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

II. Structure of growth rings in regenerating stems in relation to juvenile wood formation

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Abstract:

The corewood of pine is very prone to compression wood formation, this changing the whole pattern of the tree ring structure and the sizes of early and late wood. Compression wood always increases the formation of late wood at the expense of early wood. Tree rings with compression wood are generally wider than those without it, but there occur also tree rings without compression wood wider than those in which it is present, formed in the same year and in the same tree.

INTRODUCTION

The structure of tree rings in young stems is closely related to the organization of the zone of wood immediately surrounding the pith. This zone termed corewood or juvenile wood is interesting both from the point of view of wood formation biology as well as technology of wood, since juvenile wood has different properties than mature wood (Fielding, 1967).

Compression wood formation in trees changes the quality of wood (Côté, 1968; Krzysik, 1957), and it was of interest to study the influence of this wood on the structure of tree rings, and the possible participation of compression wood in young pine stems with damaged leaders. It was also of interest to establish whether it is possible to refer as it is usually done (Wardrop, 1965; Esau, 1965; White, 1965; Côté, 1968; Côté and Day, 1965; and others), compression wood formation to hyponasty and, thus, with the eccentricity of growth.

MATERIALS AND METHOD

The pine trees used for the study are described in detail in the first part of this publication (Molski, 1969) and so is the method. Only the main points of the method concerning the problems discussed in this part are described here. All measurements were done on cross sections of the stem in all annual height growths (referred to in brief as internodes lateron), a few centimetres above the branch whorls in order to avoid any deformation due to nodal swelling. Two damaged trees and a control pine were investigated. Cross sections of all the pieces of main stems of the studied 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 radial directions of the cardinal point under $\times 100$ a magnification. The tracheids were classified to early, late and compression wood in every cardinal direction. In this way the necessary data of tracheid layers was obtained for each of the tree ring quarters in all the investigated annual height growths.

The cell wall thickness was the main feature allowing differentiation of the tracheids into early and late wood. Proceeding from 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 7.1-micron thick or more were considered as late ones, and all 7-micron thick or less as early ones. Usually lignification of the cell walls was much higher in late wood than early, and was also helpful in classification.

In the first-year tree rings, or tree with compression wood, the border cells were measured and averages established; these averages were the guiding figures in the classification into late and early wood.

The distinction between normal and compression wood was not difficult since only tracheids with a specific rounded shape on the cross-section and large intercellular spaces were considered as compression wood. They are nearly always heavily lignified what helps in classification.

All the results were compiled in tables for each of the cardinal directions separately in order to visualize clearly the differences. The number of different cells in each of the tree rings formed in the consecutive years are presented in the form of diagrams and tables. The figures were analysed statistically and the results are presented in the form of tables. It is necessary to clearly understand the fact that all the figures and percentages refer to the particular places in the stems (a few centimetres above the branch whorls) where the cross sections were made, and not to the stem as a whole, there is, however, no question of the representation of the compression wood appearance in the stem. Nevertheless in the upper parts of the stem close to the branches usually

compression wood is more abundant than at the sites where the cross sections were made. It should be remembered also that the figures represent layers of different kinds of wood, and not the volume or area of the particular types of tissue.

RESULTS

Influence of compression wood on the size of the tree ring quarters

Comparison of the number of tracheid layers of the growth rings in all three pines showed that the damaged trees with compression wood grew slower than the control pine. This should be obvious, since the total number of needles of the damaged pines had been reduced, therefore, their assimilation ability was handicapped, and this in turn influenced the width of the tree rings. The control pine produced on the average 97 layers of tracheids in one tree ring — the minimum being 49 layers, and the maximum 164 (see Table 1). The damaged pines produced on the average less wood in one tree ring. Pine No. 1 produced about 10 per cent less, and pine No. 2 about 30 per cent less. It was interesting to see the differences between the widest and the narrowest growth ring quarters.

Table 1

Total number of tracheid layers in tree ring quarters of the investigated pines

	N	$n_{\min}$	$n_{\max}$	$\bar{x}$	$t_{\text{for } 5\%} \bar{s}_x$	$t_{\text{for } 1\%} \bar{s}_x$
Total number of tracheid layers in all the tree rings						
Control. pine	144	49	164	97.33	3.9	5.2
Pine No. 1	180	13	205	86.17	5.7	8.4
Pine No. 2	264	22	138	69.22	2.4	3.2
Total number of tracheid layers in tree rings without compression wood						
Control pine	143	49	153	96.86	3.9	5.2
Pine No. 1	136	13	148	74.4	5.5	7.3
Pine No. 2	224	22	122	68.20	2.3	3.0
Total number of tracheid layers in tree rings with compression wood						
Control pine	1	—	164	164.00	—	—
Pine No. 1	44	60	205	123.45	11.5	15.5
Pine No. 2	40	29	138	75.17	9.2	12.4

N — number of investigated quarters of tree rings

$n_{\min}$; $n_{\max}$ — minimum and maximum number of layers of tracheids in the investigated quarters of tree rings

$\bar{x}$ — average number of layers of tracheids

$t_{\text{for } 5\%} \bar{s}_x$ — confidence limits of the average number of tracheid layers, with a 5% probability of being exceeded in random sampling.

$t_{\text{for } 1\%} \bar{s}_x$ — confidence limits of the average number of tracheid layers, with a 1% probability of being exceeded in random sampling.

Fig. 1a

Fig. 1 Diagrams representing the structure of tree rings of the control pine; as they were formed in the consecutive years (from 1952 to 1959) in all height growths marked with Roman numerals from the highest one (I) produced in 1959 to the lowest one investigated (VIII) produced in 1952 in all four quarters; O — east and W — west in Fig. 1a, and S — south and N — north in Fig. 1b. The black area represents compression wood, the dotted one the early wood, and the hatched area represents late wood in the form of wood layers in the

Fig. 1b

particular quarter (see vertical axis). In the figures it is seen clearly that the juvenile wood (or corewood) is in the youngest five or six years; having much of early wood — almost twice as much as in the normal mature tree ring. It is seen also in Fig. 1a that compression wood appearance in a tree causes more layers of wood to be produced, and a high increase of late wood in this particular tree ring quarter (1959, 2nd internode, W — west quarter). It should be noted that if the tree is not damaged or bent, no compression wood is produced.

The differences in the control pine were not so wide, just 1 to 3, but in the damaged pine No. 1 they were 1 to 16, and in pine No. 2—1 to 6. It was clearly visible that compression wood formation connected with the regeneration of the damaged leader caused very uneven growth ring formation in various internodes and directions of the main stem. While pine No. 1 in 1958 had to regenerate the damaged leader from a lateral branch of the highest whorl and produced in the three highest internodes 150—180 wood layers (see Fig. 2, 1958), in the same year in the internode close to the ground it produced only about 20 layers of wood. Therefore, just three internodes below the place of maximum wood production the pine produced about 10 times less wood. The tree can translocate its nutrient substances from one place to another in the stem producing in the particular places more or less wood, in dependence on the whole gravitation equilibrium of the tree. Therefore, probably the flow of growth substances on the one hand, and the production of these growth substances throughout under the influence of the available light supplied to the crown on the other, which depends on the environment and branch relationships regulate tree growth and preserve its genetically established shape.

If the tree is not damaged severely and has sufficient assimilation ability, as was the case for pine No. 1, then the rate of regeneration is quite fast and the tree produces tree rings varying in size, very wide in some places and very narrow in others. But if the tree is damaged severely and regeneration is slow owing to the insufficient supply of food products for fast action, then the tree rings do not differ so greatly, and are generally much smaller. One might say that the tree with growth equilibrium upset acts by differences in growth ring formation in different internodes and on different sides of the tree; but if the damage increases in size, the tree loses this ability and may die completely, not being able to follow the other surrounding trees. Any damage, however, reduces the rate of growth, even if the tree still keeps pace in growth to some extent with the other trees around.

When considering separately the tree ring quarters with and without compression wood, it was seen clearly that, generally speaking, the tree ring quarters with compression wood were wider than those without compression wood (see Table 1), but the figures for different types of wood often varied greatly.

In the control pine the tree ring quarter with compression wood, which appeared only once, was very big having 164 layers of wood (Fig. 1), but the biggest tree ring quarter without compression wood had 153 layers of wood; so the tree ring quarter with compression wood was only about 7% larger (that is by 11 layers of wood) in comparison with the two biggest growth ring quarters. But as compared with the average size of

Table 2

Number of early, late and compression wood tracheid layers in tree ring quarters of the investigated pines

	N	% ¹	n _{min}	n _{max}	$\bar{x}$	% ²	t _{for 5%} $\bar{s}_x$	t _{for 1%} $\bar{s}_x$
Number of early wood tracheid layers in the pines								
Control pine	144	71	28	123	69.59	71.35	3.0	4.0
Pine No. 1	170	46	7	102	41.74	48.44	3.6	4.8
Pine No. 2	252	58	4	88	42.24	61.03	2.0	2.6
Number of late wood tracheid layers in the pines								
Control pine	133	29	15	47/110	27.86	28.83	1.0	1.4
Pine No. 1	173	38	4	117	34.44	39.96	1.7	2.3
Pine No. 2	259	34	3	61	23.82	34.41	1.2	1.7
Number of compression wood tracheid layers in the pines								
Control pine	1	—	28	—	28.00	17.07	—	—
Pine No. 1	44	16	3	158	53.82	43.59	11.2	15.7
Pine No. 2	40	8	2	138	38.00	50.55	11.8	15.2

N — number of investigated quarters of tree rings

%¹ — percentage of wood in relation to all the wood in the tree

n_{min}; n_{max} — minimum and maximum number of layers of tracheids in the investigated quarters of the tree ring

$\bar{x}$ — average number of layers of tracheids

%² — percentage of wood in relation to all the wood in the tree rings where this kind of wood occurred

t_{for 1%} $\bar{s}_x$ — confidence limits of the average number of tracheid layers with a 5% probability of being exceeded in random sampling

t_{for 5%} $\bar{s}_x$ — confidence limits of the average number of tracheid layers with a 1% probability of being exceeded in random sampling

growth ring quarters, the growth ring quarters with compression wood was about 60% larger than the average for this pine.

Compression wood appeared in 44 tree ring quarters in pine No. 1 accounting for 24% of all the investigated tree ring quarters of this tree; and in 40 tree ring quarters in pine No. 2, accounting for 15% of all the investigated tree ring quarters. Both pines had their leaders damaged the same number of times but pine No. 2 produced less compression wood than pine No. 1; this was due to the fact that pine No. 2 was more severely damaged and restored its leader slower and longer than pine No. 1 (compare Figs. 2 and 3). It was interesting to note that the frequency curve of the number of layers in tree ring quarters without compression wood for the three pines differed in location and shape. The curve for the control pine decreased proportionally from the mean (97 layers) and there was the same number of smaller and bigger tree ring quarters. Pine No. 1 had on the average 74 wood layers, but the highest number of tree ring quarters had 96% layers of wood. In pine No. 2 the mean was

Fig. 2b

and N — north in Fig. 2b. The black area represents compression wood, the dotted one early wood, and the hatched area represents late wood in the form of wood layers in the particular quarter (see vertical axis). In the damaged pine very often compression wood is produced in different seasons of year. Mostly when compression wood is produced, there is more late wood than usual. Sometimes production of compression wood in one internode causes a decrease of wood formation in other internodes (see 1958 and 1959). Formation of compression wood usually upsets the proportion of early and late wood in juvenile wood

Fig. 3a

Fig. 3. Diagrams representing the structure of tree rings of the damaged pine No. 2 as they were formed in the consecutive years (from 1949 to 1959) in all height growths marked with Roman numerals from the highest one (I) produced in 1959 to the lowest one investigated (XI) produced in 1949 in all four quarters: O — east and W — west in Fig. 3a, and S — south

Fig. 3b

and N — north in Fig. 3b. The black area represents compression wood, the dotted one early wood, and the hatched area represents late wood in the form of wood layers in the particular quarter (see vertical axis). Compression wood formation upsets the proportion of early and late wood in juvenile wood, but the usual proportion of early and late wood is restored with straight growth restoration.

Fig. 4. Frequency curves representing the number of tracheid layers in tree ring quarters without reaction wood compared in the investigated pines.

Continuous line — control pine dotted line — pine No. 1, and broken line with dots — pine No. 2. Fig. 4A represents the total numbers of tracheid layers in the tree ring quarters. The control pine has the same number of smaller and bigger tree ring quarters from the mean (which has 97 layers), that is the curve proportionally decreases from the mean. Pine No. 1 has on the average 74 wood layers, but the highest number of the tree ring quarters with 90 layers of wood. In pine No. 2 the mean is 68, but the highest number of tree ring quarters have 60 layers of wood; therefore the curve for the control pine is normal, for pine No. 1 it is shifted to the right (towards the bigger tree quarters) and for pine No. 2 it is shifted to the left (towards smaller tree ring quarters). Fig. 4B represents the number of early wood tracheid layers, and Fig. 4C the numbers of late wood tracheid layers in the tree ring quarters without compression wood. The distribution of tree ring quarters in all compared curves is similar. Number of tracheid layers in the tree ring quarters are indicated on the horizontal axis, and the number of quarters with particular tracheid layers on the perpendicular axis.

68 layers, but the highest number of tree ring quarters showed 60 layers of wood. The frequency curve for the control pine was normal, the curve for pine No. 1 was shifted in location to the right (towards the bigger tree ring quarters) and the curve for pine No. 2 was shifted to the left (towards smaller tree ring quarters) (see Fig. 4).

Table 3

Differences (right upper corner of the figure blocks) and confidence limits (left lower corner of the figure blocks) in terms of the number of tracheid layers in tree rings between the investigated pines, with 5% and 1% probability of being exceeded in random sampling

	Control pine	Pine No. 1	Pine No. 2
Total number of tracheid layers in all the tree rings			
Control pine	—	+11**	+28**
Pine No. 1	6.9	—	+17**
	9.0		
Pine No. 2	4.5	6.1	—
	5.8	8.0	
Total number of tracheid layers in tree rings without compression wood			
Control Pine	—	+23**	+29**
Pine No. 1	6.8	—	+6**
	9.0		
Pine No. 2	4.6	6.0	—
	6.0	7.0	
Total number of tracheid layers in tree rings with compression wood			
Control pine	—	—	—
Pine No. 1	—	—	+48**
Pine No.2	—	15	—
		20	

Difference denoted by one asterisk is significant ($t_{for 5\% \bar{S}_X$) and differences with two asterisk are highly significant ($t_{for 1\% \bar{S}_X}$).

Analysis of the frequency curves of tree ring quarters with compression wood showed the differences between the investigated pines, but they were similar to the curves for the tree ring quarters without compression wood described before. This conclusion is very important, showing that the appearance of compression wood does not change the general distribution of tree ring quarters in relation to the wood layers in the tree ring quarters; thus they have the same pattern regardless whether compression wood is present or not. However, there were differences in the total number of wood layers and pine No. 1 showed a wide difference in the tree ring size with and without compression wood; and pine No. 2 had both types of tree ring quarters of very similar size. It can be concluded that the differentiation of the tree ring proceeds in accordance with the same rules, independently of the fact whether there are compression wood cells or not.

The frequency distribution curves of tree ring sizes were normal in the control pine, having the average size in the centre of the curve, they were asymmetrical in pines with compression wood, but in the weak pine

No. 2 which regenerated slowly, the asymmetry was towards small tree ring sizes (that is, there were more small tree rings) and in the strong pine No. 1, which regenerated faster, bigger tree rings were more frequent (see Fig. 5).

The variations in size between tree ring quarters without compression wood were smallest in the control pine and widest in pine No. 1. In the control pine the ratio of the smallest tree ring quarter to the biggest one

Fig. 5. Frequency curves representing the number of tracheid layers in tree ring quarters with reaction wood are compared in the investigated pines.

Continuous line control pine; dotted line — pine No. 1, and broken line with dots — pine No. 2. Fig. 5A represents the total numbers of tracheid layers in the tree ring quarters with compression wood. The frequency distribution curves of the tree ring quarters are asymmetrical as in Fig. 4; that is the asymmetry is towards the small tree ring quarters in pine No. 2 and towards larger ones (than the average) in pine No. 1. Fig. 5B represents the numbers of compression tracheid layers in tree rings. The distribution is here completely different — the largest quantity of tree ring quarters have small number of compression tracheid layers, and quantity of quarters with higher numbers of tracheid layers decreases gradually. Number of tracheid layers in the tree ring quarters, as in Fig. 4, are indicated on the horizontal axis, and the number of quarters with particular tracheid layers on the perpendicular axis.

was 1 to 3, in pine No. 2 it was by 40—50% smaller than in pine No. 1. The mean of the tree ring quarters with compression wood in pine No. 1 was 123 layers of wood, which was about 50% bigger than the mean of all tree ring quarters, and about 70% bigger than the mean of the tree ring quarters without compression wood in this pine, but at the same time it should be noted that the average of the tree ring quarters with compression wood was only by about 20% smaller than the biggest tree ring quarter without compression wood in pine No. 1. And the biggest tree ring quarter with compression wood was only 30% larger than the biggest tree ring quarter without compression wood. The ratio between the smallest and the biggest tree ring quarter with compression wood was 1 to 3.5.

The average size of the tree ring quarter with compression wood in

pine No. 2 was only 10% larger than the average size of all the tree ring quarters (that is with and without compression wood). The same relationship occurred when tree ring quarters without compression wood were compared. The ratio between the biggest and the smallest tree ring quarter with compression wood was 1 to 4.5. And the biggest tree ring quarter with compression wood was 13% larger than the biggest tree ring quarter without compression wood; the average size of the tree ring quarters with compression wood was 70% smaller than the biggest tree ring quarter without compression wood.

It is interesting to compare the sizes of tree ring quarters with compression wood in the pines restoring the leader to the biggest tree ring quarter without compression wood in consecutive years:

Year of growth of the pines	Pine No. 1		Pine No. 2	
	tree ring quarters with compression wood		tree ring quarters with compression wood	
	bigger	smaller	bigger	smaller
	than the biggest tree ring quarter without compression wood		than the biggest tree ring quarter without compression wood	
1959	6	—	1	—
1958	3	7	1	—
1957	—	—	1	7
1956	1	1	2	9
1955	—	1	2	—
1954	6	5	3	5
1953	9	—	2	2
1952	4	—	—	2
1950	—	—	2	—
	29	15	15	25

It appears clearly that in pine No. 1, which was stronger, there were more larger tree ring quarters with compression wood than the biggest tree ring quarter without compression wood, and in the weaker pine No. 2 there were more smaller ones. It can be added that in pine No. 1 there were 44 tree ring quarters with compression wood; 36 of them were bigger than the average size of all the tree ring quarters, and 8 were smaller; in pine No. 2 there were 40 tree ring quarters with compression wood, 21 of them larger and 19 smaller than the average size of all the tree ring quarters in this tree.

Analysis of the thickness of tree ring quarters compared in the same year in different internodes of the tree showed an interesting trend in their formation. The highest one, just formed produced the thinnest ring, what is understandable taking into account that secondary growth starts later in the season, already after the formation of the internode has taken

Table 4

Differences (right upper corner of the figure blocks) and confidence limits (left lower corner of the figure blocks) in terms of the number of tracheid layers in tree rings between different types of tree rings in the investigated pines with 5% and 1% probability of being exceeded in random sampling

	all tree ring quarters	tree ring quarters with- out compression wood	tree ring quarters with compression wood
Pine No. 1			
all tree ring quarters	—	+12**	—37**
tree ring quarters without compression wood	8 10	—	—49**
tree ring quarters with compression wood	13 17	13 17	—
Pine No. 2			
all tree ring quarters	—	+1	—6
tree ring quarters without compression wood	3 5	—	—7
tree ring quarters with compression wood	15 20	15 20	—

Differences without asterisk denote the lack of any significance, and differences with two asteriks are highly significant (tfor 1% $s_{\bar{x}}$).

place. The ring growth sizes were larger in the second, third and sometimes fifth internode from the top in this particular year (see Figs. 1, 2 and 3). Lower down, the tree ring sizes (taking into account the number of the wood cell layers and not the width in millimetres) were smaller, what can be seen clearly in the control pine. In pines Nos. 1 and 2 the same can also be seen, but the appearance of compression wood interrupted this pattern to some extent. The differences between the tree ring quarters produced in the same year were sometimes as 1 to 2, but on opposite sides; such great differences can never be seen close to each other. Only when compression wood was produced on one side, the differences could be wide between the nearest sides reaching even double values.

Structure of the tree rings

Similarly to the differences in tree ring sizes, there were various numbers of wood cell layers of early, late and compression wood in tree rings. The control pine (see Fig. 1 and Tab. 1 and 2) had on the average 71 percent of early wood and 29 percent of late wood, that is approximately 2 to 1. A clear domination of early wood was seen almost in all tree ring quarters, except in one case where compression wood had

Table 5

Differences (right upper corner of the figure blocks) and confidence limits (left lower corner of the figure blocks) in terms of the number of tracheid layers in tree rings of different types of wood between the investigated pines, with 5% and 1% probability of being exceeded in random sampling

	Control pine	Pine No. 1	Pine No. 2
Number of early wood tracheid layers in the pines			
Control pine	—	+27**	+27**
Pine No. 1	4.7 6.2	—	0
Pine No. 2	3.7 4.8	4.1 5.4	—
Number of late wood tracheid layers in the pines			
Control pine	—	-6**	+4**
Pine No. 1	2.0 2.7	—	+10**
Pine No. 2	1.6 2.2	2.1 2.8	—
Number of reaction wood tracheid layers in the pines			
Control pine	—	—	—
Pine No. 1	—	—	+16
Pine No. 2	—	16 22	—

Differences without asterisk denote the lack of any significance, and differences with two asterisk are highly significant (for 1% $s_{\bar{x}}$).

appeared. In this tree ring quarter the relationship was opposite and there were only 31 layers of early wood, and 110 layers of late wood and finally 28 layers of compression wood. In this tree the Vith internodes in the North direction in 1959 produced 47 layers of late wood and 53 layers of early wood, the ratio of the smallest number of early wood to the highest number of late wood in one particular tree ring quarter without compression wood being 1 : 1. In the same internode in the West direction in 1956 there were 95 layers of early wood and 17 layers of late wood, the ratio of the highest number of early wood to the lowest number of late wood being 5 to 1.

Pine No. 1 had quite a different pattern of tree ring structure (see Fig. 2 and Tab. 1 and 2). Comparing the total number of early, late and compression wood layers in tree ring quarters we had; 46 percent of early wood, 38 percent of late wood and 16 percent of compression wood. Pine No. 1 in comparison with the control pine had 25 percent less of early wood and 9 percent more of late wood. The decrease of early wood can be to some extent explained by the fact of formation of compression wood

Table 6

Differences (right upper corner of the figure blocks and confidence limits (left lower corner of the figure blocks) in terms of the number of tracheid layers in tree rings between different types of wood in the investigated pines with 5% and 1% probability of being exceeded in random sampling

	early wood	late wood	compression wood
Control pine			
early wood	—	+41**	—
late wood	3.2 4.4	—	—
compression wood	—	—	—
Pine No. 1			
early wood	—	+8**	—12**
late wood	4 5	—	—20**
compression wood	12 16	12 16	—
Pine No. 2			
early wood	—	+18**	+4
late wood	2.3 3.0	—	—14*
compression wood	12 15	12 15	—

Difference without asterisk denotes the lack of any significance, difference with one asterisk is significant (for 5% $s_{\bar{x}}$), and differences with two asterisk are highly significant (for 1% $s_{\bar{x}}$).

in the site, where usually early wood should be expected (compression wood in this pine appeared 38 times, in a total of 44, in the place of early wood; see Fig. 2), and only 6 times instead of late wood. But a similar explanation is difficult in the case of a late wood increase by about 30 percent. If we assume the average size of tree rings to be 86 layers, 42 layers consisted of early wood and 34 of late wood. But if we take the average size of the tree rings with compression wood, then the respective values would be 123 and 54 layers (that is 44 percent) consisted of compression wood.

Pine No. 2 had a different tree ring structure than the control and pine No. 1. Pine No. 2 exhibited 58 percent of early wood, 34 percent of late wood and 8 percent of compression wood.

Thus, there was only 15 percent less of early wood than in the control pine, and only 5 percent more of late wood. These were much smaller differences than between the control pine and pine No. 1. Moreover, in

pine No. 2 all the 40 cases of compression wood appearances occurred in the place of early wood or between late and early wood.

In pine No. 2, the average tree ring quarter had 69 layers with 42 layers of early wood and 23 layers of late wood. In tree ring quarters with compression wood the average was 75 layers with 38 layers (51 percent) of compression wood.

Compression wood in pine No. 1 appeared in 44 tree ring quarters, that is 23 percent of them showed this type of wood and it accounted for 16 percent of the total wood in this pine. Taking into account only the tree ring quarters with compression wood, this type of wood occupied 44 percent of these tree rings. Compression wood in pine No. 2 appeared in 40 tree ring quarters, that is 15 percent of the tree ring quarters had this type of wood, and it accounted for 8 percent of all the wood in this tree, that is half of the total amount of the wood as compared with pine No. 1. Taking into account only the tree ring quarters with compression, this type of wood occupied 50 percent of these tree rings, that is more than in pine No. 1. Compression wood in pine No. 2 replaced half of the total wood as compared with pine No. 1, but in pine No. 2 it occupied more of the area of tree rings with compression wood, that is 50 percent in pine No. 2, and only 44 percent in pine No. 1. But this result (50 percent) may be due to the high amount of compression wood in the VIIth yearly longitudinal growth produced there from 1955 to 1959, that is in the course of 5 years.

It is worth noting the site of appearance of compression wood in tree ring quarters. All together there were 85 tree ring quarters with compression wood; only 4 of them were composed of compression wood entirely. In 44 cases compression wood appeared at the beginning of the growth seasons in place of the early wood which should have been there; in 6 cases compression wood appeared at the end of the growth seasons in place of the late wood; and in 30 cases it appeared between early and late wood. This shows clearly that compression wood can be produced at any time and at any place of the tree ring. In young trees compression wood was generally very seldom produced throughout the growth season.

DISCUSSION

The normal coniferous tree ring in the temperate zone can be divided into two parts: early and late wood. It would seem that early wood is better adapted by its dimensions and structure to the function of water conduction, and late wood is rather intended for mechanical functions; there are tree species which produce uniform tree rings composed of the same thinwalled tracheids without late wood in tropical environment or very often the late wood section is very narrow, having only very few layers

of thickwalled tracheids. But besides the conducting and mechanical (even rather static) function, wood plays also the role of movement (or replacement) of the already established stem and branches to a new position or of reinforcing them in the old positions in spite of the environment and forces acting against them, bending them down or sideways.

When the overall distribution of branches is changed owing to damages, or if wind, snow or any other force change the genetically established shape of the tree, compression wood formation restores the shape, moving the stem or branches towards the genetically established form of growth. The phenomenon is well known and has been several times described (Hartman, 1942; Sinnott, 1952; Wardrop, 1964, 1965; Molski, 1969, and others). If we extend this argumentation, it may be that in some of the tree rings, a new kind of wood — compression wood — is responsible for the active movement of the stem or branches, or their maintenance in proper position. In spite of all the difficulties with faultless segregation of tracheids into early and late wood, on the basis of cell wall thickness, size and shape of cells, their lignification, and finally, position in the tree ring, it is possible to establish the borders between the three types of wood.

Another problem is the interpretation of tree ring size. Very often by size of a tree ring is meant its width in centimetres or millimetres. But the number of cell layers might be also used as a measure, and then it represents rather the activity of the cambium and the manner of cell differentiation, than the thickness of the wood layer, however, both ways of approach represent the width of the tree ring and are somehow related to one another. However, by using the terms of different types of tracheid layers, it is possible to see the action of cambium and the biology of tree ring formation. Therefore, in this publication the „size” of tree rings is expressed in the number of tracheid layers and not in metric scale.

As shown by investigations the rate of tree ring formation is different in the particular seasons of the year (Kienholz, 1934; Wodzicki and Peda, 1963). For the climatic conditions in Poland, in spring the rate is higher, slower in summer and in autumn again higher, for example in *Abies pectinata* D. C. (Wodzicki and Peda, 1963) the increment is about 0.30 of a cell per day in spring, 0.11—0.15 cell per day in summer, and about 0.38 of the cell per day in autumn. This does not mean that the rate is similar in a regenerating damaged tree during formation of compression wood and irregular eccentric tree rings, as was in the case of pines No. 1 and No. 2. Wardrop and Dadswell (1948, 1950, 1952), Hartmann (1942) and others found that during compression wood formation the rate of cambium division and wood differentiation is higher, therefore the tree rings with compression wood are wider and eccentric.

Figs. 1, 2 and 3 illustrate the structure of growth rings formed in con-

secutive years in all the elongation growths. It is seen that compression wood formation might increase the overall number of wood layers, but in the same year there might be also more wood layers produced in places where compression wood did not appear at all. Therefore only statistical analysis can help in reading the right conclusions (see Tables 3, 4, 5 and 6). In spite of the general custom in biology to use confidence limits with a 5 percent probability of being exceeded in random sampling, because of quite uniform material (that is uniform size of tracheids) the level of 1 percent probability was also used, therefore, for differences exceeding slightly the confidence limits with a 5 percent probability, the terms „significant differences”, and for differences exceeding confidence limits with 1 percent probability „highly significant differences” are applied.

Table 3 shows that all differences in the total number of tracheid layers between trees are highly significant. The control pine has much bigger tree rings than the damaged pines: by 11 and 28 layers larger than in pines No. 1 and No. 2 respectively, but there is also a highly significant difference between the damaged pines, even wider than between the control pine and pine No. 1. The differences between the sizes of tree rings without compression wood are highly significant between the control pine and between the two damaged pines. It means that tree rings are indeed reduced by damage (being smaller by 23 and 29 layers in damaged pines) but the difference between the pines is very small, only by 6 cells. There is also a very wide difference in the sizes of tree rings with compression wood. In pine No. 1 they had 48 cells more (see Tables 1 and 3). There is no doubt that damages of the stem cause a decrease in tree ring sizes owing to the leaf loss and thus decreasing photosynthesis ability, but very narrow tree rings with compression wood and much wider ones without any compression wood may be found. It means that compression wood may be found in narrow tree rings as well as in wide ones.

Table 4 shows how the tree ring quarters differ in the same tree. In pine No. 1 there are highly significant differences between all the tree ring quarters, and tree ring quarters without compression wood as well as tree ring quarters with compression wood, but similar differences in pine No. 2 are not even significant, in other words are not proved statistically. It means that tree rings with compression wood might be so insignificantly larger that there is no statistical proof, whereas in others the differences might be highly significant. The results do not support the claims of necessity of connection of compression wood with eccentricity of growth, however, very often tree rings with compression wood are wider. Nevertheless, this problem requires further studies.

Table 5 shows the participation of the different kinds of wood in tree ring formation.

There are highly significant differences in the sizes of early wood layers in tree rings of the control and the damaged pines. The control

pine had about 75 percent of early wood, the damaged pine No. 1 — 46 percent and pine No. 2 — 58 percent. The control pine had 27 layers of early wood more than the damaged pines — that is almost six times more than the confidence limits. But there is no difference in the number of layers between both damaged pines (see Table 5); nevertheless there are differences in percentages of early wood participation in the trees (see Table 2) — in pine No. 1 there is about 46 percent of early wood, and in pine No. 2 — 58 percent. It may be said on the whole that compression wood formation reduces the amount of the early wood in the trees.

The differences in the number of late wood tracheid layers in the pines are highly significant. The control pine had less late wood (29 percent) and the damaged pines more (38 percent in pine No. 1, and 34 percent in pine No. 2) — see Tables 2 and 5. There were also wide differences in the amount of compression wood in the damaged pines, however, the differences were not proved statistically. Pine No. 1 had 16 percent of compression wood and pine No. 2 only 8 percent of the total number of the wood layers (see Table 2). But if only tree ring quarters with compression wood are taken into consideration, with exception of the tree ring quarters without such wood, then compression wood takes up about 50—44 percent of the tree rings on the average. The above situation in the changes in amounts of different kinds of wood, when compression wood is formed, is interesting — in both damaged pines there was less early wood and more late wood than in the control pine. It means that compression wood formation increases late wood formation, that is wood which is more suitable for mechanical functions, and both types of wood: compression wood and surplus of late wood are produced at the expense of early wood.

Table 6 shows the differences between different types of wood in the particular investigated tree; the differences are nearly always highly significant.

The juvenile wood of pine from the point of view of the tree ring structure is very prone to compression wood formation, this changing the whole balance of early and late wood, and hence the variability of wood structure from the point of view of wood technology. Formation of compression wood can be induced by damages of the leader by animals, snow, wind or other environmental factors, but it might be reduced through proper silviculture and forest protection.

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SUMMARY

The structure of tree rings in young stems is interesting from the point of view of the wood formation biology as well as the technology of wood, since the juvenile wood has different properties than mature wood; particularly interesting is the influence of compression wood in young trees on tree ring structure. The pines which were the subject of the investigation have already been described in the first paper (Molski, 1969). Tree rings were analysed with the use of a microscope on microtome sections. The figures in Tables (from 1 to 6) and diagrams (see Figs. 1 to 5) represent the counts of tracheid layers and not metric units or any other methods of measurements.

The damaged pines obviously grew slower than the control pine, the average tree ring of the control pine had 97 layers of tracheids, and the damaged pines: No. 1 — 86 layers, and No. 2 — 69 layers. The control pine had tree rings of 49 to 164 layers that is 1 to 3, the damaged pine No. 1 — from 13 to 205, that is 1 to 16, and the damaged pine No. 2 — from 22 to 138 layers, that is 1 to 6. The figures show that compression wood formation connected with the regeneration of the damaged leaders causes very uneven growth ring formation in the particular internodes and directions of the main stem.

Tree rings with compression wood are in general wider than those without compression wood (see Table 1). The control pine which was not damaged had the highest number of tree rings similar to the average one, and the same number of narrower and wider ones, but the damaged pine No. 1 which was stronger and damages regenerated faster had more wider tree rings (wider than the average) and less narrower ones, and pine No. 2 which was more severely damaged and regenerated slowly had more narrower tree rings than the average and less wider ones. But it has to be pointed that in both damaged pines there were many tree ring quarters without compression wood which were wider than the tree ring quarters with compression wood. Statistical analysis of the tree ring quarters with compression wood and without it, shows that in both pines the distribution curves were the same for both kinds of rings, in spite of differences in size (see Figs. 4 and 5). It means that the appearance of compression wood does not change the general distribution of tree ring quarters in relation to the wood layers in the rings, so they have the same pattern regardless whether there is compression wood or not.

There are also differences in the number of wood cell layers of early, late and compression wood in tree rings. The control pine had 71 percent of early wood and 29 percent of late wood (that is 69 layers of early wood and 28 layers of late wood (as the average in the tree). In pine No. 1 there was 46 percent of early wood (25 percent less than in the control pine), 38 percent of late wood (9 percent more than in the control pine), and 16 percent of compression wood. Compression wood appeared 38 times in the place of early wood and 6 times in the place of late wood. The pine No. 2 had 58 percent of early wood, 34 percent of late wood and 8 percent of compression wood, that is 13 percent of early wood less and 5 percent of late wood more than in the control pine. Compression wood appeared in pine No. 2 always in the place of early wood or between the early and late wood. Compression wood in pine No. 1 accounted for 16 percent of the total wood in this pine, and in pine No. 2 for 8 percent of the total wood. Compression wood can be produced at any time and any point of the tree ring, depending only on the actual growth situation. Nevertheless compression wood production always increases the formation of late wood, that is wood which is more suitable for mechanical functions, at the expense of the early wood, changing the pattern of the structure of tree rings.

The corewood of pine, from the viewpoint of the tree ring structure, is very prone to compression wood formation, which changes the whole pattern of tree ring structure and proportions of early and late wood. The changes in tree ring structure may cause differences in the technological properties of corewood. Formation of compression wood is induced by damages of the leader by environmental factors, such as animals, wind, snow, etc., but they might be reduced by proper forest protection and silviculture.

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*Rola drewna reakcyjnego w regeneracji pędu głównego
u sosny zwyczajnej (Pinus silvestris L.) zgryzionej przez łosie (Alces alces).*

*II. Struktura przyrostów rocznych w regenerujących pęd przewodni sosnach
w świetle tworzenia drewna przyrzeniowego*

Streszczenie

Budowy słoików rocznych w młodych pniach sosny jest interesująca zarówno z punktu widzenia biologii tworzenia drewna, jak również technologii drewna, gdyż tworzące się drewno młodociane (lub przyrzeniowe) tuż przy rdzeniu ma inne własności techniczne niż drewno starego pnia sosny. Szczególnie interesujący jest wpływ pojawiania się drewna kompresyjnego na strukturę słoików rocznych. Sosny będące przedmiotem badań zostały już opisane przez autora w poprzedniej publikacji (Molski, 1969) tej samej serii. Struktura słoików rocznych badana była pod mikroskopem na skrawkach mikrotomowych i wyniki pomiarów i obliczeń przedstawiono w formie tabel (od 1 do 6) oraz formie wykresów (od 1 do 5). Należy podkreślić, że liczby przedstawiają liczbę warstw komórek drewna w słoikach rocznych w badanych kierunkach, a nie wielkości stref poszczególnych rodzajów drewna wyrażanych mikronami, czy też milimetrami.

Sosny, które były uszkodzone przez łosie, rosły wolniej, co oczywiście nie powinno być niespodzianką. O ile średnia ilość drewna w słoju rocznym w drewnie kontrolnym wynosiła 97 warstw cewek, to w sośnie No. 1 wynosiła ona 86 warstw, a w sośnie No. 2 — 69 warstw. O ile w sośnie kontrolnej wielkości słoików rocznych wahała się od 49 do 164 warstw, to jest 1 do 3, a w sośnie Nr 2 od 22 do 138 warstw, a więc 1 do 6. Ryciny obrazujące pojawienie się drewna reakcyjnego i strukturę słoików rocznych (patrz 1 do 3) wykazują, że regeneracja zniszczonego pędu głównego z gałęzi bocznych powoduje tworzenie się bardzo nierównych słoików rocznych, zarówno w poszczególnych przyrostach na wysokość, jak w różnych kierunkach od rdzenia.

Ogólnie stwierdzić można, że słoje roczne w miejscach, gdzie tworzy się drewno reakcyjne, są szersze od słoików bez drewna reakcyjnego (patrz tabela 1). Sosna kontrolna, która nie była uszkodzona, miała normalny symetryczny rozkład wielkości słoików rocznych, to jest miała taką samą ilość słoików większych i mniejszych od średniej wielkości. Lecz sosna Nr 1, która była silniejsza pod względem wzrostu i szybciej regenerowała zniszczony pęd szczytowy, miała rozkład asymetryczny z większą ilością słoików większych niż średnia arytmetyczna, zaś sosna Nr 2, która była uszkodzona silniej i wolniej regenerowała pęd szczytowy, miała również rozkład asymetryczny, mając jednak więcej mniejszych słoików od średniej arytmetycznej, a więc przesunięty w lewo. Należy jednak podkreślić, że w obu sosnach regenerujących pęd przewodni z gałęzi bocznych było wiele słoików rocznych bez drewna reakcyjnego, które miały więcej warstw cewek niż słoje z drewnem kompresyjnym. Przeprowadzona analiza statystyczna słoików rocznych z drewnem kompresyjnym i bez takiego drewna w każdym z poszczególnych drzew wykazała, że rozkład tych słoików był bardzo podobny dla obu typów słoików rocznych w danym drzewie bez względu na to, czy było tam drewno reakcyjne, czy też nie, a więc jego pojawianie się nie ma zasadniczego wpływu na rozkład wielkości słoików pod względem ilości warstw cewek w przyrostach rocznych.

Budowa wewnętrzna słoików rocznych pod względem ilości warstw cewek drewna wczesnego, późnego i reakcyjnego kształtowała się bardzo różnie w poszczególnych drzewach. Sosna kontrolna miała 71 procent drewna wczesnego i 29 procent drewna późnego (a więc 69 warstw cewek drewna wczesnego i 28 warstw drewna późnego). W sośnie Nr 1 było 46 procent drewna wczesnego (25 procent mniej niż

w sośnie kontrolnej), 38 procent drewna późnego (9 procent więcej niż w sośnie kontrolnej) oraz 16 procent drewna kompresyjnego. Drewno reakcyjne pojawiło się 38 razy w miejscu drewna wczesnego oraz 6 razy w miejscu drewna późnego. W sośnie Nr 2 było 58 procent drewna wczesnego, 24 procent drewna późnego oraz 8 procent drewna reakcyjnego, a więc o 13 procent mniej drewna wczesnego i 5 procent więcej drewna późnego niż w sośnie kontrolnej. W sośnie Nr 2 drewno reakcyjne pojawiała się zawsze w miejscu drewna wczesnego lub między drewnem wczesnym i późnym. A więc drewno reakcyjne w sośnie Nr 1 zajmowało 16 procent warstw, a w sośnie Nr 2 — 8 procent warstw całkowitej ilości drewna. Było ono produkowane w bardzo różnych miejscach w przyroście rocznym w zależności od aktualnej sytuacji wzrostu danego drzewa. Jednakże zawsze pojawianie się drewna reakcyjnego powodowało zwiększenie się produkcji drewna późnego, a więc tego, które jest bardziej dostosowane do pełnienia funkcji mechanicznych, zmniejszając jednocześnie ilość drewna wczesnego, co powoduje zmianę w strukturze słoików rocznych.

Ogólnie stwierdzić można, że drewno młodociane, czy też przyrzeniowe może zawierać drewno kompresyjne w bardzo różnych, zazwyczaj nieznacznych, ilościach, co powoduje zmianę struktury przyrostów rocznych — zwiększa się wtedy ilość drewna późnego i zmniejsza ilość drewna wczesnego. Zmiany w strukturze słoików rocznych muszą pociągać za sobą zmianę we właściwościach technologicznych drewna przyrzeniowego. Pojawianie się drewna reakcyjnego powodowane jest jednak uszkodzeniami pędu głównego przez zwierzęta, wiatr czy śnieg i może być do pewnego stopnia ograniczone poprzez właściwe zabiegi hodowlane i ochronę lasu.

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