Irregular Heartwood Formation in Maritime Pine (\textit{Pinus pinaster} Ait): Consequences for Biomechanical and Hydraulic Tree Functioning

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As the proportion of sapwood (SW) transformed into heartwood (HW) is irregular both radially and longitudinally in trunks of Maritime pine (\textit{Pinus pinaster} Ait.), it has been suggested that HW formation is a developmental process, regulated internally within the tree. In trees where stem growth is eccentric due to stem lean or wind action, the number of annual growth rings of SW transformed into HW is greater on the compressed side of the tree. To determine the contribution to bending stiffness, if any, of this prematurely formed HW, four point bending tests were carried out on fresh HW and SW samples taken from the same growth ring, or neighbouring growth rings, at different cross-sectional positions at a height of 2 m from six 52-year-old Maritime pines. The mean (±s.e.) modulus of elasticity (\(E\)) was 7.6 ± 0.3 GPa (longitudinal direction) for all samples. No significant differences in \(E\) were found between HW and SW; thus HW does not play a significant mechanical role in bending stiffness. To test a second hypothesis that early HW formation on the compressed side of trees may maintain a constant, optimal volume of SW between HW and SW; thus HW does not play a significant mechanical role in bending stiffness. To test a second hypothesis that early HW formation on the compressed side of trees may maintain a constant, optimal volume of SW, four point bending tests were carried out on fresh HW and SW samples taken from the same growth ring, or neighbouring growth rings, at different cross-sectional positions at a height of 2 m from six 52-year-old Maritime pines. The mean (±s.e.) modulus of elasticity (\(E\)) was 7.6 ± 0.3 GPa (longitudinal direction) for all samples. No significant differences in \(E\) were found between HW and SW; thus HW does not play a significant mechanical role in bending stiffness. To test a second hypothesis that early HW formation on the compressed side of trees may maintain a constant, optimal volume of SW between HW and SW; thus HW does not play a significant mechanical role in bending stiffness.

**Key words:** Heartwood, sapwood, bending test, Pipe Model Theory, \textit{Pinus pinaster}.

**INTRODUCTION**

Maritime pine (\textit{Pinus pinaster} Ait.) is a fast-growing, drought- and salt-resistant species found in large plantations mainly in the south-west of France, Spain, Portugal and North Africa. Although economically important for the wood and paper industry, and much studied since the 1960s (Polge and Illy, 1967; Keller and Mosnier, 1987; Maugé, 1987; Castèra, 1999), Maritime pine suffers from serious form defects. Many trees possess leaning trunks, often due to an incident in the tree’s life e.g. a storm which dislodged the tree when young. Most adult stems have highly developed eccentric growth on the leeward side of the trunk, along with large amounts of compression wood (Fourcaud, 1999). Recently, heartwood (HW) distribution in Maritime pine has been investigated with regards to wood technological properties, as the quantity of HW determines the quality of a log. HW is the non-functional wood at the centre of the trunk; it usually forms once a tree reaches a certain age which can depend on the species and local conditions (Hillis, 1987). HW is generally more durable and resistant to pathogens than sapwood (SW). Two hypotheses as to the mechanism of HW formation have been proposed; (1) Ziegler (1968) suggested that HW formation is simply due to cell death as the SW ages; and (2) Bamber (1976), hypothesized that the process is active and is triggered by an unknown signal within the tree. HW usually forms in the oldest part of the tree first, i.e. at the base, and also forms in branches, but not in roots. Most trees possess a regular HW with a periphery that is similar in shape to the outside of the stem; however, in certain species, HW can have an undulating outline which does not correspond to the growth rings (Hillis, 1987). In Maritime pine, the distribution of HW within a trunk has been found to be unusual, both longitudinally and radially (Kokutse et al., 1999; Stokes and Berthier, 2000). Less heartwood was found at the base of the trunk than further up the trunk at heights of 2-5 m and even 5-0 m. Within a cross-section, an even more surprising distribution was found as HW was not limited to a specific number of growth rings but bulged across the SW on the leeward side of the tree. In extreme cases, up to 40 annual growth rings had been transformed into HW on the leeward side of the tree, compared to only ten on the windward side. This irregularity was highly correlated with stem eccentricity, but the reason for such eccentric HW formation is not known, nor is the mechanism by which it occurs.

Several hypotheses were postulated by Stokes and Berthier (2000) regarding the phenomenon of eccentric HW formation, two of which will be presented in this paper.

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The first theory concerns the mechanical function of HW. Although HW is harder than SW, and thus resistant to pathogen and insect attack (Hillis, 1987), this does not necessarily mean that it contributes to bending stiffness in a leaning or wind blown tree. In order for a tree to benefit from a change in HW mechanical properties, HW would need a much higher modulus of elasticity than SW. The modulus of elasticity ($E$) is a measure of the elasticity of a material, and to calculate the flexural stiffness of the tree trunk, i.e. the measure of the ability of an object to resist bending, $E$ would need to be multiplied by the second moment of area ($I$). Niklas (1997a,b) found that $E$ was slightly greater in heartwood than sapwood in Black locust (*Robinia pseudo-acacia*); however, sapwood was the principal contributor to $EI$ as it was located further from the stem centre. Sapwood therefore contributes a disproportionately higher second moment of area than does heartwood in the same cross-section. Mencuccini et al. (1997) also found that in *Pinus sylvestris*, even when heartwood accounted for more than 80% of the total diameter, it only contributed about 50% to whole section flexural stiffness. This low contribution of heartwood was also attributed to the fact that it lies very close to the neutral axis of the tree and is largely made up of juvenile wood, which has lower elastic properties than normal wood (Dumail, 1999). If irregular HW was to increase bending stiffness in Maritime pine, it would need to have a much greater $E$ than that of the SW, a theory which will be examined in this paper.

A second hypothesis put forward by Stokes and Berthier (2000), concerning irregular HW formation in Maritime pine, was that it was due to a developmental process, regulated by the tree, to ensure an optimal amount of SW around the trunk. One way to test this theory would be to correlate the surface area of SW with that of the crown foliage, by applying the Pipe Model Theory. The Pipe Model Theory developed by Shinozaki et al. (1964a,b) has been used by many authors to estimate foliage biomass and sapwood production in both temperate (Waring et al., 1982; Marchand, 1983; Whitehead et al., 1984) and tropical species (Morataya et al., 1999). The Pipe Model Theory states that there is a significant relationship between the surface area of SW and that of the foliage above it. This relationship has been verified for many species, in many different habitats and stand types, as well as in different age classes. It is therefore hypothesized that the surface area of the SW is maintained at an optimum for tree functioning; if foliage is less due to e.g. high stand density, heartwood will be formed at a faster rate to avoid the production of superfluous SW. As yet, the signal for this process is not known, nor is it known if the production of irregular HW in trees with pronounced stem eccentricity could be the result of such a function.

The aim of this study was to test two of the hypotheses put forward by Stokes and Berthier (2000) concerning the formation of irregular HW in Maritime pine. Mechanical properties of both HW and SW will be measured to determine if HW serves a mechanical function. Secondly, the Pipe Model Theory will be applied to a selection of straight and leaning trees of Maritime pine to test the hypothesis that irregular HW formation allows the tree to maintain an optimal surface area of SW, which is correlated with the surface area of foliage in the crown.

### MATERIALS AND METHODS

#### Study site and experimental layout

Maritime pine trees growing in a plantation in the Forêt de l’Hermitage, Gironde, south-west France (0° 46'E, 44° 44'N, 58 m a.s.l., 45 km from the Atlantic Ocean) were examined to establish whether heartwood (HW) formation serves a mechanical role, or is due to a developmental process aimed at optimizing the proportion of functional sapwood (SW). The plantation was subjected to prevailing winds from the north-west (300°). The mean windspeed in the region is 3.3 ms⁻¹, with maximum speeds reaching over 35-0 ms⁻¹ (Météo-France). Trees were planted in 1947 at different densities, with different nutrient regimes (Lemoine and Sartoulou, 1976). Information on the genetic background of these trees is not available. A random selection of 12 trees was made; density and genetic background were not taken into consideration. Twisted and curved trees were excluded from the analysis due to the difficulty in interpreting data from such trees. Mean diameter at breast height (DBH) of all the trees was 37.4 ± 2.43 cm and mean height 29.3 ± 1.5 m (Table 1).

#### Sampling procedure for measuring the surface area of heartwood and sapwood

Stem lean between 0 and 4 m was measured using the technique described by Stokes and Berthier (2000). The azimuth towards which the tree was oriented was also measured. Trees were then felled and cross-sections (CSs) taken every 10 cm to DBH. Above DBH, CSs were taken every 2 m. HW formation is known to be highly irregular at the base of the tree (Keller and Mosnier, 1987; Stokes and Berthier, 2000), and as a detailed analysis of the evolution of HW along the length of the trunk was desired, CSs were more frequent between the base and DBH.

Cross-sections were sanded to determine the number of annual growth rings correctly. HW was easily distinguished from SW due to its darker colour. HW distribution in the cross-section was determined by counting the number of annual growth rings which had been transformed into HW and measuring the distance between the pith and the outer HW and SW boundaries along the longest axis and also those perpendicular to the longest axis (Fig. 1A). Therefore, distance of HW and SW boundaries from the pith was measured along four axes (Fig. 1A). Eccentricity of the whole cross-section was calculated using the method described in Stokes and Berthier (2000). Extension of HW, or ‘bulging’ of HW into a zone of SW was described using:

$$\Delta = \frac{n}{m}$$

where $\Delta$ is the extension of heartwood into sapwood zone, $n$ is the difference between the number of growth rings on the compressed side of the trunk (zone where there is more...
The surface area of HW and SW was calculated for each CS using the quadratic mean of the four axes measured (Parde and Bouchon, 1988):

\[ S_i = \frac{\pi}{4} \left( \sum_{i=1}^{4} R_i^2 \right) \]  
\[ S_{HW} = \frac{\pi}{4} \left( \sum_{i=1}^{4} r_i^2 \right) \]  
\[ S_{SW} = S_i - S_{HW} \]

where \( S_i \) is the total surface area of the cross-section, \( S_{HW} \) is the surface area of the heartwood, \( S_{SW} \) is the surface area of the sapwood, \( R \) is the distance from the pith to the bark along one axis and \( r \) is the distance from the pith to the heartwood boundary along one axis.

Differences in proportions of HW and SW from different regions around the trunk were determined using analysis of variance. All values are means ± s.e.

**Sampling procedure for measuring surface area of the crown**

To determine the crown area of each tree, and thus test the Pipe Model (Shinozaki et al., 1964a,b) for trees with irregular HW formation, the following method developed by Waring et al. (1982) was used. After each tree was felled, needle-bearing twigs were separated from branches. Fresh biomass for both twigs plus needles and branches was measured. Twenty needle-bearing branches were chosen randomly from the crown for a more detailed analysis of surface area. These branches were stored in a cold room at 4°C for a maximum of 6 d before being studied further. Twenty needles were removed randomly from the twigs and weighed. The surface area of each of these needles was measured using image analysis software (WinNeedle©, Regent Guay Instruments, Canada). To calculate total crown surface area [eqn (6)], the surface area of each needle measured by WinNeedle was adjusted, as the needle is a half cylinder. Projected needle area was not used as the surface area data were to be correlated with SW area. Needle surface area was thus calculated using:

\[ S_{\text{needle}} = \left( 1 + \frac{\pi}{2} \right) S_{\text{measured}} \]  

where \( S_{\text{needle}} \) is the calculated needle surface area and \( S_{\text{measured}} \) is the needle surface area measured by WinNeedle. The needles remaining on each twig were also removed and weighed, along with the twig minus needles.

The surface area of the crown was estimated using fresh biomass data, the relationship between fresh and dry weight of each needle and its surface area, as well as the fresh and dry weight of the selection of twigs (Waring et al., 1982):

\[ S_{\text{crown}} = F_{\text{w}} \left( \frac{d_{20\text{needles}}}{d_{20\text{needles}}} \right) \left( \frac{S_{20\text{needles}}}{d_{20\text{needles}}} \right) \]  

where \( S_{\text{crown}} \) is the total crown surface area, \( F_{\text{w}} \) is the total crown fresh weight, \( f_{\text{needles}}/f_{\text{twigs}} \) is the relationship between needle fresh weight and twig fresh weight, \( d_{20\text{needles}}/d_{20\text{needles}} \) is the relationship between fresh and dry weight of 20 needles and \( S_{20\text{needles}}/d_{20\text{needles}} \) is the relationship between surface area and dry weight of 20 needles.

**Mechanical tests**

Wood from six of the trees to be used for analysis in the second series of tests was used for mechanical testing. Samples of wood were cut longitudinally from logs stored at 4°C within 1 week of felling the trees. Each sample was 1 cm wide × 1 cm deep × 30 cm long. Samples were taken at different positions around the cross-section, with samples of HW and SW from above and below the lean, as well as perpendicular to the direction of lean/wind (Fig. 1B). Where possible, HW and SW samples were taken from the same growth rings, or from neighbouring rings (Fig. 1B). Three samples of both HW and SW were taken from each of the three regions of the CS, thus a total of 108 samples were measured.

Four point bending tests were carried out on wood samples immediately after they were prepared. The volume of each sample was calculated after measuring its dimensions using a pair of vernier callipers. Bending tests were carried out using an Instron Tensile Testing machine (JJ-T5002). Points were at a distance of 5 cm from each
RESULTS

Nearly all the trees were leaning away from the wind direction, towards an azimuth of 115°; three trees were leaning perpendicular to the wind direction, and in four of the trees the angle of lean was too slight to be measured using this system, therefore the trees were counted as ‘straight’. At the base of the tree, the stem was found to lean at an angle of 12.1 ± 2.6°, while at DBH, the angle of lean was 9.3 ± 1.8°. Further up the tree, at 5.0 m, the trees were not inclined. Most eccentric growth occurred underneath the direction of lean or towards an azimuth of 115° (direction of prevailing wind). Although not measured, reaction wood was observed on the compressed side in CSs of leaning trees.

Longitudinal distribution of heartwood

The proportion of HW increased progressively from the base of the trunk, where it accounted for 19% of the CS surface area, to DBH, where HW made up 24% of the CS; and at a height of 5 m, 26% of SW was transformed into HW (Table 1, Fig. 3). From DBH upwards, the proportion of HW gradually decreased, until it was non-existent at the base of the live crown.

Radial distribution of heartwood

The number of growth rings transformed into HW was variable around the trunk and between trees (Figs 3 and 4). As shown by Stokes and Berthier (2000), significantly more annual rings were transformed on the leaning or leeward side (45%) of the tree than on the opposite side or perpendicular to it (27%) (Fig. 4, P = 19.6, P < 0.001). The extension of HW into the SW zone was significantly correlated to SW eccentricity on the side of the tree held in compression during wind sway/lean (y = −1.433x + 0.818, R² = 0.66, P = 0.003, where y is the SW eccentricity and x is the HW extension).

Table 1. Mean characteristics of P. pinaster for 12 52-year-old trees

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Mean ± s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diameter at breast height (DBH) (cm)</td>
<td>34.4 ± 2.4</td>
</tr>
<tr>
<td>Total height (m)</td>
<td>29.3 ± 1.5</td>
</tr>
<tr>
<td>Height to live crown (m)</td>
<td>21.7 ± 5.3</td>
</tr>
<tr>
<td>% of sapwood at:</td>
<td></td>
</tr>
<tr>
<td>0 m</td>
<td>81.1 ± 3.1</td>
</tr>
<tr>
<td>1.3 m</td>
<td>76.1 ± 3.1</td>
</tr>
<tr>
<td>5 m</td>
<td>73.2 ± 3.3</td>
</tr>
<tr>
<td>Fresh weight of live crown (kg)</td>
<td>131.0 ± 18.4</td>
</tr>
<tr>
<td>Actual dry weight of live crown (n = 3) (kg)</td>
<td>77.0 ± 18.1</td>
</tr>
<tr>
<td>Surface area of foliage (calculated) (m²)</td>
<td>283.4 ± 34.3</td>
</tr>
</tbody>
</table>
Region where measurements were taken

**Fig. 4.** More growth rings are transformed into heartwood on the compressed side of leaning/wind-stressed trunks of *P. pinaster* than on the side held in tension or perpendicular to the direction of mechanical stress (*P* = 19:6, *P* < 0:001).

**Fig. 5.** Relationship between surface area of sapwood and foliage in *P. pinaster* for all trees considered together. Triangles and dashed line represent sapwood surface area at the base of the trunk (*y* = 259:0x + 74298, *R*^2^ = 0:85, *P* < 0:001); diamonds and complete line represent sapwood surface area at DBH (*y* = 283:8x + 103604, *R*^2^ = 0:86, *P* < 0:001); and circles and dotted line represent the sapwood surface area at a height of 5 m up the trunk (*y* = 385:6x + 81702, *R*^2^ = 0:82, *P* = 0:002).

Relationship between the surface area of the crown and that of the sapwood (*Pipe Model Theory*)

When all trees were considered together, the relationship between the surface area of SW and the crown was highly significant at the base of the trunk, at DBH, and at 5 m high (*Fig. 5*). At the base of the trunk there was a greater proportion of sapwood basal area with an equal amount of foliage surface area compared to further up the trunk. When leaning trees only were considered, regressions were still highly significant, even more so at the base of the trunk and at DBH (*Fig. 6*).

Mechanical tests

Mean *E* for the SW was slightly higher (8:1 ± 0:4 GPa) than that for HW (7:1 ± 0:4 GPa), although the difference was not significant. No significant difference in *E* was found when samples loaded on the radial face were compared to those loaded on the tangential face, for both SW and HW. However, *E* was found to be significantly lower in both HW and SW samples from the compressed side of the trunk, compared to samples taken from other regions in the stem (Table 2).

**Table 2. Mean values for the modulus of elasticity of samples taken from sap- and heartwood of *P. pinaster***

<table>
<thead>
<tr>
<th>Type of wood tested</th>
<th>Modulus of elasticity (GPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean-Sapwood</td>
<td>8:1 ± 0:5</td>
</tr>
<tr>
<td>Mean-Heartwood</td>
<td>7:1 ± 0:4</td>
</tr>
<tr>
<td>Sapwood</td>
<td></td>
</tr>
<tr>
<td>beneath lean/leeward</td>
<td>7:2 ± 0:6*</td>
</tr>
<tr>
<td>above lean/windward</td>
<td>8:1 ± 1:0</td>
</tr>
<tr>
<td>perpendicular to lean/wind</td>
<td>9:2 ± 0:6</td>
</tr>
<tr>
<td>Heartwood</td>
<td></td>
</tr>
<tr>
<td>beneath lean/leeward</td>
<td>6:4 ± 0:4**</td>
</tr>
<tr>
<td>above lean/windward</td>
<td>8:6 ± 0:5</td>
</tr>
<tr>
<td>perpendicular to lean/wind</td>
<td>8:4 ± 1:1</td>
</tr>
</tbody>
</table>

Values are means ± s.e.

**** *P* ≪ 0:01; *P* ≪ 0:05.

**DISCUSSION**

The longitudinal distribution of HW was found to vary slightly depending on distance along the trunk. The proportion of HW at 0 and 1:3 m was approx. 20% of the total surface area of the cross-section, while it was 26% at a height of 5 m. This finding confirmed the results of *Stokes* and *Berthier* (2000) who found that in the same stand, and for trees of the same age, there was a significantly smaller proportion of HW at the base of the trunk than at 2:5 m and even at 5 m. Measurements were not taken at 2:5 m; therefore, it is possible that a significant
difference may also exist at this height in the trees measured in this study. Stokes and Berthier (2000) proposed that the increase in SW area at the base of the trunk was due to a decrease in hydraulic conductivity, as cells in this zone are likely to have smaller lumens and thicker cell walls (Gartner, 1991).

Radial distribution of HW around the stem was highly irregular, depending on the direction in which measurements were taken. A greater number of growth rings were transformed into HW (45 %) on the side of the tree held in compression during wind sway/lean compared to the other sides (27 %). HW extension on the compressed side of the tree was significantly related to cross-section eccentricity. These results confirm those of Stokes and Berthier (2000), who proposed several theories concerning the function of such irregular HW. One hypothesis tested in this paper was that HW contributes to the bending stiffness of the tree in the compressed zone. However, results showed that the longitudinal $E$ of adult HW and SW of Maritime pine was not significantly different, therefore HW does not contribute specifically to the bending stiffness of leaning or wind-stressed trees. In order for HW to compensate for the fact that it is made up of a large quantity of juvenile wood, which has a low $E$ (Dumail, 1999), and is situated near the neutral axis of the trunk, the $E$ of HW would need to be much higher than that of the SW (Mencuccini et al., 1997; Niklas, 1997a,b). Niklas (1997a,b) found that values for $E$ were slightly higher in the HW of Black locust, compared to the SW: thus may be due to the fact that, in angiosperms, more extractives are produced during the transformation of SW to HW, and that tyloses may frequently form in the vessels (Hillis, 1987), thus increasing density, and hence wood strength. Relatively fewer changes occur in the transformation of SW to HW in Maritime pine (Gachet et al., 2000), therefore accounting for the fact that $E$ did not increase in HW. However, values of $E$ for wood from the compressed side of leaning trees were significantly lower than those from other regions around the trunk. Compression wood was seen in these zones, and it is well documented that compression wood has a lower $E$ than that of normal wood due to its microstructure (Timell, 1987).

A second hypothesis proposed by Stokes and Berthier (2000) concerning the formation of irregular HW, was that it is a process regulated internally within the tree to maintain an optimal and constant proportion of SW around the trunk. This proportion of SW would thus be related to the surface area of the crown foliage, and regulated so that ‘waste’ or superfluous SW is transformed into HW, which is less costly for the tree to maintain. The application of the Pipe Model Theory (Shinozaki et al., 1964a,b) to trees with irregular and eccentric HW formation confirmed that a strong relationship does indeed exist between the surface area of SW and that of the crown foliage. It can be seen that a strong link exists between the production of foliage and the senescence of SW, although whether SW production governs foliage biomass, or vice versa is not yet known.

Recently, several studies have proposed that formation of HW is a process regulated internally within the tree, rather than a passive state whereby sapwood simply becomes dysfunctional due to age. It has been shown that polyphenols and flavonoids, responsible for the durability of HW, and which are implicated in the HW formation process, are synthesized in situ in the transition zone, and are not transported from the cambium to the HW. Genes are expressed for the production of these compounds at specific times of the year; however, the signal switching on this mechanism is not yet known (Beritognolo et al., 2000). Sperry et al. (1991) showed that there was a selective embolizing of older vessels in Populus tremuloides Michx., due to a degradation of the pit membrane, thus leading to HW formation. However, this degradation of the pit membrane was not a function of age because it occurred after 1 year in vigorously-growing branches, but was much delayed in slower-growing branches. Sperry et al. (1991) therefore suggested that it is the immediate physiological environment of the xylem which governs pit degradation, but the mechanism by which this occurs is not known. It is possible that wear and tear of the pit membrane is caused by repetitive mechanical loading of the trunk and branches, as mechanical perturbation has recently been found to decrease sap flow within a tree stem, thereby having implications for embolism formation (Stokes et al., 2000). Sap flow has also been found to be lower in the regions of branches containing compression wood (Spicer and Gartner, 1998), which may be an additional factor contributing to early cell dysfunction, and hence HW formation. Both mechanical action and compression wood formation may lead to the production of ethylene, a gas implicated in both the process of HW formation (Hillis, 1987) and the adaptive growth response of plants to mechanical loading. In mechanically perturbed plants, levels of ethylene increase, prohibiting longitudinal growth and promoting radial growth (Telewski, 1990). Ethylene may be involved in the expression of certain genes implicated in HW formation, but further studies need to be carried out to confirm this hypothesis (Gachet et al., 2000).

It appears that in Maritime pine the heartwood that forms irregularly and in greater quantities on the compressed sides of leaning or wind-stressed trees does not serve a mechanical function by increasing the bending stiffness of the trunk. However, as there is a distinct relationship between the surface area of the sapwood and that of the crown foliage, heartwood formation appears to be regulated internally within the tree. Such a mechanism would allow the tree to maintain a constant and optimal sapwood surface area, an important criterion for survival in a species often subjected to severe drought for long periods.

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