

Variation in morphological and wood cell traits in coppice stems of *Populus nigra* L. and *Salix alba* L.

SERAY ÖZDEN KELEŞ*

Department of Forest Engineering, Kastamonu University, Kastamonu, Turkey

*Corresponding author: sozden@kastamonu.edu.tr

Citation: Özden Keleş S. (2021): Variation in morphological and wood cell traits in coppice stems of *Populus nigra* L. and *Salix alba* L. J. For. Sci., 67: 396–407.

Abstract: Coppice management is an ecologically important silvicultural practice to provide the quicker and higher potential of wood biomass production for industrial demands. Understanding morphological and anatomical responses of coppiced trees could help to determine the quantity and quality of wood and thus provide better management of coppiced tree plantations for short-time biomass production. However, there is a little investigation in morphological and anatomical adaptation in different fast-growing tree species. The present study, therefore, studied how morphology and anatomy vary between two fast-growing coppices of *Populus nigra* L. (black poplar) and *Salix alba* L. (white willow). Each coppiced tree was grown in a similar habitat and was at a similar age. However, each coppiced tree showed different morphological and anatomical plasticity in their stems in response to environmental factors. Poplar coppices showed better anatomical properties due to greater vessel diameter, fibre length, fibre width, fibre wall thickness, and ray height; however willow coppices had better morphological plasticity which had higher average stem height and ring width. The results suggest that willow coppices had the greater height growth potential even at 2 years of age than poplar coppices.

Keywords: coppicing; fast-growing species; wood cell anatomy; plant morphology

Environmental and ecological conditions directly affect tree growth and development in different ways. The process of rapid industrialization and globalization also has substantial environmental impacts on the forest ecosystem because the vast majority of forest biomass and resources is often used for domestic and industrial purposes. Therefore, deforestation and forest degradation may increase day by day to meet the wood energy demands, which also significantly impairs forest biomass and bioenergy (Barua et al. 2014; Wu et al. 2016; Jeelani et al. 2017; Xu et al. 2017; Zalesny Jr., Bauer 2019). Previous researches have shown that only traditionally managed forest stands or natural forests could not satisfy the massive biomass and ecosystem demands (FAO 2009, 2010, 2016; Spinelli et al. 2019). Therefore, it is crucial to offer sustainable forest management systems to respond to an inexpensive, feasible, and high production potential.

Coppicing is one of the potentially important reforestation options to provide more efficient and quick forest management inputs (Evans 1992; Fujimori 2001). The principle of coppicing is to cut trees just above the ground level on a regular rotation (every 5–35 years) and then new shoots will regrow from the cut or damaged stumps (Wilson 1968; Blake 1980, 1983; Kauppi et al. 1988; Fuller, Warren 1993; Rinne et al. 1994; Dickmann et al. 1996). The coppiced trees could regrow rather faster than the unmanaged trees since stems use soil nutrients and minerals directly, therefore they produce an extensively developed root system that makes the hydraulic resistance lower to the leaves. Coppicing thus could be considered as the renewable energy sources to meet the current increasing requirements for the wood biomass since coppicing ensures the required size of stems for particular purposes in short waiting time and in-

<https://doi.org/10.17221/208/2020-JFS>

tervals (Hardesty 1987; Buckley 1992; Kennedy 1998; Fenning, Gershenzon 2002; Jarman, Kofman 2017). However, not all tree species have the ability of coppicing; coppiced stems are naturally regenerated by mainly the hardwood tree species. Poplar and willow are the most promising tree species for coppicing plantations due to their key roles in the ecosystem which are to provide global plantation, fast-growing, coppicing ability and harvested on a short rotation, great renewable energy potential, valuable forest products, soil stabilization, rehabilitation of degraded land and erosion control on the river (Wilkinson 1999; Licht, Isebrands 2005; Tsarev 2005; Kuzovkina, Volk 2009; Weih 2009; Isebrands et al. 2014).

The success of coppice management however depends on the type of tree species, growing site, and environmental conditions. The environmental factors can affect the growth and development of tree species by changing morphological and anatomical cell properties. Trees are living organisms and the body of a tree is generated in two phases which are the growth and development in length (primary growth) and diameter (known as secondary growth). Morphologically, height growth and growth rate are both considered to be good indicators of a tree to reflect the environmental adaptivity or vitality of a tree (Dobbertin 2005). Hence, when light, soil water, and nutrients are less than ideal, the growth of a tree is limited and thus the height growth rate may be reduced (Sands, Mulligan 1990; Craine, Dybzinski 2013).

At the anatomical level, the vascular cambium is the key growth tissue in a tree that is responsible for the secondary growth (known as an increase in diameter or radial growth). Secondary growth in a stem and secondary growth in a root are interconnected axial and radial vascular systems. In the axial system, the vascular cambium is seen as a continuous cylinder of the meristematic layer between xylem and phloem. The function of the xylem is to conduct water and the phloem is responsible for sugar conduction up and down through the axis of a tree. Wood is also produced by the accumulation of the secondary xylem and therefore wood formation, quality, and biomass are the product of the activity of vascular cambium (Murmanis 1970; Panshin, de Zeeuw 1980; Larson 1994; Chaffey 1999). In the axial vascular system, secondary xylem or wood are made up of different types of tree cells. In angiosperms, the wood

xylem is made up of fibres, vessels, rays, and parenchyma cells (Crang et al. 2019). The function of the cells is to support and protect the stem, conduct water and minerals, storage, and cavitation recovery (Tyree, Sperry 1989; Brodersen et al. 2010; Crang et al. 2019). All of those cells can show alterations in their geometry, distribution, number, size, lumen width, and wall thickness depending on the ecological and environmental conditions. Under limited conditions (i.e. low water availability), the dimension of the cell decreases, and the cell wall thickness increases (Levitt 1980; Pitman et al. 1982a, b; Guerfel et al. 2009). The annual growth ring is also one of the important characteristics of the cambial activity which provide favourable information related to how trees develop and grow in a year growing period (Fritts 1976; Fritts 2001; De Luis et al. 2011a, b; Biondi et al. 2014). Trees generally exhibit wider annual growth rings when the water conditions are ideal; while the tree ring width decreases with the limited access to water (Fritts 1976; Schweingruber 1996; Hallinger et al. 2010). The processes of wood cell development are also responsible for the variation in wood density. Wood density is known as the physical property of wood which shows the amount of wood substance per wood volume, therefore higher density means more total wood biomass (Thomas et al. 2007; Nam et al. 2018). Density is mostly affected by the changes in the environment. A previous study by Thomas et al. (2007) showed that wood density increased with the increase in growth temperature (max. 30 °C), while density decreased at 35 °C. Morphology and anatomy together can therefore give significant clues of the growth and development success of the tree species and also show adaptive responses of coppice trees to the effect of local environmental changes (Schweingruber 1996; Hallinger et al. 2010; Gartner-Roer et al. 2013; Novak et al. 2013).

The specific objective of this study was, therefore, to investigate how two different fast-growing tree species exhibit variations in their morphological plasticity and wood cell anatomical characteristics under the same climatic conditions. Understanding morphological and anatomical characteristics of poplar and willow may help to ensure better processes of growth, development, and life history function in coppicing management so providing survival and ecological strategies. Furthermore, it advances to maintain the sustainable plantation

and nursery management of these species for a renewable source of biomass demands.

MATERIAL AND METHODS

Study area. The study area is located in the north-western part of the Kastamonu province, Turkey (33°24'E; 41°28'N). The altitude was 984 m a.s.l. The study was particularly conducted on this location due to the following reasons: (1) traditional and extensive regeneration of poplar and willow coppicing populations; (2) coppice populations grown near the lake (along waterways, but not waterlogged); (3) similar age and the same growth demands; (4) having the same porosity. The climate was continental, with an average annual air temperature of 9.6 °C and total precipitation of 494.4 mm·year⁻¹, recorded by the nearest weather station. The distance between weather station and research plot was approximately 4.2 km. The soil type was classified as sandy loam.

In this study, *Populus nigra* L. (black poplar) and *Salix alba* L. (white willow) were selected due to their successful coppicing ability. Poplar and willow are also known as fast-growing tree species because they occur naturally and grow faster in height. Poplar more likely grows better in highly moist soils close to the water source, while willow can grow both along waterways and in damp stony upland areas (Fung et al. 2001; Sulaiman 2006).

Tree sampling. In June 2019, coppice stems of poplar and willow were harvested at 3 cm above the ground level and one stem was collected from each coppice stump. To eliminate the effect of neighbourhood competition, coppice stems were produced 2 m away from each individual. Each cutting had 2-years-old shoots. A total of thirty-five coppice stems for each tree species (i.e. 35 stems for poplar and 35 stems for willow) was cut and all cuttings were produced from dormant shoots. All cuttings were then wrapped in wet paper and kept in closed plastic bags to prevent dehydration until tests.

Morphological and anatomical measurements. Each stem was individually sampled to measure morphological traits such as stem height, stem basal diameter, pith proportion (%), xylem proportion (%), and bark proportion (%). The stem height was measured using a metric folding ruler. The stem basal diameter was performed at the base of the stem (near the ground level). The stem diameter measurements were taken over the bark in the plane

and perpendicular plane to the stems using a digital calliper. After stem diameter measurements, the bark was removed from the stem, and then the remaining diameter was measured (including xylem and pith portions). The diameter of the pith (at the centre of the stem) was then measured both in the plane and perpendicular plane to the stems using a digital calliper. To specify the proportions of each segment (pith, bark, and xylem) in the total stem diameter, the first areas of segments were calculated. The areas were assessed using the area of a circle formula since each coppice stem was nearly circular in cross-section, i.e. the ratios in diameter between parallel and perpendicular planes were less than 1.2%. Therefore, the transverse geometry of stems could be considered as circular (Niklas 1992). Finally, the areas of pith, bark, and xylem were divided by the total stem area (over bark diameter) to indicate the proportion of each segment (Özden, Ennos 2018). To determine average tree ring width, small cross-sections were taken from each coppice stem.

For cell anatomical observations, harvested stems were transversely cut into small pieces (around 1-cm length). To cut thin slices or sections, the sticks were softened in boiling water, then kept in equal parts of water, glycerol, and ethanol (Yaltirik 1971). Softened specimens were then prepared in both cross and tangential sections of the thickness of 20–25 µm using a sliding microtome. In softened specimens, vessel diameter (VD) was measured in cross-sections; ray height (RH) and ray width (RW) were measured in tangential sections. Ten individual stems were used for both poplar and willow coppices and thus measurements were performed on total twenty stem samples for fibre cell measurements. To measure the fibre cell anatomical characteristics, the sticks were cut into small strips, then the strips were macerated using Franklin's (1945) method (1:1 equal parts of hydrogen peroxide and concentrated glacial acetic acid). Macerated pieces were then stained with safranin to measure fibre properties (fibre length – FL, fibre width – FW, fibre wall thickness FWT, and fibre lumen width – FLW). For each anatomical cell characterization, twenty-five measurements were done (IAWA 1989). All cell measurements were done using a light microscope (Leica DM750 photomicroscope, Leica Microsystems Ltd., Switzerland) and digital photographs were obtained by Leica LAS EZ Image Analysis Software (Version 3.4.0., 2016).

<https://doi.org/10.17221/208/2020-JFS>

Wood density. To calculate basic wood density, the most common method is to divide the oven-dry weight of wood by its green volume (or water-saturated volume) (Phillips 1965b; Britt 1967). In this study, therefore, first harvested fresh stems were cut into small pieces of around 2-cm length, and then all specimens were immersed in a closed container containing liquid water until all hydrated. After that, the water displacement method was used to measure the green volume of wood: each specimen was placed in distilled water utilizing a needle in a beaker standing on an electronic weighing balance that gave the mass of water displacement. Finally, water-saturated specimens were oven-dried at 103 °C. The ratio of the oven-dry weight of the specimen to its green volume gave the basic wood density (Phillips 1965b; Britt 1967; Simpson 1993; Barnett, Jeronimidis 2003).

Statistical analysis. Statistical analyses were designed to test the effects of tree species (poplar vs. willow) on the morphological (stem height, stem diameter, pith%, xylem% and bark%), ring width and cell anatomical properties (vessel diameter, fibre length, fibre width, fibre lumen width, fibre wall thickness, ray height, and ray width) and wood density traits using SPSS 19.0 statistical software package (Windows, 2010). One-way ANOVA test was used to assess whether there are any statistically significant differences between the means of morphological, anatomical, and wood density parameters between poplar and willow coppices at the $\alpha = 0.05$ level. The relationship between different properties of two coppice stems was also quantified using the linear regression tests.

RESULTS AND DISCUSSION

Stem morphological characteristics. Although each coppiced tree was grown in the same habitat and was two years old, the morphological characteristics of poplar and willow showed different patterns in their coppice stems (Figure 1). One-way ANOVA results indicated that willow coppices had significantly greater stem heights than poplar coppices ($F_{1, 69} = 5.08$; $P < 0.05$). The stem height was on average 118.6 cm in willow coppices and 105.5 cm in poplar coppices (Figure 1). This finding is consistent with that of Hussain et al. (2009), who also studied the growth performance of poplar (*P. deltoides* × *P. nigra* ‘Dudley’) and willow (*S. mat-sudana* × *S. alba* ‘Tangoio’) species at the juvenile

stage. They found that the stem height was significantly greater in willow trees than in poplar trees in the second year of the plant growth, i.e. average stem height was found to be 190 cm in willows and 135 cm in poplars. Stem diameter was also found to be significantly higher in willows than in poplars in the same study. This differs from the findings presented here because average basal stem diameter did not differ significantly between poplar and willow coppices ($P > 0.05$), that is poplar had on average 9.4 mm stem diameter and willow had on average 9.3 mm stem diameter. The variation in the growth potential of poplar and willow could be related to the management of the harvesting period since the coppice stems were harvested from 2-years-old shoots in this study. These results however seem to be consistent with other researches that revealed that willow coppices showed faster growth than poplar coppices in the young stage of their growth (Christersson 2008; Mola-Yudego, Aronsson 2008; Dimitriou, Rosenqvist 2011; Dimitriou, Rutz 2015). A study by Dimitriou and Rutz (2015) also suggested harvesting willow coppices after a short period (i.e. short rotations of 3–6 years) while poplar coppices require a longer coppice rotation period (i.e. 10–15 years). The difference in height growth between poplar and willow coppices could also be due to root growth and the concentrations of organic carbon. In a forest ecosystem, roots are a crucial part of the tree since they facilitate the vast majority of the carbon cycle and therefore provide a great contribution to total tree biomass (Keyes, Grier 1981; Fogel, Hunt 1983; Jackson et al. 1996; Schlesinger 1997; Meinen et al. 2009). Phillips et al. (2014) studied the root growth in poplar and willow species at the young growth stage (3 years old).

Their study showed that young willows had greater lateral growth than poplars. The greater proportion and depth of roots may therefore help to take up more water and minerals from soils for plant growth, so plants grow better in height and could have a longer lifespan (Jackson et al. 2000; Schenk, Jackson 2002). The higher rate of height growth in willow could also be related to the concentrations of organic carbon in the soil. A study by Dimitriou and Mola-Yudego (2017) investigated the concentration of soil organic carbon in poplar and willow. They found that the concentration of organic carbon was greater in young willows than in young poplars. It could be concluded that willows in the juvenile stage

have a better lateral root system which advances to reach soil sources more quickly, so willows grow better than poplars. In this study, therefore it could be suggested that willow coppices had the higher growth potential than poplar coppices within a few years after harvesting.

The % of pith, xylem, and bark were also measured between two coppiced trees (Figure 1). However, statistically, pith%, xylem% and bark% did not show any significant differences between poplar and willow ($P > 0.05$). Pith is one of the inner tissues that are located in the central region of the stems. The main function of pith is to provide nutrient

storage and conduction throughout the stem for internodal elongation growth and development (Kraus 1867; Brown et al. 1995). Brown et al. (1995) studied the role of pith in intermodal growth and development of American sweetgum. Their study suggested that the pith volume positively affects the internode length that is increasing in the proportion of pith and makes the internode growth greater. In this study, however, no significant relationships were found between average pith% and stem height ($P > 0.05$). Therefore, more studies are required to prove the positive effect of pith proportion on the intermodal length growth.

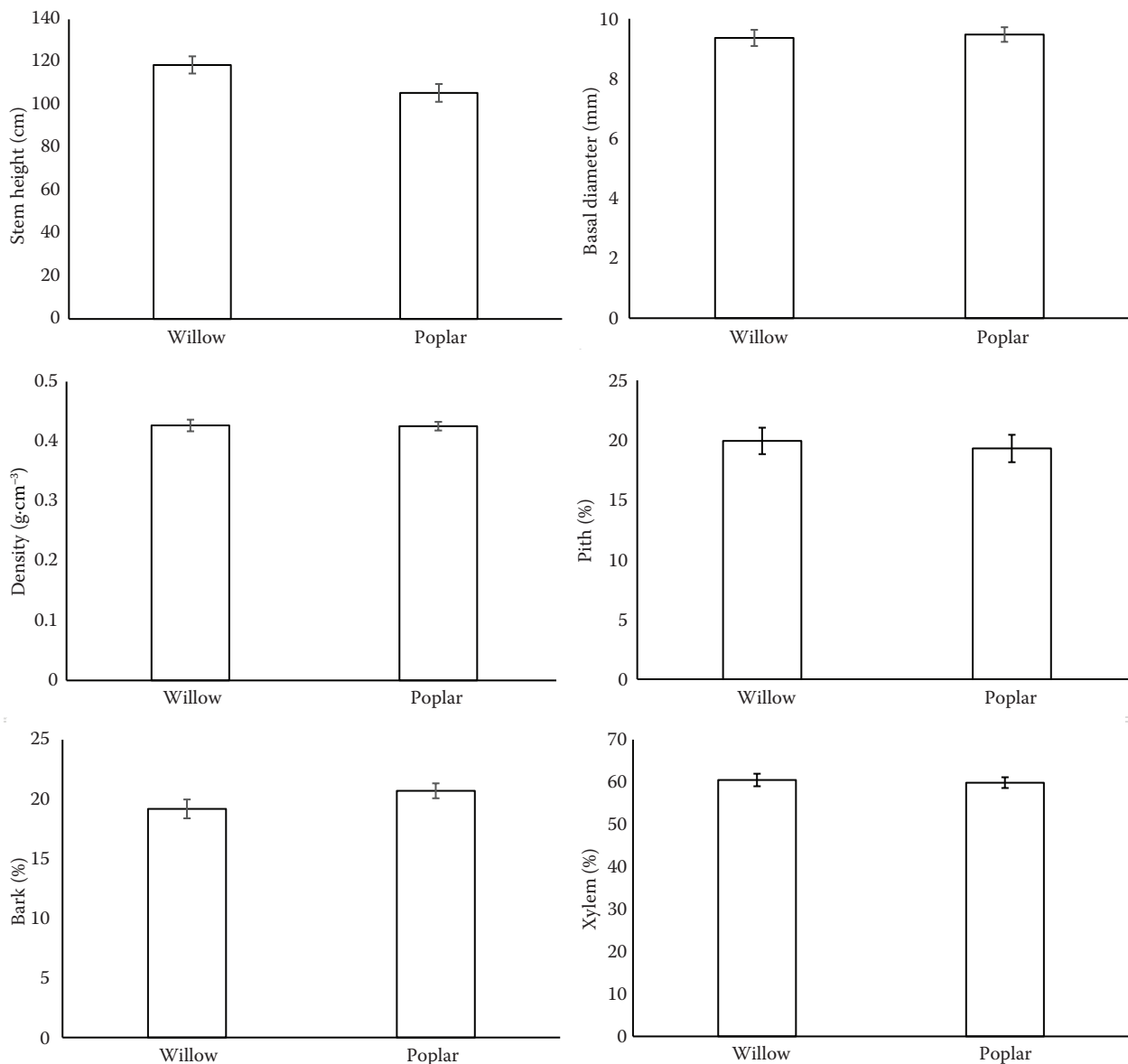


Figure 1. Average morphological and basic wood density traits (stem height, basal stem diameter, pith%, bark% and xylem%) in poplar and willow coppices. A standard error is shown by the error bars

<https://doi.org/10.17221/208/2020-JFS>

Tree ring width, wood cell anatomical properties and basic wood density

Anatomical variations and basic wood density in poplar and willow coppices were examined. Average tree ring width (TRW), vessel diameter (VD), fibre length (FL), fibre width (FW), fibre lumen width (FLW), fibre wall thickness (FWT), ray height (RH), and ray width (RW) are shown in Table 1.

Among the poplar and willow coppices, tree rings were found to be significantly wider in willow coppices than in poplar coppices ($F_{1,69} = 4.23$; $P < 0.05$); the average ring width was on average 1.43 mm in willow coppices and 1.22 mm in poplar coppices (Table 1). Annual ring width is one of the key indicators to understand the relationship between climate and growth of a tree and show how trees adapt or respond to their water availability. In general, wider annual rings show a faster-growing season with higher water availability, while smaller rings indicate there is limited water to grow (Fritts 1966). In this study, wider annual rings were observed in willow coppices than in poplar coppices. It could be suggested that willows had a higher ability to use water sources than poplar coppices, therefore the activity of the cambium cell production was greater which provides wider tree rings.

Poplar and willow coppices also showed different cell anatomical properties to their local environments (Figure 2). One of the key characteristics to determine tree adaptation to environmental conditions is xylem anatomy. The xylem of angiosperms is made up of vessels, fibres, rays, and other cell types. Vessels belong to the important conductive tissues and are responsible for sap or water

transport (Panshin, de Zeeuw 1980; Larson 1994; Pfautsch 2016). Poplar and willow are both also diffuse to semi-diffuse species which have nearly the same vessel diameter throughout the annual growth ring (Figures 1 and 2). The anatomical measurements showed that the diameter of vessel cells was significantly higher in poplar coppices than in willow coppices (average 25.1 μm for poplar and 20.8 μm willow) ($P < 0.001$). This finding is in agreement with the results of a previous study by Panshin and de Zeeuw (1980), who also investigated the difference in the size of vessels between poplar and willow. In general, the size of vessels plays a key role to understand xylem vulnerability or risk to cavitation by water stress (Sperry et al. 1988; Cochard, Tyree 1990; Davis et al. 1999; Cobb et al. 2007; Morán-López et al. 2014). Previous works showed that larger vessels more likely cause xylem embolism. It could be therefore suggested that poplar coppices could be more vulnerable to drought- or freeze-induced stresses due to their larger vessel size, thus hydraulic conductivity of a stem may decrease. However, willow coppices may show greater cavitation resistance to embolism due to their smaller vessels.

The fibres also belong to the important xylem tissues in angiosperms that provide mechanical support to a tree. In general, the fibres are considered to be a mechanical contribution to wood quality, however, the fibres may also give ecologically better insights into how trees respond to environmental changes (Hacke et al. 2001; Arend, Fromm 2007; Fonti et al. 2013; De Micco et al. 2016). Previous researches have found that the dimension of wood

Table 1. Main descriptive variables obtained for the poplar and willow coppices considering ring width and wood cell traits; the one-way analysis of variance (ANOVA) was used to assess whether there are any statistically significant differences in anatomical characteristics between poplar and willow coppice stems

Morphological and anatomical parameters		Mean \pm SE	
		poplar	willow
Average tree ring width	mm	1.22 \pm 0.06	1.43 \pm 0.07*
Vessel diameter		26.5 \pm 0.93***	21.1 \pm 1.10
Fibre length		1 018.1 \pm 38.3*	897.2 \pm 40.9
Fibre width		36.7 \pm 1.73*	32.5 \pm 2.17
Fibre lumen width	μm	4.1 \pm 0.21 ^{ns}	4 \pm 0.18
Fibre wall thickness		2.72 \pm 0.12***	2.19 \pm 0.10
Ray height		294.4 \pm 19.3**	234.7 \pm 17.8
Ray width		25.2 \pm 1.06	29.7 \pm 1.78*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns – non-significant

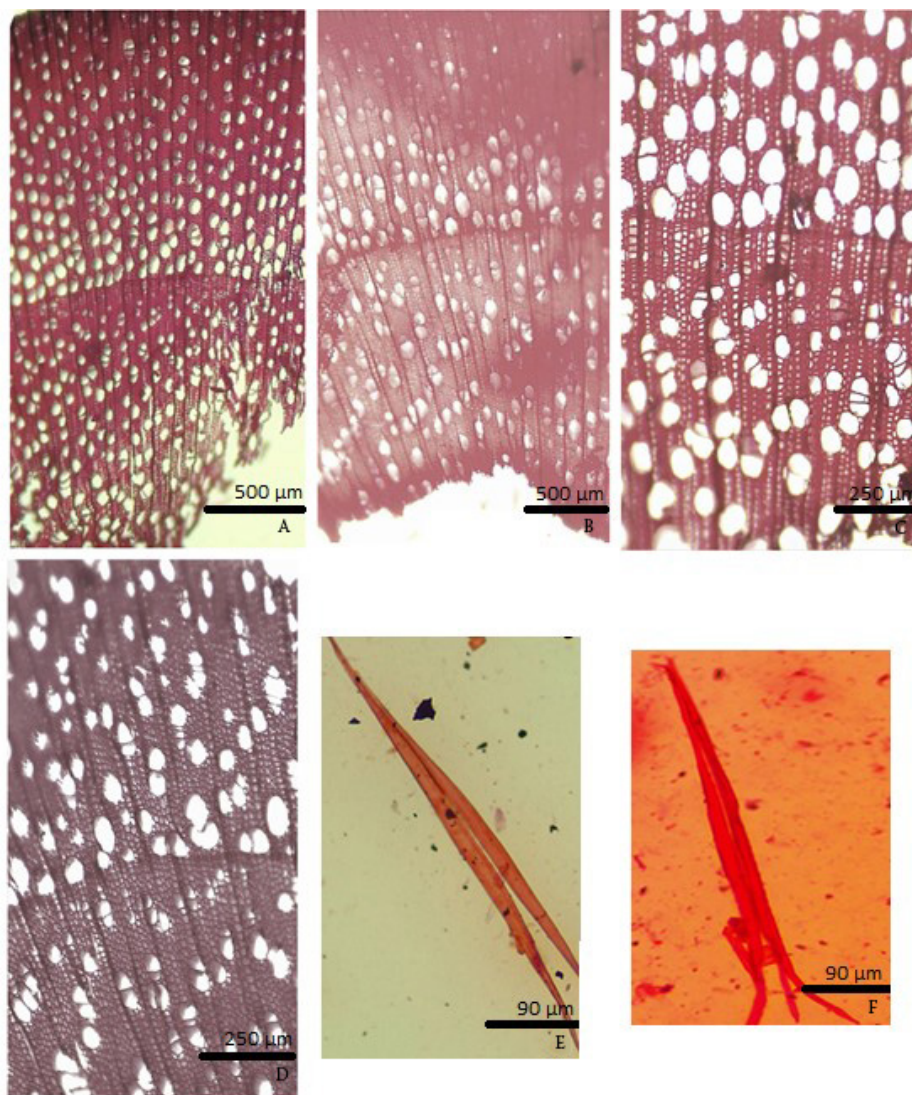


Figure 2. Light microscopy images showing the general cross-section of the stem of poplar and willow coppices; (A) cross-section of the stems of poplar coppices (4×), (B) cross-section of the stems of willow coppices (4×), (C) vessel distribution in the cross-section of the stems of poplar coppice (10×), (D) vessel distribution in the cross-section of the stems of willow coppice (10×), (E) fibre element in macerated material of the stems of poplar coppice (10×), (F) fibre element in macerated material of the stems of willow coppice (10×)

fibre cells is interestingly sensitive to the environmental changes like vessels; that is the dimension of wood fibres decreases with low water availability and drought-induced changes (Arend, Fromm 2007; de Micco et al. 2016). In this study, the fibre traits were therefore determined for each coppice stem to show whether there are any variations in fibre dimensions between poplar and willow coppices (Table 1). The anatomical analyses revealed that poplar coppice stems had longer and wider fibres than willow coppices: fibre length (FL) varied between 130 μm and 1 450 μm in poplar coppices, and from 70 μm to 1 230 μm in willow coppices; fibre

width (FW) varied between 21.3 μm and 60 μm in poplar coppices, and from 17.4 μm to 60 μm in willow coppices (Table 1). One-way ANOVA results also indicated that average FL and FW were significantly greater in poplar coppices than in willow coppices ($P < 0.05$). These results are in line with those of previous studies which showed that poplars had longer fibres than willows (Panshin, de Zeeuw 1980; Hernández et al. 1998; Schoch et al. 2004). Average FLW and FWT values showed differences related to the type of coppice species. Each coppice stem (poplar vs. willow) showed approximately similar average FLW values in their stems,

<https://doi.org/10.17221/208/2020-JFS>

so no significant difference was found in the values of FLW between poplar and willow coppices (average FLW was 4.1 μm in poplar coppices and 4 μm in willow coppices) ($P > 0.05$). However, a statistically significant difference was observed in average fibre wall thickness (FWT) between poplar and willow coppices. Poplar coppice stems had significantly greater FWT values than willow coppices ($P < 0.05$): the average FWT was 2.71 μm in poplar and 2.26 μm in willow. Cobas et al. (2013) compared wood cell traits in poplar and willow juvenile woods. However, they did not find any significant differences in average FL, FW, FLW, FWT, and VD between poplar and willow juvenile woods. This study partly agreed with the study of Cobas et al. (2013) because the average FLW did not differ significantly between poplar and willow coppices.

The characteristics of the rays were also investigated (Table 1). Rays of poplar coppices were homocellular in stem wood, while rays of willow coppices were heterocellular in stem wood. The ray height varied between eight and twenty-two cells in poplar coppices and it ranged from five to twenty cells in willow coppices. The average RH of poplar coppices was significantly greater than the average RH of willow coppices (on average 294.4 μm in poplar and 234.7 μm in willow) ($P < 0.05$). However, the average RW values showed opposite results, i.e. willow coppices had a significantly greater average width of rays than poplar coppices ($P < 0.05$) (on average 29.7 μm in willow coppices and 25.2 μm in poplar coppices) (Table 1).

Basic wood density was also measured for each coppice stem. Interestingly, wood density did not differ significantly between poplar and willow coppice stems; that is average density was 0.42 $\text{g}\cdot\text{cm}^{-3}$ in poplar coppices and 0.43 $\text{g}\cdot\text{cm}^{-3}$ in willow coppices ($P = 0.926$). No difference between the two species may be explained by similar growth conditions since each species was grown in the same environment (i.e. the same air temperature and rainfall). Klačnja et al. (2013) also studied the wood densities in poplar and willow species. In their studies, the wood density was found to be 0.33 $\text{g}\cdot\text{cm}^{-3}$ in poplar and 0.34 $\text{g}\cdot\text{cm}^{-3}$ in willow. Their study also showed no significant differences in wood densities between poplar and willow species. The present study showed rather higher wood density values than the results of Klačnja et al. (2013), the difference between mean values could be related to the difference between study sites.

CONCLUSION

This study shows differences in morphological traits, cell anatomical properties, and tree ring widths in poplar and willow coppices under the same environments. Here, the findings showed that willow coppices had greater height growth than poplar coppices. This may suggest that willows had a higher ability for coppicing than poplars and therefore willows could be more useful for short rotation coppice management since willows produced quite taller stems even at the juvenile stage (2-year age). Poplar and willow also showed specific anatomical characteristics of ring width formation and wood cell development. The size of xylem cells was greater in poplar coppices than in willow coppices, whereas annual tree ring width and RW were greater in willow coppices. The anatomical results provided valuable signs about the response of each coppice that stems from environmental changes. This study thus clearly showed that different coppice trees that were grown in a similar habitat and were of similar age could improve species-specific traits in their morphological and anatomical structure. Particularly, the difference in anatomical properties of two coppiced trees may provide a better understanding of how poplar and willow will cope with future environmental conditions. In the present study, it may be suggested that willows may more likely survive to feature unpredictable changes in the environment (drought-induced or freezing stresses) more easily than poplars due to their smaller vessel size which provides a lower risk of cavitation.

REFERENCES

- Arend M., Fromm J. (2007): Seasonal change in the drought response of wood cell development in poplar. *Tree Physiology*, 27: 985–992.
- Barnett J.R., Jeronimidis G. (2003): *Wood Quality and Its Biological Basis*. Oxford, Blackwell: 226.
- Barua S.K., Lehtonen P, Pahkasalo T. (2014): Plantation vision: potentials, challenges and policy options for global industrial forest plantation development. *International Forestry Review*, 16: 117–127.
- Biondi F., Hay M., Strachan S. (2014): The tree-ring interpolation model (TRIM) and its application to *Pinus monophylla* chronologies in the Great Basin of North America. *Forestry: An International Journal of Forest Research*, 87: 582–597.

<https://doi.org/10.17221/208/2020-JFS>

- Blake T.J. (1980): Effects of coppicing on growth rates, stomatal characteristics and water relations in *Eucalyptus camaldulensis* Dehn. *Functional Plant Biology*, 7: 81–87.
- Blake T.J. (1983): Coppice systems for short-rotation intensive forestry: The influence of cultural, seasonal, and plant factors. *Australian Forestry Research*, 13: 279–291.
- Britt K.W. (1967) Wood and fiber properties: measurement and interpretation. In: *Proceedings of 4th For Bio Conference TAPPI*, Appleton, Month Day, 1967: 84–98.
- Brodersen C.R., McElrone A.J., Choat B., Matthews M.A., Shackel K.A. (2010): The dynamics of embolism repair in xylem: In vivo visualizations using high-resolution computed tomography. *Plant Physiology*, 154: 1088–1095.
- Brown C.L., Sommer H.E., Pienaar S.L.V. (1995): The predominant role of the pith in the growth and development of internodes in *Liquidambar styraciflua* (Hamamelidaceae). I. Histological basis of compressive and tensile stresses in developing primary tissues. *American Journal of Botany*, 82: 769–776.
- Buckley G.P. (1992): *Ecology and Management of Coppice Woodlands*. Dordrecht, Springer Netherlands: 336.
- Chaffey N. (1999): Cambium: old challenges-new opportunities. *Trees*, 13: 138–151.
- Christersson L. (2008): Poplar plantations for paper and energy in the south of Sweden. *Biomass and Bioenergy*, 32: 997–1000.
- Cobas A.C., Felissia F.E., Silvia Monteoliva S., Area M.C. (2013): Optimization of the properties of poplar and willow chemimechanical pulps by a mixture design of juvenile and mature wood. *BioResources*, 8: 1646–1656.
- Cobb A.R., Choat B., Holbrook N.M. (2007): Dynamics of freeze–thaw embolism in *Smilax rotundifolia* (Smilacaceae). *American Journal of Botany*, 94: 640–649.
- Cochard H., Tyree M.T. (1990): Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiology*, 6: 393–407.
- Craine J.M., Dyzinski R. (2013): Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, 27: 833–840.
- Crang R., Lyons-Sobaski S., Wise R. (2019): *Plant Anatomy: A Concept-Based Approach to the Structure of Seed Plants*. Cham, Springer: 725.
- Davis S.D., Sperry J.S., Hacke U.G. (1999): The relationship between xylem conduit diameter and cavitation caused by freezing. *American Journal of Botany*, 86: 1367–1372.
- De Luis M., Novak K., Raventós J., Gričar J., Prislán P., Čufar K. (2011a): Climate factors promoting intra-annual density fluctuations in Aleppo pine (*Pinus halepensis*) from semi-arid sites. *Dendrochronologia*, 29: 163–169.
- De Luis M., Novak K., Raventós J., Gričar J., Prislán P., Čufar K. (2011b): Cambial activity, wood formation and sapling survival of *Pinus halepensis* exposed to different irrigation regimes. *Forest Ecology and Management*, 262: 1630–1638.
- De Micco V., Battipaglia G., Balzano A., Cherubini P., Aronne G. (2016): Are wood fibres as sensitive to environmental conditions as vessels in tree rings with intra-annual density fluctuations (IADFs) in Mediterranean species? *Trees*, 30: 971–983.
- Dickmann D.I., Nguyen P.V., Pregitzer K.S. (1996): Effects of irrigation and coppicing on above-ground growth, physiology, and fine-root dynamics of two field-grown hybrid poplar clones. *Forest Ecology and Management*, 80: 163–174.
- Dimitriou I., Rosenqvist H. (2011): Sewage sludge and wastewater fertilisation of Short Rotation Coppice (SRC) for increased bioenergy production – Biological and economic potential. *Biomass and Bioenergy*, 35: 835–842.
- Dimitriou I., Rutz D. (2015): *Sustainable Short Rotation Coppice: A Handbook*. Munich, WIP Renewable Energies: 102.
- Dimitriou I., Mola-Yudego B. (2017): Poplar and willow plantations on agricultural land in Sweden: Area, yield, groundwater quality and soil organic carbon. *Forest Ecology and Management*, 383: 99–107.
- Dobbertin M. (2005): Tree growth as indicator of tree vitality and of tree reaction to environmental stress: A review. *European Journal of Forest Research*, 124: 319–333.
- Evans J. (1992): *Plantation forestry in the tropics*. 2nd Ed. Oxford, Oxford University Press: 422.
- FAO (2009): *Enhancing Stakeholder Participation in National Forest Programmes: A Training Manual*. Rome, FAO: 121. Available at: <http://www.fao.org/3/i1858e/i1858e.pdf>
- FAO (2010): *Global Forest Resources Assessment 2010*, FAO Forestry Research Paper 163. Rome, FAO: 378. Available at: <http://www.fao.org/forestry/fra/fra2010/en/>
- FAO (2016): *Global Forest Resources Assessment 2015: How Are the World's Forests Changing?* Rome, FAO: 54. Available at: <http://www.fao.org/3/i4793e/i4793e.pdf>
- Fenning T.M., Gershenson J. (2002): Where will the wood come from? *Plantation forests and the role of biotechnology*. *Trends in Biotechnology*, 20: 291–296.
- Fogel R., Hunt G. (1983): Contribution of mycorrhizae and soil fungi to nutrient cycling in a Douglas-fir ecosystem. *Canadian Journal of Forest Research*, 13: 219–232.
- Fonti P., Heller O., Cherubini P., Rigling A., Arend M. (2013): Wood anatomical responses of oak saplings exposed to air warming and soil drought. *Plant Biology*, 15: 210–219.
- Franklin G.L. (1945): Preparation of thin sections of synthetic resins and wood-resin composites and a new macerating method for wood. *Nature*, 155: 51.
- Fritts H.C. (1966): Growth-rings of trees: Their correlation with climate. *Science*, 154: 973–979.
- Fritts H.C. (1976): *Tree Rings and Climate*. London, Academic Press: 582.

<https://doi.org/10.17221/208/2020-JFS>

- Fritts H.C. (2001): Tree-Rings and Climate. Caldwell, The Blackburn Press: 567.
- Fujimori T. (2001): Ecological and Silvicultural Strategies for Sustainable Forest Management. Amsterdam, New York, Elsevier: 398.
- Fuller R.J., Warren M. (1993): Coppiced Woodlands: Their Management for Wildlife. Peterborough, JNCC: 29.
- Fung L., Charles J., Hurst S., Rowan D., Allan D., Ainge G., Horgan D., Greer D., Norling C., Ma H.C., Pickering A., van den Dijssel C., McIvor I. (2001): An integrated programme for willow sawfly research. Annual progress report to the river managers group. HortResearch Client Report No. 2002/41: 61.
- Gärtner-Roer I., Heinrich I., Gärtner H. (2013): Wood anatomical analysis of Swiss willow (*Salix helvetica*) shrubs growing on creeping mountain permafrost. *Dendrochronologia*, 31: 97–104.
- Guerfel M., Baccouri O., Boujnah D., Chaibi W., Zarrouk M. (2009): Impacts of water stress on gas exchange, water relations, chlorophyll content and leaf structure in the two main Tunisian olive (*Olea europaea* L.) cultivars. *Scientia Horticulturae*, 119: 257–263.
- Hacke U.G., Sperry J.S., Pockman W.T., Davis S.D., McCulloh K.A. (2001): Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, 126: 457–461.
- Hallinger M., Manthey M., Wilmking M. (2010): Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist*, 186: 890–899.
- Hardesty L.H. (1987): Coppicing: Using a forester's tool on rangelands. *Rangelands Archives*, 9: 129–132.
- Hernández R.E., Koubaa A., Beaudoin M., Fortin Y. (1998): Selected mechanical properties of fast-growing poplar hybrid clones. *Wood Fiber Science*, 30: 138–147.
- Hussain Z., Kemp P.D., Horne D.J., Jaya I.K.D. (2009): Pasture production under densely planted young willow and poplar in a silvopastoral system. *Agroforestry Systems*, 76: 351–362.
- IAWA Committee (1989): IAWA List of microscopic features for hardwood identification by an IAWA Committee. *IAWA Bulletin n.s.*, 10: 219–332.
- Isebrands J.G., Aronsson P., Carlson M., Ceulemans R., Coleman M., Dickinson N., Dimitriou J., Doty S., Gardiner E., Heinsoo K., Johnson J.D., Koo Y.B., Kort J., Kuzovkina J., Licht L., McCracken A.R., McIvor I., Mertens P., Perttu K., Riddell-Black D., Robinson B., Scarascia-Mugnozza G., Schroeder W.R., Stanturf J., Volk T.A., Weih M. (2014): Environmental applications of poplars and willows. In: Isebrands J.G., Richardson J. (eds): *Poplars and Willows: Trees for Society and the Environment*. Boston, CABI: 258–336.
- Jackson R.B., Canadell J., Ehleringer J.R., Mooney H.A., Sala O.E., Schulze E.D. (1996): A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108: 389–411.
- Jackson R.B., Schenk H.J., Jobbágy E.G., Canadell J., Colello G.D., Dickinson R.E., Field C.B., Friedlingstein P., Heimann M., Hibbard K., Kicklighter D.W., Kleidon A., Neilson R.P., Parton W.J., Sala O.E., Sykes M.T. (2000): Belowground consequences of vegetation change and their treatment in models. *Ecological Applications*, 10: 470–483.
- Jarman R., Kofman P.D. (2017): Coppice in Brief. COST Action FP1301 Reports. Freiburg, Albert Ludwig University of Freiburg, Germany: 1-12.
- Jeelani N., Yang W., Xu L., Qiao Y., An S., Leng X. (2017): Phytoremediation potential of *Acorus calamus* in soils co-contaminated with cadmium and polycyclic aromatic hydrocarbons. *Scientific Reports*, 7: 8028.
- Kauppi A., Rinne P., Ferm A. (1988): Sprouting ability and significance for coppicing of dormant buds on *Betula pubescens* Ehrh. stumps. *Scandinavian Journal of Forest Research*, 3: 343–354.
- Kennedy A.D. (1998): Coppicing of *Tarconanthus camphorates* (Compositae) as a source of sustainable fuelwood production: an example from the Laikipia Plateau, Kenya. *African Journal of Ecology*, 36: 148–158.
- Keyes M.R., Grier C.C. (1981): Above- and below-ground net production in 40-year old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research*, 11: 599–605.
- Klašnja B., Orlović S., Galić Z. (2013): Comparison of different wood species as raw materials for bioenergy. *South-East European Forestry*, 4: 81–88.
- Kraus G. (1867): Die Gewebespannung des Stammes und ihre Folgen. *Gebauer-Schwetschke*: 70. (in German)
- Kuzovkina Y.A., Volk T.A. (2009): The characterization of willow (*Salix* L.) varieties for use in ecological engineering applications: Co-ordination of structure, function and autecology. *Ecological Engineering*, 35: 1178–1189.
- Larson P.R. (1994): *The Vascular Cambium: Development and Structure*. Berlin, Springer-Verlag: 725.
- Levitt J. (1980): *Responses of Plants to Environmental Stress: 1. Chilling, Freezing and High Temperature Stresses*. New York, London, Toronto, Academic Press: 497.
- Licht L.A., Isebrands J.G. (2005): Linking phytoremediated pollutant removal to biomass economic opportunities. *Biomass and Bioenergy*, 28: 203–218.
- Meinen C., Hertel D., Leuschner C. (2009): Biomass and morphology of fine roots in temperate broad-leaved forests differing in tree species diversity: is there evidence of below-ground overyielding? *Oecologia*, 161: 99–111.
- Mola-Yudego B., Aronsson P. (2008): Yield models for commercial willow biomass plantations in Sweden. *Biomass and Bioenergy*, 32: 829–837.

<https://doi.org/10.17221/208/2020-JFS>

- Morán-López T., Poyatos R., Llorens P., Sabaté S. (2014): Effects of past growth trends and current water use strategies on Scots pine and pubescent oak drought sensitivity. *European Journal of Forest Research*, 133: 369–382.
- Murmanis L. (1970): Locating the initial in the vascular cambium of *Pinus strobus* L. by electron microscopy. *Wood Science and Technology*, 4: 1–14.
- Nam V.T., Anten N.P.R., van Kuijk M. (2018): Biomass dynamics in a logged forest: the role of wood density. *Journal of Plant Research*, 131: 611–621.
- Niklas K.J. (1992): *Plant Biomechanics: An Engineering Approach to Plant Form and Function*. Chicago, University of Chicago Press: 607.
- Novak K., de Luís M., Raventós J., Čufar K. (2013): Climatic signals in tree-ring widths and wood structure of *Pinus halepensis* in contrasted environmental conditions. *Trees*, 27: 927–936.
- Özden S., Ennos R. (2018): The mechanics and morphology of branch and coppice stems in three temperate tree species. *Trees*, 32: 933–949.
- Panshin A.J., de Zeeuw C. (1980): *Textbook of Wood Technology: Structure, Identification, Properties and Uses of the Commercial Woods of the United States and Canada*. 4th Ed. New York, McGraw-Hill: 722.
- Pfautsch S. (2016): Hydraulic anatomy and function of trees – Basics and critical developments. *Current Forestry Report*, 2: 236–248.
- Phillips E.W. (1965b): Methods and equipment for determining the specific gravity of wood. IUFRO Meet Section 41 Melbourne: 14.
- Phillips C.J., Marden M., Suzanne L.M. (2014): Observations of root growth of young poplar and willow planting types. *New Zealand Journal of Forestry Science*, 44: 15.
- Pitman G.B., Larsson S., Tenow O. (1982a). Stem growth efficiency: an index of susceptibility to bark beetle and sawfly attack. In: Waring R.H., ed. *Carbon uptake and allocation in subalpine ecosystems as a key to management*. Corvallis, OR: Oregon State University, Forest Research Laboratory, 52–56.
- Pitman G.B., Perry D.A., Emmingham W.H. (1982b): Thinning to Prevent Mountain Pine Beetles in Lodgepole and Ponderosa Pine. Extension Circular 1106. Corvallis, Oregon State University Extension Service: 4.
- Rinne P., Saarelainen A., Junttila O. (1994): Growth cessation and bud dormancy in relation to ABA level in seedlings and coppice shoots of *Betula pubescens* as affected by a short photoperiod, water stress and chilling. *Physiologia Plantarum*, 90: 451–458.
- Sands R., Mulligan D.R. (1990): Water and nutrient dynamics and tree growth. *Forest Ecology and Management*, 30: 91–111.
- Schenk H.J., Jackson R.B. (2002): Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, 90: 480–494.
- Schlesinger W.H. (1997): *Biogeochemistry. An Analysis of Global Change*. 2nd Ed. San Diego, Academic Press: 588.
- Schoch W., Heller I., Schweingruber F.H., Kienast F. (2004): *Wood anatomy of central European Species*. Available at: <http://www.woodanatomy.ch/>
- Schweingruber F.H. (1996): *Tree Rings and Environment: Dendroecology*. Bern, Paul Haupt: 609.
- Simpson W.T. (1993): *Specific Gravity, Moisture Content, and Density Relationships for Wood*. (General technical report FPL, GTR-76). Madison, U.S. Department of Agriculture, Forest Service, Forest Products Laboratory: 13.
- Sperry J.S., Donnelly J.R., Tyree M.T. (1988): A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment*, 11: 35–40.
- Spinelli R., Visser R., Björheden R., Röser D. (2019): Recovering energy biomass in conventional forest operations: a review of integrated harvesting systems. *Current Forestry Report*, 5: 90–100.
- Sulaiman Z. (2006): *Establishment and silvopastoral aspects of willow and poplar*. [Ph.D. Thesis.] Palmerston North, Massey University.
- Thomas D.S., Montagu K.D., Conroy J.P. (2007): Temperature effects on wood anatomy, wood density, photosynthesis and biomass partitioning of *Eucalyptus grandis* seedlings. *Tree Physiology*, 27: 251–260.
- Tsarev A.P. (2005): Natural poplar and willow ecosystems on a grand scale: the Russian Federation. *Unasylva*, 56: 10–11.
- Tyree M.T., Sperry J.S. (1989): Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40: 19–38.
- Weih M. (2009): Genetic and environmental variation in spring and autumn phenology of biomass willows (*Salix* spp.): effects on shoot growth and nitrogen economy. *Tree Physiology*, 29: 1479–1490.
- Wilkinson A.G. (1999): Poplars and willows for soil erosion control in New Zealand. *Biomass and Bioenergy*, 16: 263–274.
- Wilson B.F. (1968): Red maple stump sprouts: development the first year. *Harvard Forest Paper*, 18: 10.
- Wu J., Albert L.P., Lopes A.P., Restrepo-Coupe N., Hayek M., Wiedemann K.T., Guan K., Stark S.C., Christoffersen B., Prohaska N., Tavares J.V., Marostica S., Kobayashi H., Ferreira M.L., Campos K.S., da Silva R., Brando P.M., Dye D.G., Huxman T.E., Huete A.R., Nelson B.W., Saleska S.R. (2016): Leaf development and demography explain photosynthetic seasonality in Amazonian evergreen forests. *Science*, 351: 972–976.
- Xu L., Saatchi S.S., Shapiro A., Meyer V., Ferraz A., Yang Y., Bastin J.-F., Banks N., Boeckx P., Verbeeck H., Lewis

<https://doi.org/10.17221/208/2020-JFS>

- S.L., Muanza E.T., Bongwele E., Kayembe F., Mbenza D., Kalau L., Mukendi F., Ilunga F., Ebuta D. (2017): Spatial distribution of carbon stored in forests of the Democratic Republic of Congo. *Scientific Report*, 7: 15030.
- Yaltirik F. (1971): Taxonomical Study on the Macro- and Micro- Morphological Characteristics of Indigenous Maples (*Acer L.*) in Turkey. Istanbul, Istanbul University Press: 232.
- Zalesny Jr. R.S., Bauer E.O. (2019): Genotypic variability and stability of poplars and willows grown on nitrate-contaminated soils. *International Journal of Phytoremediation*, 21: 969–979.

Received: December 16, 2020

Accepted: June 22, 2021