layers of normal late wood are formed.

Sometimes cambium ceases for a few years to produce compression wood in any particular quarter, but when the crown of the tree grows upwards, the centre of gravity changes, and the new forces acts on the lower part of the tree increasing its inclination, then the cambium starts production of compression wood again in the curved parts of the stem in order to straighten it or prevent further inclination.

All investigations done so far on the problems of compression wood indicate that it plays a very important role in the preservation of the characteristic habitus of the species and helps to regenerate the damaged parts of the tree by their replacement by others. Reaction wood helps the trees to survive and produce offspring for a very long time in spite of such difficulties and disturbances as heavy snow, frost, large yields of friut, animal damages, etc., which damage the leader of the tree of the leaders of main branches. This might be of great importance in the first stages of survival on the way to adaptation before the genetic mutations occur. Therefore reaction wood might play an important function in the evolutionary trends of transformation of trees. Reaction wood might mediate in the early stages of such transformation as from monopodial to sympodial growth, and from high tree-growth shape to low shrub-growth of woody plants enabling them to survive and produce offspring before suitable genetic mutations occur in the population well adjusted to the new environmental conditions.

The reaction wood function might therefore not only be of morphogenetic importance, but also be an adaptation of higher woody plants of great evolutionary significance as well.

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## *Rola drewna reakcyjnego w regeneracji pędu głównego u sosny zwyczajnej (Pinus silvestris L.)*

### I. Rozmieszczenie i funkcja drewna reakcyjnego w pędach głównych

### Streszczenie

Tworzenie drewna reakcyjnego przez drzewa i krzewy jest jednym z interesujących problemów wzrostu roślin drzewiastych, ściśle związanych z morfologicznym utrzymaniem kształtu danego osobnika zgodnie z genetycznie odziedziczonymi cechami, pomimo przeszkód, a nawet i uszkodzeń powodowanych przez środowisko. Jednakże możliwość regeneracji uszkodzonych pędów głównych lub pędów przewodnich gałęzi bocznych poprzez zajmowanie ich miejsca przez ukształtowane już gałęzie niższego rzędu w drodze ich przemieszczania w przestrzeni ma szczególne znaczenie w walce o byt ze środowiskiem i utrzymanie się populacji danych drzew lub krzewów pomimo zniszczeń. Jednym z wycinkowych, lecz bardzo charakterystycznych zjawisk, jest regeneracja uszkodzeń sosny zwyczajnej przez łosie, a przede wszystkim regeneracja zgryzanych pędów głównych.

Autor w celu zbadania regeneracji pędów głównych poddał dokładnej analizie anatomicznej pędy główne sosny zwyczajnej dwóch sosen, które miały kilkakrotnie niszczone wierzchołki, oraz jako kontrolne jedno drzewko, które nigdy nie miało uszkodzeń pędu głównego. Aby odtworzyć historię tych drzew i prześledzić pojawianie się drewna reakcyjnego na wszystkich wysokościach przyrostów na długość, każdy z przyrostów na wysokość badany był na przekroju poprzecznym pod mikroskopem w celu bezbłędnego odróżnienia drewna reakcyjnego od drewna normalnego. Za drewno reakcyjne u sosny uznano jedynie cewki o okrągłych kształtach na przekroju poprzecznym. Przekroje badano na czterech kierunkach zgodnych z kierunkami świata.

Sosna kontrolna wytworzyła tylko jeden raz, i to na jednym z kierunków drewno reakcyjne, prawdopodobnie w celu wyprostowania zgiętego przez śnieg ostatniego przyrostu na wysokość. Sosny, które miały kilkakrotnie zgryzane przez łosie pędy szczytowe wytwarzały drewno reakcyjne wielokrotnie i to na różnych kierunkach od rdzenia. Dokładna analiza występowania drewna reakcyjnego u sosny, oraz odtworzona historia wzrostu drzew pozwalają na sformułowanie kilku uogólnień.

Drewno reakcyjne pojawia się kiedy utworzony jest już pęd i rozpoczął się przyrost wtórny. Pojawia się ono w warunkach zmian w otoczeniu (nowy dopływ światła na skutek wycięcia drzew) lub częściowym zniszczeniu korony drzewa lub pędu szczytowego, na skutek czego pozostałe gałęzie mogą rozrastać się inaczej niż poprzednio i zmienić kierunek wzrostu i położenia gałęzi, lub też gałęzie te są odkształcone od normalnego położenia przez czynniki zewnętrzne, takie jak

śnieg, duża ilość owoców lub przygniecenie przez zwierzynę. Pojawiające się drewno reakcyjne na skutek odpowiednich bodźców fizjologicznych wywiera presję jednostronną gałęzi i zmienia jej położenie. Dzięki możliwości wytworzenia drewna reakcyjnego drzewo lub krzew może utrzymać genetycznie ustalony kształt i kierunek wzrostu pomimo zniszczeń i uszkodzeń. Dzięki drewnu reakcyjnemu zniszczony pęd główny może być bardzo szybko zastąpiony przez jedną z gałęzi bocznych.

Drewno reakcyjne pojawia się w bardzo różnych ilościach w zależności od wielkości gałęzi, odchylenia czy szybkości zmiany położenia. Ilość wytwarzanego drewna reakcyjnego regulowana jest substancjami wzrostowymi stymulowanymi dopływem światła lub grawitacją oraz genetycznie ustalonym kształtem korony drzewa. Czasami pojawia się zaledwie 2—3 warstwy drewna reakcyjnego, czasami zaś aż 100 — czy 200 warstw. Drewno reakcyjne obejmuje większą lub mniejszą część przyrostu rocznego, czasami dochodząc aż do trzech kierunków, obejmując przyrost na kształt półksiężyca. Nigdy jednak w tym samym czasie nie tworzy się na wszystkich czterech kierunkach dokoła przyrostu rocznego. Oczywiście można go znaleźć w tym samym przyroście rocznym; lecz na przeciwnych kierunkach tworzone ono jest w różnym czasie, na przykład w kierunku północnym na wiosnę, a w kierunku południowym na jesieni lub lecie.

Ilość drewna reakcyjnego wytwarzanego zależy od grubości pędu który je wytwarza. Jeśli gałązka boczna jest cienka — jednoroczna — i może bardzo szybko zająć nową pozycję w układzie korony bez współzawodnictwa z innymi gałązkami, wtedy pojawia się dużo drewna reakcyjnego i gałązka ta już w pierwszym roku może dobrze dopasować się do nowego układu. Jeśli drewno reakcyjne wytwarza się na skutek przychylonego pnia drzewa, wtedy będzie pojawiało się bez przerwy i w dużych ilościach, gdyż może ono jedynie wzmocnić w ten sposób pień nie będąc zdolnym przesunąć go na nowe miejsce w przestrzeni.

Drewno reakcyjne pojawia się z dużą precyzją nie tylko pod względem ilości w przyrostach rocznych, ale także jego rozmieszczenia w całym pędzie. Jeśli na przykład drewno reakcyjne pojawi się w dolnym międzywęźlu zmieniając jego położenie ku północy, dzięki czemu cała górna część drzewa przesunie się ku północy, wtedy w wyższym międzywęźlu nieco później w czasie drewno reakcyjne pojawi się również, lecz w przeciwnej stronie i przechyli pęd w kierunku południowym. I tak zmieniając swe położenie na przeciwnych stronach działa w ostateczności jako prostująca siła cały pęd przez kolejne przechylenia z przeciwnej strony na coraz to innej wysokości.

Drewno reakcyjne pojawia się w różnych porach roku, czasami tak wcześnie na wiosnę, że później wytworzą się jeszcze normalne komórki drewna wczesnego; czasami tak późno w lecie, że jeszcze po drewnie reakcyjnym pojawiają się cewki drewna późnego; a jeszcze w innych sytuacjach już po wytworzeniu się kilku warstw drewna późnego. Czasami w danym międzywęźlu i na danym kierunku przez kilka lat nie powstaje drewno reakcyjne, i po paru latach pojawia się ponownie, prawdopodobnie na skutek wzrostu korony i działania nowych sił przekrzywiających pęd w niższych położeniach.

Drewno reakcyjne na skutek swego precyzyjnego działania spełnia doniosłą rolę morfogenetyczną pozwalając utrzymać drzewom genetycznie ustabilizowany kształt korony i wzrost na wysokość. pomimo uszkodzeń i przeszkód środowiska. Dzięki temu całe populacje mogą przetrwać niekorzystne okresy wzrostu drzew lub krzewów umożliwiając im przetrwanie aż do czasu powstania nowych mutacji genetycznych umożliwiających egzystencje w zmienionych warunkach. Drewno reakcyjne spełnia więc doniosłą rolę w pierwszych etapach rozwoju populacji w zmienionych warunkach i umożliwia doczekanie osobników przystosowanych do tych zmienionych warunków.

Przykładem na to mogą być wierzby. Stare historycznie gatunki są monopodialne, współczesne, młode filogenetycznie zaś sympodialne. Do zmian tych według Szafera (1959, 1963) doszło na skutek wypiętrzeń górskich i ciągłego uszkadzania wierzchołków. Pierwszy okres niepomyślny dla wierzb monopodialnych mogły one przetrwać przez regenerację pędu przewodniego z gałązek bocznych dzięki drewnu reakcyjnemu, tak samo jak niszczone przez łosie sosny we współczesnych lasach mogą egzystować i wyrastać nawet na duże drzewa, pomimo kilkukrotnego niszczenia pędów szczytowych. Dzięki drewnu reakcyjnemu sosna górska może każdego roku podnosić przygięte śniegiem gałęzie boczne, a sosna zwyczajna na dalekiej północy w Laponii może utrzymać się na stanowiskach normalnie dla niej niedostępnych (Molski, 1962). Zdolność tworzenia drewna reakcyjnego jest więc nie tylko problemem morfogenetycznym (Sinnott, 1960), ale również mechanizmem anatomicznym w walce o byt umożliwiającym przetrwanie przeciągających się nowych niekorzystnych warunków aż do pojawienia się nowych spontanicznych i przypadkowych mutacji przystosowanych do nowego środowiska genetycznie, spełniając w ten sposób doniosłą rolę w filogenezie gatunków roślin drzewiastych.

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