Changes in angle width between the main axis and a branch in young pines (*Pinus silvestris* L.)

Zmiany w wielkości kąta między osią główną a gałęzią w młodych sosnach
(*Pinus silvestris* L.)

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There are rather scarce data concerning branch angle formation in young pines. Baranetzky (1901) have observed that very young pine shoots, after being emerged from the bud were growing straight upward and showed strong geotropism. After few weeks they began to deviate gradually from the original vertical position due to their increasing weight — as he claimed. Münch (1938) have shown that besides geotropism and the weight of a branch also the third factor — epinasty plays an important role in branch angle formation. Epinasty counteracted geotropism and contributed to the downward movement of a branch. According to Münch epinasty in branches is induced due to a hormonal message transported from the leader and superjacent branches.

Another factor which may take part in the branch angle formation was suggested by Jankiewicz (1964). Shoot deviation in young apple trees may be caused by mechanical pressure generated by tissues situated in the crotch.

It is a well known fact that compression wood is formed in conifers on the lower side of a branch (Westing 1965). Compression wood counteracts in this case the downward curvature caused by branch weight. On the other hand Hejnowicz (personal communication — 1965) observed compression wood on the upper side in the basal part of one-year-old pine branches.

Shoot growth in pine as in many woody plants of Temperate Zone is a two year process (Kozłowski 1963). Winter buds contain unextended internodes with the primordia for all needles. During the subsequent season only extension of the already formed internodes takes place (Sacher 1954).

The author believes that detailed observations of branch angle formation should precede the attempt of explaining the mechanism of this

phenomenon. This paper presents the results of observations carried out during 1—3 years on branch angle formation in intact and decapitated trees. It seemed also necessary to collect some data on shoot and needle growth.

MATERIAL AND METHODS

The experiments were always started with 6-year-old trees of *Pinus silvestris* L. of the height of about 180—200 cm. The trees were growing in two plantations in the vicinity of Skierniewice in Central Poland. Plantation A was located on loose sand and plantation B on medium sand

Fig. 1. The branches were not straight so their position in relation to vertical was defined by four angles:

c_1 — the basal crotch angle measured 0.5 — 1 cm from the main axis, c_2 — the angle between the vertical and the tangent to the branch in 1/3 of the branch length, c_3 — as in c_2 but in 2/3 of the branch length, c_4 — about 3 cm below the first year apex. In very short branches the angles c_2 and c_3 were omitted, or instead of them one angle c_x in the middle of the branch was measured.

with appreciable amount of organic matter. Only the trees which were not shaded or lightly shaded by the neighbours were chosen for the experiment.

The trees were subjected to different treatments as described later and were measured several times during the year. In the plantation A the same branches and their angles were measured throughout 3 seasons (April 1963 — October 1965). In the plantation B one-, two-, and three-year-old branches and their vertical angles were measured during one season 1965.

Since the branches were not straight the angle with the vertical was measured in two to four places as indicated in fig. 1. During the second and third year of branch growth only that part of a branch which was formed during the first year was taken into account and the angles were

measured in the same points as during the first year (Fig. 1). The accuracy of angle measurements was about $\pm 6^\circ$. In each whorl the angles and the lengths of all branches were measured.

The presence of compression wood was checked with the naked eye. Only in some dubious cases microscope with polarized light was used.

The buds in the apical whorl of the main axis were never of equal size (Fig. 2) so they could not be considered jointly. The 4—6 buds which were adjacent to the central bud were the strongest. They were named "upper buds" in this paper, and the shoots sprouting from them were

Fig. 2

Fig. 3

Fig. 2. The apical whorl of buds in pine during winter: *cn* — central bud, *up* — „upper buds”, *lw* — „lower buds”, *in* — interfascicular bud.

Fig. 3. „Decapitated and partly disbudded tree”. All buds except two „upper” ones were removed.

named "upper shoots" in the whorl. Few mm below them were situated several smaller buds which were called "lower buds" (Szymański and Szczerbiński 1955). They were adjacent to the "upper buds" but not to the central bud. Below the „lower buds” there were found sometimes interfascicular buds (Debazac, 1962). They were always very small and were situated between the pair of living needles.

The three treatments used in this work were as follows: 1. control, intact trees, 2. "decapitated trees" in which the central bud in the apical whorl was removed just before the growth started, 3. "decapitated and partly disbudded trees" in which the central bud and the buds of the apical whorl except two were removed (Fig. 3). Each treatment was repeated at least in two years.

The experimental trees were grouped in 6—14 randomized blocks one tree being a plot. The results were in most cases analyzed with the analysis of variance using "t" test for significance.

RESULTS

1. *Growth of the shoots in the uppermost whorl.* The period of extension growth was about 2—3 weeks longer in 1965 than in 1963 and 1964, due to very cold spring and cold early summer 1965. Shoot growth was about twice as vigorous in the plantation B than in A (Fig. 4 and 5).

The central shoot in the whorl have finished its growth later than the lateral shoots. There were considerable differences in the length of the lateral shoots: the lower a bud was situated in the whorl the less vigorous shoot have sprouted from it.

Decapitation did not stimulate significantly the longitudinal growth of current year branches in the experiment of 1963. In the experiment

Fig. 4

Fig. 5

Figs. 4. and 5. Shoot and needle growth in the apical whorl. Fig. 4. — The trees in the plantation A (in 1963), Fig. 5. The trees in the plantation B (in 1965).

Solid lines — the shoots of control trees: 1 — the leader, 2 — the „upper” shoots, 3 — the „lower” shoots, 4 — the shoots which grew out of the interfascicular buds. Dashed line: 5 — the „upper” shoots of decapitated trees. Dashed and dotted line: 6 — the shoots of „decapitated and partly disbudded trees”. Dotted lines — the needles of control trees in fig. 5, a — on the leader, b — on the „upper” branches, c — on the „lower” branches, d — on the branches which grew out of the interfascicular buds (date for August based on very scarce material).

of 1964 the branches of decapitated trees were longer than those of controls, but the results were not analysed statistically. In „decapitated and partly disbudded trees” the two remaining „upper shoots” were much stronger than analogical shoots of control trees (Fig. 5). As it was found earlier by Rutter (1957), the growth of the needles lasted considerably longer than the growth of shoots. The „lower shoots” in the apical whorl possessed shorter needles than those of the central and „upper shoots”. Especially short were the needles of the branches which have grown from interfascicular buds.

2. *Branch angle formation during the first year of branch growth.* The buds composing the apical whorl of control trees formed not uniform angles with the vertical: the "upper" buds about 18° , the "lower" ones about 32° , and the interfascicular ones about 80° .

As the branches began to grow, they were initially strongly geotropic and were growing vertically upwards except interfascicular branches (Fig. 6). After about two weeks the basal part of the branches began to deviate from the main axis, but their apical part remained vertical (Fig. 7, and 8 a, b). Only during the end of May or beginning of June the

Fig. 6

Fig. 7

Fig. 6. During the first two weeks of growth the branches showed strong geotropism.

Fig. 7. On the beginning of June the bases of the branches continued to deviate from the main axis whereas the apical part remained almost vertical.

apical part of the branches began to deviate gradually from vertical and continued this process to the beginning or middle of August. It has to be pointed out that branch angles continued to enlarge long after the shoots stopped to grow. The angles of the „upper” branches in the whorl were always much narrower than those of "lower" branches. The process of branch angle formation was similar in both plantations, but the branches of trees on more fertile soil (plantation B) acquired finally more upright position (Fig. 8 and 9). Very weak branches which grew out of the inter-

fascicular buds possessed from the beginning large basal angles with the main axis, their apical parts, however, were changing the position from upright in middle June to about 45° in August (Fig. 9c).

Fig. 8

Fig. 9

Figs 8 and 9. The changes in branch position during the first year of branch growth. Fig. 8. — the control trees in plantation A, 1963.

Fig. 9. — the control trees in plantation B, 1965.

a — the „upper” shoots, b — the „lower” shoots, c — the shoots which grew out of the interfascicular buds.

For other details see Figs 1 and 2.

Decapitation exerted significant influence on branch angle — the branches acquired more upright position than in control trees (Fig. 10). The process of re-establishment of the new leader was commenced during the second year.

In decapitated and partly disbudded trees the branches were almost vertical and only their bases were slightly deviated from vertical — usually less than 20° (Fig. 10).

Compression wood was present in all even very young branches which were investigated. Dark red compression wood was always situated on

the upper side of a branch in its basal part adjacent to the main axis (Fig. 11a). Light colored compression wood occurred also in many cases on the lower side of the branches especially in those very weak. Unexpectedly

Fig. 10. The angles of „upper” branches in control trees (solid lines), in decapitated trees (dashed lines), and in „decapitated and partly disbudded trees” (dotted lines). The initial position of the branches on May 22-nd was the same for all trees. The differences between the treatments were significant for the last date (1.IX.).

Fig. 11. Compression wood (dotted) in the branches and in the main stem. a — the „upper” branch of the control tree, b — the branch of „decapitated nad partly disbudded tree”.

tedly compression wood of dark red color was observed also in the main axis adjacent to the upper side of branch base. In the branches of decapitated and partly disbudded trees compression wood was present in negligible amount on the upper side of a branch but was very well visible on the lower side (Fig. 11b).

3. *The changes in branch position during the second year of branch growth.* During the spring the position of the branches in relation to

vertical changed very little up to the second half of May (Fig. 12a, b). Afterwards the branches moved gradually downward. This process ended in 1964 before August 31-st and in 1965 one or two weeks later.

Fig. 12. The changes in branch position during the second year of branch growth. Control trees in plantation A.

a — the „upper” branches, b — the „lower” branches. In „lower” branches the angle c_x was measured in the middle of a branch. Dashed line: the last position during the first year of growth (1963) was given for comparison. Dotted line: the last position during 1964. The differences for the dates May 25-th and August 31-st highly significant for the angles c_3 and c_4 .

Fig. 13. The changes in branch position during the second year of branch growth in decapitated trees. Plantation A, 1964. The branch which tended to replace the leader — solid lines, the other branches — dashed lines. The method of presenting the results as in fig. 1.

The period of most considerable changes in branch position coincided with most intensive needle growth (Fig. 5) and with marked increase of the weight of new shoots formed at the branch top (Tab. 1). Therefore it seems probable that the weight of new whorl of shoots formed at the apex of a branch was the main cause of its downward movement.

In decapitated trees majority of branches moved downward during their second season of growth (Fig. 13). In each whorl, however, one branch took the leadership and was moving in opposite direction — upwards.

Table 1

Average weight of the whorl of new shoots formed at the top of „upper” branches. The second year of branch growth
Plantation A, 1964

Dates	April 7-th	May 23-rd	June 25-th	August 31-st
Weight* of new shoots in grams	2.0	5.8	26.4	39.9

* From each of 12 trees one „upper” branch was taken at random

4. *The changes in branch position during the third year of branch growth.* In control trees the snow caused consistant but not very large downward displacement of the branches (Fig. 14, compare the curves for December 22-nd before snow-fall and for January 27-th after snow-fall). After the snow melted away (Fig. 14 — the curve for April 7-th), the branches have returned to their original position. During the subse-

Fig. 14. The changes in branch position during the third year of branch growth. The control trees, plantation A.

a — the „upper” branches, b — the „lower” branches. Dashed line — the last position during the second year of growth (1964) was given for comparison. The difference in the angle α for the dates: April 7-th and October 16-th were significant for „upper” branches.

quent period, up to the autumn the positions of the branches changed very little and in 1965 non significantly. It has to be mentioned that the growth of new shoots on the top of these branches was excellent during the third year in both plantations.

Those results would suggest that the snow cover had small and fully reversible effect on branch position in control trees. However, in quiet sites protected from wind the branches of some trees which were not included into the experiment were heavy loaded with snow and remined bent down even after snow thaw.

In decapitated trees the process of leader re-establishment was markedly accelerated by the snow. In each whorl the branch which tended to replace the leader suffered very little from snow because wind shook

Fig. 15. Decapitated tree in snow. The branch which have replaced the leader is upwight and its ramifications are not covered with snow (due to wind). The other branches are strongly bent down by the snow.

it off. The other branches were bent strongly downward by the load of snow (Fig. 15). After snow thaw those branches did not return to the previous position (Fig. 16, compare the differences between the curves

Fig. 16. The changes in branches position in decapitated trees during the third year of branch growth. Plantation A.

The branches which took the leadership are marked with solid lines, the other branches with dashed lines. With dashed and dotted lines was marked the last position of the branches during the second (1964) year of growth. On January 27-th, 1965 the branches were covered with snow. For other details see fig. 1.

for December 22 — before snow-fall and for April 7-th after snow thaw). The changes which occurred in branch position during the summer

were minute, only the branches which replaced the leader acquired more and more vertical position.

DISCUSSION

Branetzky (1901) and Münch (1938) gave only short general description of the branch angle formation in pine presenting only scarce quantitative data. The results presented in this paper show that during the first year of branch growth mainly the basal part of a branch enlarged its angle with the main axis. The more distal parts compensated initially that process by negative geotropic bending. Later in the season the apical part of a branch followed rather passively the gradual downward movement of branch base.

The factors responsible for branch angle enlargement during the first year of branch growth are not clear. Branch weight does not seem to play an important role in this process, since the strongest and heaviest branches form the narrowest angles. This fact was also noted by other authors (Eklund and Huss 1946).

The influence of the leader contributes to the changes in the branch position inducing epinasty in the branches (Münch 1938). We may suppose that the decline of geotropic reaction in the apical parts of the branches during the second half of the season is the result of increasing epinastic effect. According to Lyon (1963) epinasty results from the accumulation of auxin on the upper side of a branch. This may explain the presence of compression wood on the upper side of the youngest branches. Nečesany (1958) gave evidence that auxin stimulates compression wood formation in conifers.

Compression wood in the basal part of the youngest branches may be also the result of mechanical pressure between the tissues of a branch and those of the main axis since the diameters of a branch and the main axis increase markedly during spring and summer. Presence of compression wood both in the branch and in adjacent part of the main axis supports this supposition. Further experiments will throw probably more light on those phenomena.

It was characteristic that during the second year of branch growth the basal branch angles (c_1) did not change. Only the middle and distal parts of a branch moved to more horizontal position. The results of this work suggest that the increasing weight of the branches is the main factor causing that downward movement.

It was shown that the load of snow cover may cause irreversible changes in branch position. It is possible that this factor may contribute

to gradual increase of branch angle during the life of a branch in larch and spruce (Saarnijoki 1955; Morby and Wareing 1963).

SUMMARY

Branch angle formation was investigated in 6—8 year old pines in Central Poland. The observations were carried on during one year or in another experiment during 3 years period on the same branches. Besides of branch angle shoot growth and needle growth was measured.

Part of experimental trees were decapitated by removing the central bud, part were decapitated and partly deprived of buds in the apical whorl, and part were left intact as controls. The experiment was set up in 6—14 randomized blocks and the results were analysed statistically.

During the first year of branch growth the basal part of a branch deviated markedly from the main axis. The apical part was initially strongly geotropic, later in the season its geotropism diminished and it deviated from the vertical similarly as the basal part.

The branches of decapitated and partly disbudded trees were straight upward.

Dark red compression wood was found in the basal part of all one-year-old branches on their upper side. In decapitated and partly disbudded trees compression wood was found in minute amount on the upper side of the base of uppermost branches but was very distinct on their lower side.

During the second year of growth the basal part of a branch did not change its angle with the main axis, only the middle and apical part moved consistently downward. It was suggested that this downward movement was due to increasing weight of apical whorl of the branch.

During the third season of growth changes in branch position were very little and in most cases non significant.

Leader re-establishment was observed in decapitated trees during the second season of branch growth.

The weight of snow cover caused irreversible changes in branch position in some trees.

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Research

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STRESZCZENIE

Badano formowanie się kątów między główną osią a gałęziami w 6—8-letnich drzewkach sosny rosnących w okolicach Skierniewic. Obserwacje prowadzono przez jeden rok, a w jednym z doświadczeń te same gałęzie były obserwowane

przez 3 kolejne lata. Poza pomiarami kątów gałęzi przeprowadzono również obserwacje nad ich wzrostem i nad wzrostem igieł.

Drzewka doświadczalne traktowano w trojaki sposób: część z nich dekapitowano przez usunięcie centralnego pąka z najwyższego okółka, część dekapitowano i pozbawiano większości pąków w najwyższym okółku; drzewka kontrolne pozostawiano bez zabiegów. Doświadczenia zakładano w 6—14 blokach losowych, a wyniki były analizowane statystycznie.

W czasie pierwszego roku wzrostu gałązki jej podstawowa część odchyłała się silnie od głównej osi. Środkowa i wierzchołkowa część początkowo wykazywały silny geotropizm. W późniejszym okresie geotropizm tych części zmniejszał się i następowało ich odchylenie się zgodnie ze zmianami położenia podstawowej części gałązki.

Gałązki drzewek dekapitowanych miały mniejsze kąty z osią główną niż gałązki drzewek kontrolnych. Gałązki drzewek dekapitowanych i częściowo pozbawionych pączków rosły prawie pionowo.

Silnie zabarwione drewno reakcyjne było wytwarzane u drzewek kontrolnych w podstawowej części gałązki po jej górnej stronie, w pierwszym roku wzrostu. W dekapitowanych drzewkach częściowo pozbawionych pąków w najwyższym okółku drewno kompresyjne wytworzyło się po górnej stronie gałązek w znikomej ilości, za to było widoczne po dolnej ich stronie w podstawowej części gałązek.

W drugim roku wzrostu gałązki kąt między jej podstawą a osią główną pozostawał nie zmieniony. Jedynie część środkowa i wierzchołkowa przyjęła bardziej poziome położenie, przypuszczalnie dzięki wzrostowi ciężaru wierzchołkowego okółka gałęzi.

W trzecim roku wzrostu gałązki zmiany w jej położeniu w czasie wiosny i lata były znikome i w większości wypadków nieistotne. W czasie zimy jednak ciężar śniegu wywoływał nieodwracalne zmiany w położeniu gałązek szeregu drzewek.

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