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**Abstract**

The formations of compression wood and eccentric radial increment are two phenomena that are so closely associated that they cannot be readily discussed separately. However, various studies suggest that their formation is stimulated by different mechanisms and that there is no functional relationship. While the formation of compression wood is a reaction of coniferous trees to negative gravitropic scenarios which enables the trees to recover from displacement, one-sided radial growth promotion is stimulated by unilateral mechanical strain on the cambium for lowering stress peaks. This study offers an approach to quantify the relation of both phenomena in stem cross-sections and single growth rings.

Samples of 56 Norway spruces (*Picea abies* [L.] Karst.) from sites differing in slope and exposure to the prevailing wind direction were examined for their cross-sectional compression wood distribution and eccentricity in radial increment. The assessment of both phenomena on stem cross-sections was based on their spectral properties in reflected light. Hyperspectral image analysis allowed detection of compression wood distribution as well as measurement of annual radial increment along eight radii, oriented by compass direction.

Since the distributions of both phenomena comprise both a directional component as well as amplitude in annual reference, these data were handled as vectors. Circular statistics were applied to describe and quantify their relationship and to test both phenomena for the inducing environmental factor that stressed the tree.

The direction of compression wood formation and eccentric growth is significantly positively correlated. In the majority of observations a unimodal distribution of both phenomena is given. Mostly strong one-sided compression wood formation is associated with a coincident direction of eccentric radial increment. However, stem cross-sections with a distinct direction of compression wood were observed without a dominating direction of eccentric growth, and vice versa.

Bivariate statistics that consider vector direction as well as vector length have proved to be very helpful in retrospectively identifying possible initiating environmental factors for both phenomena at a given site. The location of standard and confidence ellipses in relation to the assumed direction of action is a strong indication for or against an assumed environmental factor.

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Introduction

Studies have shown that the formation of compression wood is a reaction of coniferous trees to negative gravitropic scenarios (Westing, 1965; Timell, 1983). It is interpreted as enabling the tree’s recovery from displacement, so it regains its original orientation in the earth’s field of gravity (Hartmann, 1942). However, the correction is often only effectively observed at the apical meristem by the appearance of a sweep. Therefore, compression wood is considered a reaction to an external stress that puts a strain on the tree. Hartig (1901) has pointed out that the formation of compression wood and eccentric growth occur together in the vast majority of cases. Thus, Timell (1986) concludes that the two phenomena are so closely associated in conifers that they cannot be readily discussed separately. However, this close association does not necessarily mean that they are causally related. Experimental evidence for the lack of functional correlation of formation of compression wood and eccentric growth through one-sided radial growth promotion is given by Westing (1961) and Riech and Ching (1970). The latter state that radial growth promotion is influenced by compressive stress on the lower side of a leaning stem, while compression wood formation is correlated with the gravitational stimulus.

It is well known that unilateral strain stimulates one-sided radial growth promotion leading to eccentric stem cross-sections. Steucek and Kellogg (1972) demonstrated promoted growth in regions of increased mechanical strain. In consequence, Mattheck (1991) and Mattheck and Kubler (1995) explain the distribution of growth as related to lower stress peaks. This is in agreement with the hypothesis of constant-strain (Wilson and Archer, 1979).

Clinostat experiments have demonstrated that gravity is involved in formation of compression wood (Hartig, 1901; Jaccard, 1939; Hartmann, 1942). Hartmann (1932) realized that something more than gravity must be involved, and suggested that each part of a tree strives to remain in its genetically predetermined, static equilibrium position. The formation of compression wood is arranged so as to bring back displaced organs to their original position by the shortest possible route. The experiments carried out by Hartmann (1932, 1942), Münch (1937, 1938) and Sinnott (1952) demonstrate that compression wood formation regulates and maintains tree form as a whole, and thus is of morphogenetic importance (see as well Sinnott, 1951, 1960; Spurr and Hyvärinen, 1954; and Firn and Digby, 1997). This allows us to predict the location of compression wood formation in a displaced stem or branch. It must be stated that gravity probably does not function as the primary cause, at least not invariably (Timell, 1986).

In spite of being under different control, both phenomena are closely associated. This study offers an approach to quantify the relationship of compression wood distribution and eccentric radial growth in stem cross-sections and single growth rings. Since the distributions of both phenomena are related to directional information, circular statistics are applied. In addition, suitable methods are provided to test both phenomena for a common stimulating environmental factor. In addition to the methodological approach discussed here, further applications to test and model the influence of tree characteristics, i.e. tree height, various crown parameters and social tree class, on the distribution and amount of compression wood and pith eccentricity at a given site are discussed in detail in Duncker (2006).

Material and methods

The material used for this study was collected from 56 Norway spruces growing on five different sites in the Black Forest, south-western Germany. The sites were selected to be as similar as possible, differing only in slope and in exposure to the prevailing wind direction. The sites are located at sub-mountain to high-mountain altitudes and vary in degree of slope from almost level (1°) to strongly inclined (29°). The sample trees had a mean diameter (dbh) at 1.3 m height of 46.5 cm (34.5 cm min–66.1 cm max) and a mean tree height of 30.7 m (24.1–36.8 m). An average of 8.6 stem cross-sections from defined heights along the stem (i.e. 1.3, 6.5, 11.5, 17.5, 20, 22.5, 25, 27.5, 30 and 32.5 m) was cut from each tree for compression wood and growth ring analysis. Over 500 sample discs were taken, including those for age determination at a height of 0.3 m. The tree age ranged from 49 up to 171 years. However, within the five homogeneous, one-layered sample sites, tree ages were clustered around 51, 80, 92, 101 and 135 years, respectively.

Methods for compression wood detection and growth ring analysis

Compression wood was detected in dried stem cross-sections after polishing with fine abrasive paper. Compression wood can be discriminated from other wood features in reflected light using hyperspectral image analysis with correct positional arrangement. The spectral range used for classification was 400–1000 nm; spatial resolution was <0.07 mm² per pixel. Due to the fact that annual growth ring boundaries can be located in reflected light as well, compression wood formation can be related to single calendar years and the annual radial increment is measurable. For this purpose, a polar
Compression wood distribution and annual radial growth

The data on compression wood distribution and radial growth obtained with this sample design comprise both a directional component as well as amplitude with annual reference. This suggests that such data are often best handled not as numbers, but as vectors \((\theta, r)\). The direction \((\theta)\) results from the orientation of the radius in relation to the cardinal point. The amplitude or the length of the vector is given by the annual radial increment or the amount of compression wood, which is reduced to a linear measure by division though the sector height.

An approximate estimate for the relative amount of compression wood on the growth ring surface based on the symmetric sample design can be obtained with the following formula:

\[
\text{relCW} = \sum_{i=1}^{8} \left( \frac{\pi/8 \times (r_{ir})^2}{\pi \times \bar{l}} \right) \times \frac{r_{CW}}{r_{ir}}
\]

simplified \(\text{relCW} = \sum_{i=1}^{8} \frac{r_{ir} \times r_{CW}}{8 \times \bar{l}^2}\)

where \(\text{relCW}\) is the relative amount of compression wood on growth ring surface; \(r_{CW}\) is the length of compression wood vector in radius \(i\); \(r_{ir}\) is the length of eccentric radial growth vector in radius \(i\); \(\bar{l}\) is the quadratic mean of radial increment in radii 1–8.

The amount of compression wood within the eight radial samples is set in relation to the corresponding radial increment (2nd term). This relation is weighted by the portion of the radius on the total ring surface (1st term) estimated by the quadratic mean of all eight radii. The quadratic mean is used as best approximation of the basal area increment (Siostrozné, 1958).

If the eight vectors of one growth ring from the radii are added, a single growth ring vector results for compression wood distribution \(\text{“CWc”}\) or radial increment \(\text{“IRc”}\), respectively. This single growth ring vector describes the direction seen from the pith in which compression wood is formed \((\theta_{CW})\) or radial increment \((\bar{r})\). The length of the vector can be seen as a measure of strength of compression wood formation \((r_{CW})\) or eccentricity \((r_{ir})\). The latter is not to be confused with mean annual increment \((\bar{r})\). The degree of eccentricity can be set in proportion to the mean increment to a dimensionless measure \(r_{ir\text{rel}} = r_{ir} / \bar{l}\).

The tangential spread of the compression wood distribution can be assessed by the number of radii with \(r_{CW} > 0\). The tangential spread of the compression wood crescent within a growth ring may exceed 180°. If \(r_{CW} > 0\) holds true for more than five radii, \(r_{CW}\) tends to become smaller, since opposing amounts of compression wood cancel each other out. This is in accordance with a functional understanding of this tissue.

Analogous to derivation of single growth ring vectors, corresponding vectors of stem cross-sections will result in (“CW_c” and “IR_c”) when summing all single growth ring vectors of a disc. These vectors express the mean direction of compression wood distribution \((\theta_{CW})\) or eccentric increment \((\bar{r})\), respectively. The division of the sum of all growth ring vector lengths by the number of growth ring vectors gives the mean resultant lengths, \((r_{CW})\) and \((r_{ir})\), respectively, and lie in the range \((0, 1)\). Its extreme values have some interesting properties. \(\bar{r} = 1\) implies that all directions are coincident. However, \(\bar{r} = 0\) does not imply uniform dispersion around the circle (Fisher, 1993). Analysing the change in (“CW_c” or “IR_c”), when the single growth ring vectors are added year by year, will allow one to draw first conclusions on the nature of the driving environmental factor initiating both phenomena. Does the driving force keep a constant direction or is it changing over time or with tree age?

Descriptive circular statistic and bivariate methods

For descriptive analysis of vectorial data, specific methods of circular statistics exist. Directional data are obviously of interest in problems related to forest ecology or growth ring analysis, although circular statistics have only been applied in few cases. Robertson (1987, 1990, 1991) describes the form of tree crowns and the centroid of compression wood, wood density, and tree-ring width in stems under the influence of vector winds by circular statistics. A comprehensive
introduction in this sub-discipline of statistics is provided by Batschelet (1981) and Fisher (1993).

Besides calculating mean direction \( \bar{\rho} \) and mean resultant length \( r = \bar{\rho}/n \), further circular measures for dispersion are given by the sample circular variance \( V = 1 - \bar{r} \). Note, as mentioned above, the interpretation of \( \bar{\rho} = 0 \), \( V = 1 \) does not necessarily imply a maximally dispersed distribution. The sample circular standard deviation is defined as \( v = (-2\log(1-V))^{1/2} \). In addition, in order to describe the spread, the sample circular dispersion \( d \) is defined; for calculation see Fisher (1993). It is important for calculating a confidence interval for the mean direction, and for comparison with other directions.

The sampled data are tested for uniformity and unimodality. After initial graphical exploration, we have to decide on a test of any significant difference from uniformity – this might be the \( V \) test as described by Batschelet (1981) – or a test of randomness vs. a unimodal alternative. A test known as the Rayleigh test is appropriate for the latter purpose (Fisher, 1993).

For calculating the correlation between a pair of directions, modified circular methods are needed. If both directions are uniformly distributed, the difference in direction is calculated for each pair and the analysis is based on these differences. The variable is circular and is clustered around a certain mean angle in the case of positive correlation. The extent of clustering is represented by the mean vector length \( r \). Since \( r \) ranges between 0 and 1, it can be used as a circular correlation coefficient. Whether \( r \) differs significantly from zero or not can be tested by the Rayleigh test. In circular statistics, two variates may be positively and negatively correlated at the same time, which is in contrast to linear statistics (Batschelet, 1981). For testing negative correlations, the sum of both directions is used instead of the directional difference between both directions of less than 90°. In fact, it has been observed that compression wood formation and eccentric radial increment as given in Fig. 1 suggests a positive correlation of both directions within single growth rings. Since it is to be expected that the directions are not uniformly distributed, a correlation between \( \theta_{\text{CW}} \) and \( \theta_{\text{ir}} \) was tested. For positive correlation, the coefficient \( r_+ = 0.429 \) and negative correlation \( r_- = 0.060 \) for the test statistic \( r^2 \) proposed by Marida is used. Thus, \( r^2 = 0.148 \)

Results

Direction of compression wood formation and eccentric radial growth

In total, 485 stem cross-sections were analysed for compression wood distribution and annual radial increment and corresponding growth ring vectors were calculated. In all 14,484 out of 22,538 growth ring vectors for compression wood have \( r>0 \), which corresponds to 64.3%. If compression wood is formed, it comprises a mean of about 3.2% of the total growth ring surface. High relative amounts of compression wood occur in <1% of the observations, but may exceed 30%, up to 37% of the ring surface in an extreme case. In about 42% of the observations, the relative amount of compression wood does not exceed 4% of the growth ring surface.

The two directions of the growth ring vectors for compression wood (\( \theta_{\text{CW}} \)) and radial increment (\( \theta_{\text{ir}} \)) may have an angular difference \( \delta \in [0°, 180°] \). In fact, it has been observed that compression wood formation and eccentric growth are located in almost opposite directions, but in less than 1% of the growth rings. Fig. 1 shows the absolute (columns) and relative incidence of the directional difference between \( \theta_{\text{CW}} \) and \( \theta_{\text{ir}} \) for single growth rings. The relative incidence of single classes of angular differences is approximately given on the right scale, if divided by 10. Most frequent are angular differences of up to 5°, comprising about 9% of the observed cases; 60% of the observations comprise angular differences between both directions of less than 45°.

The frequency distribution of angular differences between the direction of compression wood formation and eccentric radial increment as given in Fig. 1 suggests a positive correlation of both directions within single growth rings. Since it is to be expected that the directions are not uniformly distributed, a correlation between \( \theta_{\text{CW}} \) and \( \theta_{\text{ir}} \) was tested. For positive correlation, the coefficient \( r_+ = 0.429 \) and negative correlation \( r_- = 0.060 \). For the test statistic \( r^2 \) proposed by Marida, \( r = \text{Max}(r_+, r_-) \) is used. Thus, \( r^2 = 0.148 \).
and $P \approx 0.05$ demonstrate a significant positive correlation ($z = 0.05$) between the direction of compression wood formation and eccentric radial increment in single growth rings. The correlation of both directions calculated for stem cross-sections based on $\bar{y}_\text{CW}$ and $\bar{y}_\text{ir}$ is even stronger with $r^2 = 0.333$ ($r_+ = 0.577$, $r_- = 0.061$) and $P < 0.01$.

For each stem cross-section, the mean direction $\bar{\theta}$ and mean resultant length $f$ for compression wood formation and eccentric radial increment were calculated, respectively. In addition, each sample of single growth ring vectors of one stem cross-section was tested for randomness against a unimodal alternative with a Rayleigh test. The tests demonstrated that for 26 stem cross-sections (5.36%) with compression wood formation and for 18 stem cross-sections (3.71%) with eccentric radial increment, the null hypothesis ($z = 0.05$) was not rejected. The stem cross-sections with uniform distribution of compression wood or eccentric radial increment predominately originate from higher stem segments within the green crown of the trees. The small number of stem cross-sections where the null hypotheses were not rejected shows that in the majority of observations there is a unimodal distribution of both phenomena. For compression wood this comprises 94.64% of the stem cross-sections and for eccentric radial increment 96.29%, respectively. Thus, we might expect an initiating environmental factor for both phenomena that does not change direction from year to year. Fig. 2 shows that the incidence of mean direction of compression wood ($\bar{\theta}_\text{CW}$) and eccentric radial increment ($\bar{\theta}_\text{ir}$) in stem cross-sections was most often oriented towards north-east.

**Fig. 1.** Angular difference between the direction of compression wood formation and eccentric radial increment in single growth rings. The columns show the absolute incidence of angular difference in classes of 5°; the line shows the relative cumulative incidence of the angular difference classes.

**Fig. 2.** Frequency distribution of mean directions for compression wood (black columns) and eccentric radial growth (white columns) in stem cross-sections. In order to allow the eye to assess the circular distribution in a linear histogram better, the data are replicated by a complete cycle.
The mean resultant lengths \( \bar{r} \) for stem cross-section vectors are given in Fig. 3. It is worth noting that values close to \( \bar{r} = 1 \) indicate a coincident direction of the sample, while \( \bar{r} = 0 \) does not imply uniform dispersion around the circle. Fig. 3 demonstrates that the measures are concentrated in the upper right corner close to mean resultant length \( \bar{r} = 1 \), for both compression wood formation and eccentric radial growth. This again illustrates that both phenomena lie in one major direction. In only 30 observations (6.4\%) for compression wood and 63 (13\%) for eccentric radial growth are values of \( \bar{r} < 0.4 \). In contrast, 297 observations (63.5\%) of compression wood and 163 (33.5\%) of eccentric radial increment show \( \bar{r} > 0.8 \). In consequence, compression wood has a stronger tendency to be one-sided than eccentric radial growth does. Further, Fig. 3 illustrates that stem cross-sections with a distinct direction of compression wood and without a dominating direction for eccentric radial growth exist, and vice versa.

In Fig. 4, the stem cross-sections of the trees from a steep (29°) south-western slope are depicted to demonstrate the use of standard and confidence ellipses in identifying the initiating environmental factor for both phenomena. All tips of the stem cross-section vectors for compression wood were plotted. They are concentrated in the first quadrant, which is the north-eastern segment. The standard ellipse for describing the variance is given in black. Further, the confidence ellipse is given in grey, covering the population centre. It does not include the origin, proving a significant direction. The grey tangents starting at the origin provide the confidence limits for the mean compression wood direction. The two grey lines starting at the origin delimit the confidence interval for the mean compression wood direction. The dashed lines delimit the confidence interval for the mean eccentric radial increment at the site. The arrow indicates the downhill direction of slope (29°) at the site.

Fig. 3. Mean resultant length \( \bar{r} \) of stem cross-section vectors for compression wood and eccentric radial increment.

Fig. 4. Standard ellipse (black) and confidence ellipse (grey) for the compression wood distribution in the stem cross-sections at a steep south-western slope. The tip of the mean vector is marked with ‘×’ in the centre of the grey confidence ellipse. The two grey lines starting at the origin delimit the confidence interval for the mean compression wood direction. The dashed lines delimit the confidence interval for the mean eccentric radial increment at the site. The arrow indicates the downhill direction of slope (29°) at the site.

In Table 1, the portion of observations within the corresponding ninth of area is shown for compression wood and eccentric radial increment. It can be observed that compression wood has a stronger tendency to be one-sided than eccentric radial increment does. Further, the null hypothesis (\( \alpha = 0.05 \)) that there is a significant difference in the mean direction of compression wood formation and eccentric radial increment in stem cross-sections at this steep site cannot be rejected. The fact that both directions are not oriented downhill might be explained by the predominant south-western wind and storm direction, as measured at a nearby meteorological station (“Elzach No. 30”), from which data were provided by the Landesanstalt für Umweltschutz Baden-Württemberg-Abt.3 (2004).
Discussion and conclusions

Compression wood formation and eccentric radial growth occur together so frequently Timell (1986) concluded that the two phenomena cannot be readily discussed separately. However, experimental evidence for the lack of a functional correlation of both phenomena is given (Westing, 1961; Riech and Ching, 1970). When studied in stem cross-sections, the annual increment of trees in temperate zones is formed in additional outer rings around a centre, which is the pith. These rings are only exceptionally concentric. Most often, promoted one-sided radial increment leads to eccentric growth. Further, the structure of the wood can be altered, which is the case when compression wood is formed. If the distribution of both phenomena is to be assessed, directional as well as intensity information is needed. This is best done in a vectorial way based on single-growth-ring measurements. By choosing the growth ring as the basic unit, the level of observation and functional formation of the phenomena become identical. The quantification of the relation of compression wood formation and eccentric radial growth has to take both dimensions of information into account. Specific methods are provided by the sub-discipline of circular and bivariate statistics.

The relation of both phenomena on a sample of stem cross-sections from 56 Norway spruce trees is quantified using these methods. This analysis shows that in the majority of observations compression wood was formed in the same direction as eccentric radial growth. Although compression wood formation and eccentric growth may rarely oppose each other within one growth ring, both vectors are significantly positively correlated. In addition, tests prove the unimodal distribution of both phenomena in more than 95% of observations, indicating that they follow major directions. Further, these major directions are not significantly different in the observed trees. Assuming that compression wood is formed in reaction to a displacement disturbing the static equilibrium position of the tree in earth’s field of gravity (Hartmann, 1942; Sinnott, 1952) and one-sided static equilibrium position of the tree in earth’s field of gravity (Hartmann, 1942; Sinnott, 1952), tests prove the unimodal distribution of both phenomena become identical. The quantification of the relation of compression wood formation and eccentric radial growth has to take both dimensions of information into account. Specific methods are provided by the sub-discipline of circular and bivariate statistics.

Although the comparison of the mean resultant length for compression wood and eccentric radial increment vectors revealed that pronounced compression wood is formed in stem cross-sections without distinct eccentricity, and vice versa, the results in total suggest that a common initiating environmental factor can be assumed for both phenomena. For retrospectively identifying this initiating environmental factor at a given site, defining confidence ellipses proves to be very helpful. Their location in relation to the possible direction of action is a strong indication in favour of or against an assumed environmental factor.

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