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Phenomenon of Trunk Twist during the Growth of Woody Plants (Using the Example of *Pinus sylvestris* L. and *Picea obovata* Ldb.)

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Abstract—The phenomenon of trunk twisting in *Pinus sylvestris* L. and *Picea obovata* Ldb. during a vegetation period has been revealed and described by direct measurements. The frequency of this phenomenon, magnitude, and direction of twists and their 2-year dynamics have been studied on five sample plots located in different forest-growing conditions. The average rotation angle is 0.2°–0.5°, while its maximum values reach 1.3°–1.7°. These characteristics depend on forest type and weather conditions. Next year more, than half of the trees change their twisting direction to the opposite one, whereas 8–19% of pine trees keep it unchanged. Based on an analysis of our results and the data of other authors, a qualitative model of morphogenetic processes has been proposed to explain the mechanism of this phenomenon.

Keywords: Pinus sylvestris, *Picea obovata*, radial growth, morphogenesis of woody plants, timber spiral grain, trunk twisting

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INTRODUCTION

Crown transformation and the development of special trunk forms (bending or twisting) during tree growth are well-known phenomena. Changes in the orientation of tree trunks are considered to be connected with various tropisms (gravitropism, phototropism, chemotropism, etc.). The basic mechanisms determining these adaptation reactions at the cell and tissue level are connected with changes in the gradient of phytohormones, assimilates, ions, and endogenous electric fields (Polevoi, 1989; Medvedev, 1996; Alekhina et al., 2007). Nevertheless, to date no information about the possibility of changes in the growth-related spatial orientation of a trunk (twisting) is available, though wood experts and specialists working in the field of wood processing are often confronted with compression wood, spiral grain, and various trunk defects (Miller and Vakin, 1938; Vakin et al., 1969; Kofman, 1986), as well as mechanical stresses, the explanation of which occurrence is limited by the characterization of anatomical features.

According to some data, trees are able to redirect (bend) their trunks and branches (Ormarsson et al., 2010). Continuous changes in the illumination level and irregular loads of trunk tissues caused by a growing crown result in the formation of reactive wood along the whole trunk or one of its parts (Knigge, 1958; Richter, 2006a). Modeling mechanical properties of tissues from different trunk parts shows that compressive wood is formed in response to a negative gravitropism (Coutand et al., 2007). Among the main factors determining changes in the trunk or branch forms, one should note mechanical tensions occurring in tissues and organs. For example, tensions influencing the formation of a new annual increment are stipulated by wood-fiber differentiation processes (Ormarsson et al., 2010; Mikshina et al., 2013), which are accompanied by the appearance of elastic and viscoelastic forces able to cause trunk tissues to twist in a spiral grain timber. The twisting phenomenon is determined by many ecological factors (wind, illumination intensity, soil conditions, exposition, etc.), but no unambiguous cause-and-effect relation has been established (Burger, 1941; Houkal, 1982; Harris, 1989). In some cases, the formation of compression wood as a response to ecological impacts does not occur, and a tangential plane of spiral grain is formed (Raunecker, 1957). The presence of compression wood is always connected with a trunk bending, whereas spiral grain is associated with twisting, which occurs during the formation of spiral structures by conductive fibers. The number of spiral structures in a trunk varies from a complete absence to two or more spirals (Harris, 1989).

The tendency of spiral growth accompanied by the formation of left- and right-handed forms is typical for most woody species at early ontogenetic stages and may keep or even be enhanced by some external factors (Khokhrin, 1977; Harris, 1989; Richter, 2015). A high prevalence of this phenomenon is confirmed by statistical studies (Durst, 1955), according to which

78% of pine trees in the forests of Western Siberia and 88% of pine and larch trees of Ural mountain forests are characterized by a spiral grain formation. Left-handed forms are typical for young coniferous trees, while fibers of older trees have the opposite rotation angle (Harris, 1989).

According to the earlier proposed hypothesis, trees with spiral grain have some advantages concerning the transpiration flow distribution around the trunk periphery (Vité, 1958, 1967). In addition, such structures provide better bending and breaking strength (Richter, 2008b). There are probably several reasons for spiral grain, among which the role of anticlinal division of cambium and cell growth direction is especially emphasized (Bannan, 1964b). In addition, this phenomenon may be determined by processes such as cell death and the turn of cambial domains, which serve as controllers able to break the twisting development. This study also assumes that excess twisting appears in the case of a failure of cambial control structures and that cambial domains (this term was introduced by Hejnowicz (1964) to describe cambial zones with unidirectional anticlinal divisions) are able to periodically change their direction. The formation of anticlinal cells is accompanied by their extension (Bannan 1963a, 1963b, 1964a, 1964b, 1966; Hejnowicz, 1961, 1964; Krawczyszyn and Romberger, 1980), and the domain shift makes about 0.7 mm per 1 mm of a xylem increase. The average angle of rotation of a spiral grain from a horizontal line is about 35° (Richter, 2015), while in a Scotch pine it may reach 90° (Hartig, 1895).

An analysis of factors and mechanisms determining the form of trunks and crowns during tree growth made it possible to reveal some anatomy-determined mechanical principles of spatial transformation (Richter, 2015). These principles include tension/compression of the external part of a trunk; a change in fiber orientation during diameter growth, which may cause the formation of spiral structures; and segmentation of trunk parts, which determines the relatively independent growth of concentrically connected twistings accompanied by the correction of a trunk axe direction. The first principle explains the appearance of compression wood and vertical bends, while the second and thirds ones determine trunk twisting and spiral grain formation.

The afore-cited information allows one to suppose that spiral grain formation in the zone of a cambial complex during the growth of conifers should result in a change in a spatial orientation of external timber layers (xylem). In connection with this, the purpose of this study was to describe and investigate trunk twisting phenomenon in Scotch pine (*Pinus sylvestris* L.) and Siberian spruce (*Picea obovata* Ldb.) trees growing in different habitats, including an analysis of the frequency of this phenomenon in a standing timber and the dynamics of the twisting magnitude and directions measured for a 2-year period.

MATERIALS AND METHODS

The trunk twisting phenomenon in Scotch pine trees was studied using five sample plots (SPs) located in different afforestations. SPs 1–3 and 5 were situated on the eastern macroslope of the Ural ridge near the Novouralsk city (Sverdlovsk region), while SP 4 was located in the protected part of the arboretum of the Botanical Garden of the Ural branch of the Russian Academy of Sciences (Yekaterinburg).

According to a physico-geographical zoning (*Fiziko-geograficheskoe raionirovanie SSSR*, 1968), the studies were carried out in the southern part of the Mid Trans-Ural province of the Middle Ural region of the Novozemelsk-Ural mountain country. According to the forest zoning proposed by Kolesnikov et al. (1974), this territory is a part of the southern taiga subzone of the Mid-Ural low-mountain province of the Ural mountain–forest region. The soil cover of the territory was represented by primitive accumulative mountain–forest types (Pogodina and Rozov, 1968; Rzhannikova, 1972; Firsova, 1977, 1978).

An examination of forest stands was carried out using a sample plot method. Temporary SPs were arranged in accordance with the Industry Standard 56-69-83 (1984). Average valuation parameters were determined according to standard methods (Anuchin, 1982). The valuation description of pine forests on SPs of the Novouralsk raion and the Arboretum of the abovementioned Botanical garden was as follows:

SP 1: forest type: grass pine forest; tree composition: 8P2L, single S; age class: XII; growth class: III; light forest; density: 0.6; average diameter: 34.6 cm; average height: 24.3 m; reserve: 180 m^3/ha; brown mountain–forest strongly podzol soil.

SP 2: forest type: dark mossy–berry pine forest; tree composition: 10P, single S; age class: VII; growth class: III; density: 0.6; average diameter: 28.6 cm; average height: 22.4 m; reserve: 210 m^3/ha; brown mountain–forest strongly podzol soil.

SP 3: forest type: dark mossy–berry pine forest; tree composition: 10P, single S; age class: VII; growth class: IV; density: 0.6; average diameter: 24.5 cm; average height: 20.6 m; reserve: 180 m^3/ha; brown mountain–forest strongly podzol soil.

SP 4: forest type: grass pine forest; tree composition: 10P, single B; age class: VII; growth class: III; density: 0.8; average diameter: 25.8 cm; average height: 25.4 m; reserve: 220 m^3/ha; podzol soil.

SP 5: forest type: grass–mossy spruce forest; tree composition: 8P2S, single B; age class: III–V; growth class: IV; density: 0.6; average diameter: 24.2 cm; average height: 19.2 m; reserve: 190 m^3/ha; mountain–forest strongly podzol soil.

Table 1. Characteristics of trunk twists in Scotch pine and Siberian spruce in 2015

Twisting characteristic, SP number, tree species	Number of trees/Percentage, %					Percentage of trees from the total number of twisted trees, %	
twisting direction; chord magnitude range, cm	$(R + L)$; 0.5–1.0	$(R + L)$; ≥1.0	R; ≥1.0	L; ≥1.0	total number of trees	R	L
1, pine	24 25.81	55 59.14	47 50.54	8 8.60	93	85.45	14.55
2, pine	14 13.08	62 57.94	49 45.79	13 12.15	107	79.03	20.97
3, pine	13 15.66	57 68.67	15 18.07	42 50.60	83	26.32	73.68
5, spruce	1 5.56	12 66.67	8 44.44	4 22.22	18	66.67	33.33

Table 2. Characteristics of trunk twists of Scotch pine and Siberian spruce in 2016

Twisting characteristics, SP number, tree species	Number of trees/Percentage, %					Percentage of trees from the total number of twisted trees, %	
twisting direction; chord magnitude range, cm	$(R + L)$; 0.5–1.0	$(R + L)$; ≥1.0	R; ≥1.0	L; ≥1.0	total number of trees	R	L
1, pine	20 21.74	50 54.35	9 9.78	41 44.57	92	18.00	82.00
2, pine	20 19.05	70 66.67	10 9.52	60 57.14	105	14.29	85.71
3, pine	23 27.38	46 54.76	39 46.43	7 8.33	84	84.78	15.22
4, pine	0 0.0	50 52.08	26 27.08	24 25.00	96	52.00	48.00
5, spruce	1 5.26	18 94.74	3 15.79	15 78.95	19	16.67	83.33

A trunk twisting magnitude was measured for each tree growing within SP borders. A metal rod (6 mm in diameter and 18 cm in length) was attached to the trunk to a depth of 5 cm at a height of 2 m transversely to a generatrix surface of a trunk. A hollow coal-plastic tube (3.1 m in length) was fixed on the prominent part of the rod, and a flexible thread with a load was attached to its end. The length of the thread corresponded to the distance to the ground. A marker was established and fixed in the upper soil layer where the load contacted ground. Clockwise and counterclockwise deflections of the rod were measured using the size of the chord between two points of a circle with the radius equal to 3.1 m + r (where r is a trunk radius). The chord size was measured by a caliper. The measuring construction provided a rigid connection between the rod and the tube, which did not depend on the number of repeated connections and made it possible to determine the position of the contact point with the absolute error value not exceeding 0.5 cm. Due to this fact, values exceeding this limit were registered separately. The metal rod was left in the tree trunk for the whole period of measurements. Rotation angles in 2015 and 2016 were determined based on the position of markers fixed on May 5, 2015, and September 15, 2015 or May 5, 2016, and September 15, 2016, respectively. Due to the relatively small values of the measured angles, the analysis of trunk twistings considered only the values of measured chord lengths. The angle of rotation was calculated in degrees based on the chord length. In addition, the direction of rotation, clockwise (L) or counterclockwise (R), was determined.

RESULTS AND DISCUSSION

The analysis of data on tree twists obtained in 2015 (Table 1) and 2016 (Table 2) for SP 1–3 and SP 5 provided an evaluation of the percentage of trees that fell into different ranges of chord length with allowance for

Table 3. Number and percentage of trees that changed or kept their twisting direction in 2016 in relation to 2015

SP number, tree species	Trees that changed their twisting direction		Trees that kept their twisting direction	
	number	percentage of the total number of twisted trees, %	number	percentage of the total number of twisted trees, %
1, pine	60	69.77	7	8.14
2, pine	56	56.00	11	11.0
3, pine	45	54.22	16	19.28
4, pine	9	18.36	3	6.12
5, spruce	10	52.63	4	21.05

the direction of rotation (Table 1) and a percentage of trees with L and R twists.

According to the results, the twisting phenomenon was observed in 72.2–84.9% of trees. The ratio of L and R twists registered for different SPs varied. In the case of SP 1 and SP 2, the number of R twists exceeded that of L twists in 3.5 or more times, while in the SP 3 the number of L twists exceeded that of R twists in almost three times. The maximum values of rotation angles for SP 1, SP 2, and SP 3 were 0.78°, 0.8°, and 0.97°, respectively. The number of measured trees at SP 5 was 18; the calculated $R : L$ ratio was 2 : 1. The average rotation angle for pine trees growing on SP 1–3 was 0.26° ± 0.02°, 0.29° ± 0.02°, and 0.32° ± 0.02°, respectively; in the case of spruce (SP 5), this value was 0.32° ± 0.04°.

To explain the trunk twisting phenomenon observed in 2015 during the vegetation period, the following qualitative model, connected with morphogenesis at the level of cambial complex functioning, was proposed. During radial growth, the periclinal division of cambial cells is accompanied with anticlinal division, which provides a continuity, sufficient density, and mechanical strength of external timber layers during the increase in the external perimeter of the horizontal trunk section. The frequency of clinal cell formation varies depending on the growth rate (Bannan, 1960) at different perimeter areas (Harris, 1989) and is accompanied by the appearance of significant tangential stresses (Leelavanichkul and Cherkaev, 2004; Ormarsson et al., 2010). These stresses cause shifts in external xylem layers in a tangential direction and the corresponding clockwise or counterclockwise deflection of a metal rod in a horizontal plane depending on the direction of the stress-causing force.

In 2016, the cycle of measurements was repeated for all SPs. An analysis of the results showed an insignificant difference in the number of twisted trees between 2015 and 2016 (Table 2). At the same time, most twisting trees changed their twisting direction to the opposite one. For example, the $R : L$ ratio at SP 5 significantly changed and became 1 : 5. A comparative analysis of the results obtained for a 2-year period showed that the number of trees on SPs 1, 2, 3, and 5, which changed their twisting direction, was 69.8, 56, 54.2, and 52.6%, respectively (Table 3). Table 3 shows data which take into account only trees which twisted in both 2015 and 2016. The number of trees twisting only during one of these two seasons is not shown, but they were taken into account during the counting of the total number of twisting trees. Obviously, mechanical stresses in the xylem arising during growth processes may activate compensatory mechanisms connected with anticlinal cell division in the cambium and resulting in the opposite twisting of a trunk in the next season. Thus, in most tree species, trunk growth is accompanied by a clockwise and counterclockwise twisting of external timber layers by small angles with a change in rotation direction. The next-year compensation for the rotation angle may be either complete or partial. The phenomenon of a change in the direction of spiral grain fibers (left or right form) is well-known and usually occurs only once in the course of ontogenesis. In the case of coniferous trees (pine, spruce, fir, or larch), the direction of wood fibers is changed from left to right at a tree age of 40–80 years (Burger, 1941). A spiral grain arrangement is also height-dependent (Schmelzer, 1977).

An analysis of rotation angles measured in 2015 and 2016 at SPs 1, 2, 3, 4, and 5 showed their maximum values in 2016 increased to 1.27°, 1.33°, 1.39°, 1.70°, and 1.54°, respectively. This phenomenon is most likely connected with differing weather conditions (in the mid-Urals, the summer season of 2016 was hotter and drier than the previous one). In 2016 the average rotation angles for SPs 1, 2, 3, and 4 were 0.3° ± 0.03°, 0.33° ± 0.02°, 0.3° ± 0.03°, and 0.51° ± 0.05°; in the case of spruce (SP5), this value was 0.71° ± 0.1°.

The data on the ratio of trees with L and R twists in 2015–2016 (Tables 1, 2) indicate that in 2015 R twists dominated in SPs 1, 2, and 5, while L twists dominated in SP 3. In 2016, the dominating twist direction on each SP changed to the opposite one. At the same time, no domination was observed on SP 4, where the number of L and R twists was almost equal. These regularities are explained by differences in the forest-growing conditions on the SPs studied, as well as by differences in weather and climatic factors. Moreover,

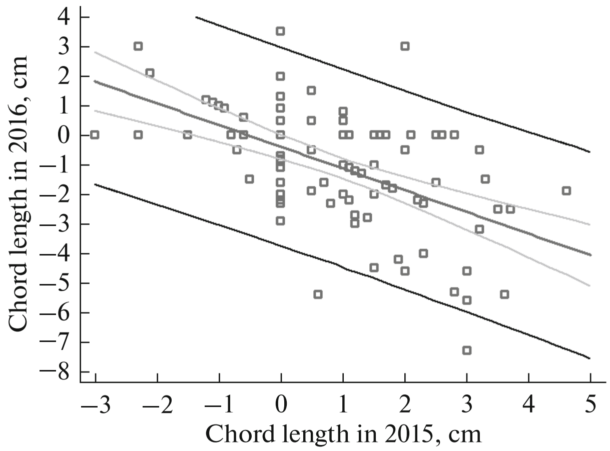

Fig. 1. Magnitudes and directions of pine-tree twistings on SP 1 in 2015–2016. Positive and negative values indicate *R* and *L* twists, respectively.

a comparative analysis of results allows us to suppose the actuation of the mechanism of sequential change of twist direction in the largest part of trees that prevents a significant twisting of trees.

Note that in 2016 some trees on SPs 1, 2, 3, and 5 kept the twisting direction that was observed in 2015 (8.14, 11.0, 19.28, and 21.1%, respectively; Table 3). Probably no stress compensation occurred in these trees, so the external layer of the growing xylem continued to twist in the same direction, forming a spiral grain.

Results of rotation-angle measurement obtained on SP 1 in 2015–2016 may serve as a good illustration of the above-described regularities (Fig. 1). A correlation analysis confirmed a significant negative correlation between rotation parameters (linear regression equation: $y = -0.737x - 0.39$; $r = -0.548$, $p < 0.05$). The number of trees which maintained the same rotation direction during 2-year periods (I and III quadrants) is relatively low. Similar regularities were observed for all SPs studied.

A study of angle magnitude distribution for both *L* and *R* twists on SPs 1–5 showed that, in most cases, they are reliably exponential (Table 4) and are described by the formula $y(x) = \lambda\exp(-\lambda(x))$. The character of distribution suggests that the magnitudes of trunk rotation angles are determined by a random Poisson type process; however, this fact does not allow

Table 4. Values of the fitting criterion χ^2 and the corresponding significance levels and λ parameters for exponential distributions on SPs 1–5.

SP number, tree species	Year	Twisting direction	χ^2 criterion			λ
			df	value	*p*	
1, pine	2015	*R*	5	4.546	0.474	0.712
		L	2	1.044	0.593	1.34
	2016	*R*	2	0.037	0.982	1.145
		L	4	2.07	0.723	0.553
2, pine	2015	*R*	4	8.677	0.07	0.908
		L	1	0.446	0.504	2.046
	2016	*R*	3	2.24	0.524	1.119
		L	3	12.77	*0.005*	0.49
3, pine	2015	*R*	2	6.54	*0.038*	1.314
		L	4	4.917	0.329	0.624
	2016	*R*	3	4.449	0.217	0.556
		L	1	0.934	0.339	0.897
4, pine	2016	*R*	4	6.795	0.147	0.722
		L	3	3.381	0.337	0.604
5, spruce	2015	*R*	1	0.437	0.509	0.890
		L	–	–	–	–
	2016	*R*	–	–	–	–
		L	2	1.045	0.593	0.233

Cases of doubtful distribution are indicated with italics.

us to unambiguously judge the stochasticity of the twisting initiation.

CONCLUSIONS

(1) The phenomenon of twisting of external trunk layers, which is connected with radial growth processes and causes changes in a spatial orientation of a trunk and branch surface, has been revealed. During vegetation season, more than half of trees turned around a trunk axis. The angle of rotation may reach 1.5° or more.

(2) Twisting of tree trunks may occur both clockwise and counterclockwise (*L* and *R* twists). At the second year, the twisting direction in the majority of trees changed to the opposite one. At the same time, 8–19% of trees kept the same twisting direction; in other trees the twisting either occurred during one of the two years of observation or was absent.

(3) Twisting characteristics probably depend on forest-growing conditions and other environmental factors, including weather and climatic conditions.

(4) General regularities of twisting of external trunk layers revealed in Scotch pine were also observed in spruce fir.

(5) The analysis of obtained data and their comparison with known information on the appearance of spiral grain in a xylem made it possible to propose a qualitative model for the mechanism of trunk twisting. The development of a quantitative model requires additional data on the magnitudes of stresses caused by cambial cell divisions and the turgor of conductive pathways.

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