



The mechanics and morphology of branch and coppice stems in three temperate tree species

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Abstract

Key message Sycamore and ash trees were found to be greater E in their coppices, but horse chestnut was stiffer in its branches, this could be related to node frequency.

Abstract In this study, mechanical and anatomical properties of branch and coppice shoots of sycamore, horse chestnut and common ash were investigated along the length of their shoots and to relate these differences to their morphology and wood density. A series of 3-point bending tests were made along the lengths of the branches and coppices shoots at different diameters to determine the mechanical properties. The morphology was also characterized. Our results showed clearly that sycamore and horse chestnut trees were found to have greater flexural stiffness (EI) in their branches than the coppices, but coppices were stiffer (higher E) than branches in ash. Sycamore also surprisingly showed greater flexibility (higher E) in its coppices than the branches. The differences between branch and coppice shoots were explained by the morphology. Since the clearest morphological differences between the branches and coppices were in leaf node frequency, and linear regression analysis showed that the mechanical properties were negatively affected by higher leaf node frequency. Sycamore and ash had more leaf nodes in their branches than coppice shoots and consequently the mean E was lower in the branches; conversely horse chestnut had more leaf nodes in its coppice shoots which consequently had a lower mean E . The leaf nodes could also provide greater flexibility in the parallel plane since there is gap in nodal region and the arrangement of fibres are quite different here. The morphological differences could explain lower mechanical properties around the nodal region. The results also showed that mechanical properties were higher at the base and lower at the tips of branch and coppice shoots. These results cast light on the use of coppicing in particular tree species.

Keywords Leaf node · Green wood · Coppice stem · Branch stem

Introduction

There has long been interest in the biomechanics of trees, which all show a similar hierarchical architectural design (Cannell and Morgan 1987; Almeras and Fournier 2009; Fournier et al. 2013). Basically, the skeleton of a tree is

formed from the root, trunk, branches and leaves. The roots transport water and minerals from the soil and anchor the tree in the ground (Thomas 2000; Ennos 2001). The trunk is the main stem of the tree which provides mechanical support and transports water and nutrients from the roots to the branches and leaves. Finally, the branches hold up the leaves and fruits, while being able to reconfigure in the wind to reduce forces on the trunk and root system (McMahon 1973; Grace and Russell 1977; Niklas 1996; Ennos 1997, 2001; Jackson et al. 2002; Smith and Ennos 2003). Under wind loading, the branches can also act as mass dampers or harmonic absorbers, to minimize sway amplitude (James et al. 2006; Spatz and Theckes 2013; James and Haritos 2014). Oscillation damping is very important control strategy of dissipating vibrational energy from wind and so limits the risk of the damaging oscillations (Niklas 1992; Spatz et al. 2007; James et al. 2014).

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A tree thus has an excellent task-sharing mechanism at all its organs, which all show a similar hierarchical architectural design (Cannell and Morgan 1987; Almeras and Fournier 2009; Fournier et al. 2013). A tree manages its own geometric structure, growth process and vital functions to both remain alive and withstand the environmental stresses by means of those body elements. The biomechanical structure of tree has been, therefore, extensively investigated as to understand how trees provide both growth performance and mechanical stability together (Niklas 1992; Dahle and Grabosky 2010; Lundström 2010).

Management of trees can cause them to produce another type of terminal shoot, however—coppice stems—which have the same underlying structure as a branch, but which are oriented more vertically. Coppicing is a traditional and an alternative reforestation method to produce small diameter stems by providing a wide range of structures and tools. Trees are cut back just above the ground level every 5–35 years, depending on the species and growth period. From the cut stumps, regrowth occurs (Fuller and Warren 1990). Growth rates of coppiced stems are usually faster than unmanaged trees partly because they directly use the root's resources (Wilson 1968; Blake 1980, 1983; Kauppi et al. 1988, 1990; Rinne et al. 1994a, b; Dickmann et al. 1996) and partly because without a trunk there is lower hydraulic resistance to the leaves. Although, branch and coppice shoots can withstand heavy wind forces, there are many factors that might affect the development of branch and coppice stem growth and their morphology (Ennos 1997; Vollsinger et al. 2005; Eugster 2008; Utsumi et al. 2010; Telewski 2012). Trees grow in two ways: primary- and secondary growth. Growth in length of branches, twigs, coppice stems, trunks, leaves and roots results from the primary growth. The increment in thickness, in contrast, results from secondary growth (Haberlandt 1928; Thomas 2000). Primary growth takes place at the apical meristem which builds up new organs such as nodes and internodes. Nodes are the attachment regions for the growth of lateral buds and leaves; and internodes are the regions of the stem between two nodes (Zimmermann and Sperry 1983; Salleo and LoGullo 1986; LoGullo et al. 1995; Tyree and Zimmermann 2002). The growth is formed from either terminal buds on the branch or lateral buds. Branches thus add new internodes every year of primary growth to increase their length. Secondary growth then occurs, making the previous year's twigs thicker than the current year's so increasing the strength and flexural rigidity of the branch away from its base, as these are mainly related to the diameter (Thomas 2000). Previous studies showed that nodes are the 'constriction zones' in trees to prevent large cavitation (Zimmermann 1978a, b; Zimmermann and Sperry 1983). It was also suggested that nodes are hydraulic bottlenecks which provide less water potentials so provide stem hydraulic conductivity during

growing period (Zimmermann and Sperry 1983; Salleo and Lo Gullo 1986; Lo Gullo et al. 1995; Tyree and Zimmermann 2002). However, there is little investigation related to the mechanical role of nodes and internodes in stems (Spatz et al. 1990, 1995, 1993; Schulgasser and Witztum 1992; Spatz and Speck 1994; Niklas 1997; Bergman et al. 2009; Caringella et al. 2014). Niklas (1997) studied the mechanical role of nodes in stems and found that when internodes of stems are bent, the bending and tensile stresses are carried to nodal regions and the nodes act as a 'spring-like joints'. Bergman et al. (2009) also investigated the effect of leaf node frequency on the properties of stems. In their study, flexural modulus and modulus of rupture were negatively affected by increased leaf node frequency and they suggested that the regions of the leaf nodes make a stem mechanically weak. Similarly, a study by Caringella et al. (2014) has recently found that the nodal region of the branches of *Cercis occidentalis* was flexible, and less stiff.

The arrangement of the leaves may also influence the mechanics of tree shoots (Richter 1970; Caringella et al. 2014). However, little attempt has been made to compare different leaf arrangements and branching patterns and relate these differences to shoot mechanics. Leaves are arranged in different ways across the twigs: either opposite, alternate or whorled. Caringella et al. (2014) investigated the effect of alternate leaf arrangement on the properties of tree shoots of *C. occidentalis* and suggested that an alternate arrangement of the leaves makes shoots more flexible when they are bent in the same plane as the leaf nodes.

There are fewer studies on coppice shoots than on normal branches (Fegel 1941; Beismann et al. 2000; Gurau et al. 2003; Dahle and Grabosky 2010; van Casteren et al. 2012). A previous study by van Casteren et al. (2012) investigated the bending failure of coppice stems of three angiosperm species. In their study, they found that each species failed in different failure manner. Denser woods showed either clean greenstick fracture or diffuse greenstick fracture, but lighter woods exhibited more buckling in their wood (van Casteren et al. 2012). The properties of branches and coppice stems also vary along their length, depending on the shoot diameter, age and wood density (Lindstrom et al. 1998; Lichtenegger et al. 1999; Bruechert et al. 2000; Spatz and Bruechert 2000; Dahle and Grabosky 2010). So far, however, there has been relatively little discussion about how properties along branches and coppice shoot. Previous studies reported that there is a variation in flexural modulus along the length of shoot that is modulus of elasticity is higher at the base than the branch tips; this is because long lever arms are theoretically expected to expose to significant surface to wind and so branches tips are subjected to higher loads (Hakkila 1969; Yoshida et al. 1992a, b; Spatz and Bruechert 2000; Woodrum et al. 2003; Sone et al. 2006; Spatz et al. 2007; Gurau et al. 2008). A study by Dahle and Grabosky (2010)

also investigated the variation of flexural modulus between branch tip and base along the length of branch shoots. In their study, the flexural modulus was found to be higher near the branch base than the apex (Dahle and Grabosky 2010).

However, there is a need for a greater understanding of the effect of different patterns of tree shoot growth on their biomechanical properties. Comparing branches and coppices from single tree species is one way of doing this and this could also improve our understanding of how trees respond to loading stresses at the individual levels. Our specific objectives in this study were (1) to investigate the flexural properties (strength and stiffness) of branch and coppice shoots in three species of broadleaved trees, and to investigate which species produce good coppice shoots, (2) to understand how properties change or vary along the length of branch and coppice shoots, and (3) to test how the stem morphology, particularly node frequency, influences the mechanics of branch and coppice shoots. The results of this study should shed light on the exploitation of trees by man, and therefore, the effectiveness of coppicing at producing wooden poles with useful properties in different tree species. Knowledge of how material properties change along the length of branches and coppice shoots would also help us understand how trees withstand loading events. In this study, therefore, the branch and coppice shoots of sycamore (*Acer pseudoplatanus* L.), horse chestnut (*Aesculus hippocastanum* L.), and common ash (*Fraxinus excelsior* L.) were investigated by performing a series of 3-point bending tests and studying their leaf arrangement and morphology.

Materials and methods

The fresh branch and coppice stems of three tree species were chosen as the test subjects: sycamore (*Acer pseudoplatanus* L.), horse chestnut (*Aesculus hippocastanum* L.) and common ash (*Fraxinus excelsior* L.). The samples were

collected from woodland at Thwaite Botanical Gardens in University of Hull, UK in May 2014. Ten lateral (horizontal) branch stems and ten vertical coppice stems per species were cut 2–3 m above the ground. The branch and coppice shoots were randomly selected and the inclinations of shoots were not determined. The shoots were approximately 65 cm long, and ranged in age from 1 to 7 years and 3 to 10 mm in diameter depending on the shoot types (branch vs. coppice). The age of stems was determined by leaf scar nodes. The species were selected because they all produced coppice shoots readily. However, of these three species, only ash is commonly managed by coppicing, whereas this practise is less seldom seen in sycamore, and especially horse chestnut. The leaf arrangement (phyllotaxy) and branching types of each species were characterized. The three different angiosperm species had two different types of leaf arrangement (phyllotaxy) and branching shapes: horse chestnut and ash both had a monopodial branching with an opposite leaf arrangement whereas sycamore had a zig-zag branching with an alternate leaf arrangement. These three tree species were chosen to have two different ring porosity patterns: diffuse porous (*A. pseudoplatanus* L. and *A. hippocastanum* L.) and ring porous (*F. excelsior* L.) patterns.

Trees sampling and 3-point bending tests

65 cm long shoots of branches and coppices were cut into 15, 20 and 30 cm long segments: the terminal 15 cm (proximal to the terminal bud), a central 20 cm length (middle point) and a 30 cm basal length (near base). The central point of each length was, therefore, 7.5, 25 and 50 cm from the shoot tip (Fig. 1). 60 shoots per species (30 branches and 30 coppice shoots) were taken, making 180 specimens in all.

To investigate mechanical properties, intact specimens of green branches and coppice shoots (including bark, xylem, phloem and pith) were subjected to the three point flexural tests conducted on a Lloyd EZ50 Universal Materials Testing

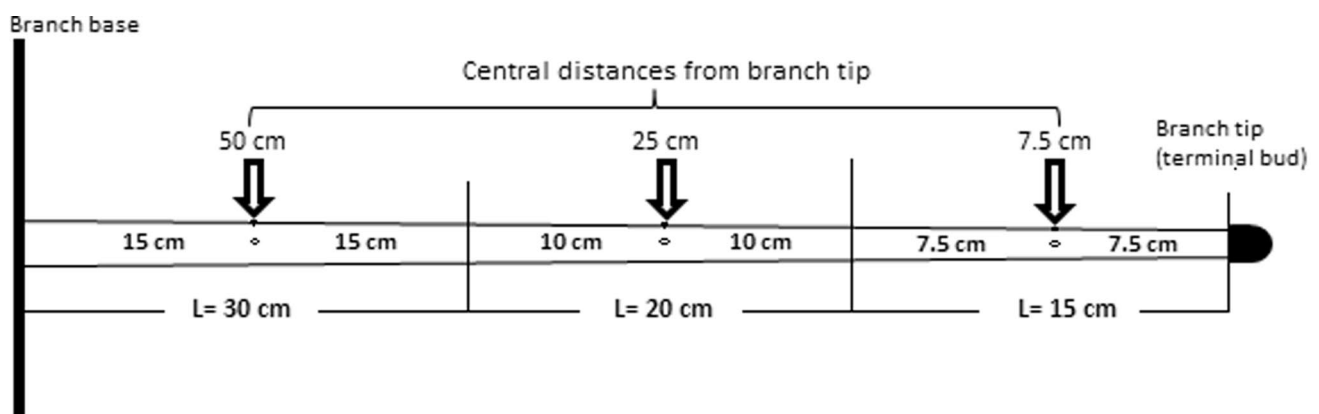


Fig. 1 The sampling locations through branches and coppice shoots of three tree species (L is length)

Machine. The maximum loads were obtained by the flexural tests and flexural rigidity (EI), flexural modulus or modulus of elasticity (E), flexural strength (M_{\max}), and the breaking stress ($\sigma_{B\max}$) were calculated. The effect of shear makes flexural stiffness calculations from three point bending tests rather complicated. To minimize this effect, therefore, we used a minimum span-to-depth ratio of 15–20 (Vincent 1992), so the shear effect can be neglected. The specimens were placed on a steel-bending rig which had two support points. The load actuator was applied at the centre point of the span and the crosshead was lowered at a speed of 60 mm min⁻¹ until the branch or coppice shoots buckled, while the force required was simultaneously measured using a 1 kN load cell. The flexural rigidity (EI) of the branch and coppice shoots was calculated using the equation

$$EI = \frac{dF}{dx} \times \frac{L^3}{48}, \quad (1)$$

where dF/dx is the initial slope of the load–displacement curve and L is the span length of the specimen between the supports. Excel was used to plot the force and displacement results and estimated initial slope (dF/dx) which is the slope of the initial linear region of the curve (Beismann et al. 2000; Woodrum et al. 2003; van Casteren et al. 2012).

The branch and coppice shoots of each three species were approximately circular in their cross-sections at the internodes, such that the ratios in diameter between parallel and perpendicular planes were around 1% (Niklas 1992; Caringella et al. 2014). However, nodes did not have perfect circles in their cross-sections; they were more likely to have elliptical cross-sections rather than nearly circular cross-sections. There was also a very small degree of tapering, less than 1.7% for sycamore, 1.3% for horse chestnut, 1.5% for ash, in going from the base to tip point of each shoot length (50, 25 and 7.5 cm). Due to the slight degree of tapering, we did our tests and calculations for regarding branch and coppice shoots as untapered or non-conical beams, so the tapering of each shoot length was neglected in our calculations (Anten and Schieving 2010). The second moment of cross-sectional area (moment of inertia) calculations was, therefore, based on the assumption that the branch and coppice shoots have a circular cross-section (as untapered beams). For each sample, two measurements of diameter were obtained at the central (mid) point of each length, both in the plane and perpendicular to the plane of the shoots using a digital calliper, and a mean diameter was then obtained. Considering this, the second moment of area (I) of a circular beam can be calculated by the following Eq. (2) (Niklas 1992)

$$I = \frac{\pi (R^4 - r^4)}{4}, \quad (2)$$

where R is the radius of outer stem and r is the radius of the pith. The structural flexural modulus (E) of wood which describes the rigidity of the wood material was then calculated by dividing EI by I (Niklas 1992; Rowe and Speck 1999; Speck and Rowe 1999; Niklas and Spatz 2012b). The Eq. (3) that describes the E calculation is as follows:

$$E = \frac{EI}{I}. \quad (3)$$

To determine the specimens' ability to resist deformation under load, the bending strength or flexural strength (M_{\max}) was calculated using Eq. (4)

$$M_{\max} = \frac{F_{\max} \times L}{4}, \quad (4)$$

where F_{\max} is the maximum force. Determining the maximum longitudinal stress ($\sigma_{B\max}$) in bending, we used the following expression for the maximum longitudinal stress as:

$$\sigma_{B\max} = \frac{M_{\max} \times r}{I}. \quad (5)$$

Density measurements

After the experiments, tested samples were cut into 3-cm-long pieces and kept at 4 °C in sealed plastic bags in a cold room for density measurements. For each samples, the small specimens were then held in distilled water in airtight containers until they all were fully hydrated. To ensure the specimens were fully hydrated and constant mass was obtained, the water soak specimens were weighed at 6-h intervals over a period of 1–2 days. The water displacement method was used to measure the wet volume of wood specimens (cm³) (top pan balance, Archimedes principle, Hacke et al. 2000). The specimens were fully sunk by means of a thin needle in a glass beaker of water that was put on an electronic balance; the volume then was recorded by the displacement weight that resulted divided by the density of water (0.998 g cm⁻³). To obtain the dry mass of specimens, the samples were placed in a drying oven at 65 °C for a minimum of 3 days until they had a consistent weight (0% moisture content). The weight of the oven-dried specimens was then measured using an electronic balance. The relative density measurement is described by the following equation (Eq. 6):

$$\text{Density} \left(\frac{\text{g}}{\text{cm}^3} \right) = \frac{\text{oven dry weight (g)}}{\text{volume (cm}^3\text{)}}, \quad (6)$$

The ratio of the pith, bark, xylem, and node frequency measurements

First, we measured the outer diameter of the stem (including bark, xylem and pith) and diameter of pith (centre of the

stem). The bark was then simply removed from each of the stem and the remaining diameter was measured (including xylem, and pith). To calculate mean diameters, the measurements were done as before in both the horizontal and vertical axes. The areas of each segment were then calculated based on the assumption that branch and coppice shoots have a circular transverse geometry.

To calculate bark area in the stem, we first calculated the area of stem (πc^2), area of pith (πa^2) and area of xylem + pith (πb^2), and then the area of the xylem + pith was subtracted from the area of the stem (Fig. 2). The % of pith, bark and xylem area was then calculated. To calculate node frequency, we counted the number of leaf nodes per each shoot length (15, 20 and 30 cm) and the numbers of leaf nodes then per cm were calculated.

Statistical analyses

Two-way and three-way analysis of variance (ANOVA) tests were employed using SPSS 20 statistical software with a 5% significance level. A Chi-square (χ^2) test of independence was performed to examine the failure patterns of wood species, wood types and internode distances. Additionally, logistic (log) and logarithmic regression analysis were employed.

Results

Failure patterns

Overall, the classification of the failure modes of branches and coppices is summarized in Table 1, the type of failure being characterized as either being due to clean fracture, or

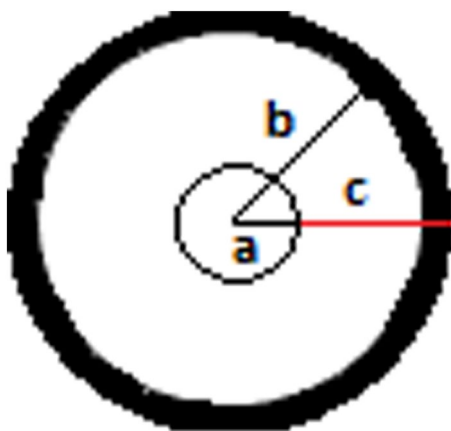


Fig. 2 Demonstrating the pith, xylem, and bark measurement points: **a** is the radius of pith, **b** is the radius of stem removing bark extract (radius of xylem and pith circle together), and **c** is the radius of the stem (biggest outer radius)

Table 1 The results of a χ^2 analysis comparing the frequency of different failure modes between the two shoot types

Shoot types (branch vs. coppice)	Clean fracture	Transverse buckling
Branch	52	38
Coppice	13	77
Total	65	115
χ^2	36.626	
<i>df</i>	1	
Crit value	3.84	

transverse buckling. Each species presented more buckling than clean fracture, but a χ^2 test showed that there were no differences between the incidence in the different species ($\chi^2_1 = 2.36$, $p > 0.05$). The failure mode results in Table 1 demonstrate that buckling was much more common in coppice shoots than branches, a difference between wood types that a χ^2 test showed was significant ($\chi^2_1 = 36.63$, $p < 0.001$).

This pattern was particularly strongly shown in sycamore (Table 2a, $\chi^2_1 = 18.468$, $p < 0.001$) and horse chestnut (Table 2b, $\chi^2_1 = 33.611$, $p < 0.001$), though the difference was not significant in ash (Table 2c, $\chi^2_1 = 0.278$, $p > 0.05$).

Bending tests In the 3-point flexural bending tests, we measured mean diameter, I , EI , E , M_{\max} , $\sigma_{B\max}$, specific modulus (E/D) values for 180 specimens of green branches and coppice shoots in three individual trees between three central distances from the branch and coppice tips.

Diameters

The mean diameters of each tree species between branch and coppice shoots at each of the three shoot locations (50, 25 and 7.5 cm) are summarized in Fig. 3. Overall, a three-way ANOVA of the mean diameters between three species showed that there were significant differences ($F_{2,162} = 42.849$, $p = 0.000$); post hoc analyses using the Tukey post hoc criterion for significance showed that the mean diameters of all three species were significantly different from each other ($p < 0.05$). Overall, the average diameters were significantly larger in horse chestnut followed by sycamore and ash. Overall, the three-way ANOVA also revealed that mean diameters differed significantly between branches and coppice shoots ($F_{1,162} = 57.198$, $p = 0.000$). Each species had larger diameter in their branches than coppice shoots. It can be seen in Fig. 3 that branches were significantly thicker than coppice shoots, but the difference was most pronounced in sycamore with branch diameter being on average 27.8% higher ($F_{1,58} = 15.41$, $p = 0.000$), whereas in horse chestnut the differences were only 9.8% ($F_{1,58} = 6.116$, $p = 0.016$) and in ash, the diameters of the two types were not significantly different ($F_{1,58} = 1.255$, $p = 0.267$). The three-way ANOVA

Table 2 The incidence of different failure types in branches and coppice shoots during three point bending tests in (a) sycamore (b) horse chestnut and (c) ash

Shoot types (Branch vs. Coppice)	Shoot lengths (7.5–25–50 cm)	Clean fracture	Transverse buckling
(a)			
Branch	7.5 cm	5	5
	25 cm	8	2
	50 cm	7	3
	Total	20	10
	χ^2	5.089	
	<i>df</i>	2	
	Crit value	5.99	
	Coppice		
Coppice	7.5 cm	0	10
	25 cm	1	9
	50 cm	0	10
	Total	1	29
	χ^2	2.069	
	<i>df</i>	2	
	Crit value	5.99	
	(b)		
Branch	7.5 cm	7	3
	25 cm	9	1
	50 cm	7	3
	Total	23	7
	χ^2	1.491	
	<i>df</i>	2	
	Crit value	5.99	
	Coppice		
Coppice	7.5 cm	0	10
	25 cm	1	9
	50 cm	0	10
	Total	1	29
	χ^2	2.069	
	<i>df</i>	2	
	Crit value	5.99	
	(c)		
Branch	7.5 cm	2	8
	25 cm	8	2
	50 cm	3	7
	Total	13	17
	χ^2	8.416	
	<i>df</i>	2	
	Crit value	5.99	
	Coppice		
Coppice	7.5 cm	2	8
	25 cm	6	4
	50 cm	3	7
	Total	11	19
	χ^2	3.732	
	<i>df</i>	2	
	Crit value	5.99	

also indicated significant differences in the diameters experienced by shoot locations from the tip ($F_{2,162} = 159.498$, $p = 0.000$); post hoc analyses using Tukey's post hoc test showed that all shoot locations were significantly different from each other ($p < 0.05$). Overall, the highest diameters were 50 cm from the tip, with a mean of 8.2 mm followed by 6.9 mm at 25 cm and 5.4 mm at 7.5 cm a pattern seen in all three species.

Second moment of area (*I*)

Not surprisingly, the second moment of area *I* (Fig. 4) shows the same pattern of differences between branches and coppice shoots and an increase away from the tip as diameter. The three-way ANOVA found that there was a statistically significant difference between the three species ($F_{2,162} = 55.436$, $p = 0.000$). Horse chestnut overall showed greater *I* values than sycamore and ash, respectively. A post hoc Tukey test found *I* values of horse chestnut and sycamore being greater than ash, but there were no significant differences in *I* values between horse chestnut and sycamore ($p > 0.05$). The three-way ANOVA also indicated that there were significant differences in the mean *I* values between branch and coppice shoots for each species ($F_{1,162} = 156.53$, $p = 0.000$). Overall, the mean *I* was around 1.9 times bigger in branches (93.8 mm⁴) than coppices (49.1 mm⁴), with sycamore showing the biggest differences (around three times bigger, $F_{1,58} = 19.81$, $p = 0.000$) and horse chestnut ash the least (both around 1.4 times bigger, $F_{1,58} = 6.116$, $p = 0.016$ and $F_{1,58} = 4.073$, $p = 0.048$, respectively).

Overall, there were also significant differences in the mean *I* values of the three shoot locations ($F_{2,162} = 297.38$, $p = 0.000$); a post hoc Tukey test indicated that each shoot location was significantly different from each other ($p < 0.05$). In particular, the mean *I* values of 50 cm specimens were around 2–3 times greater than that of the other two locations, a pattern seen in all three species.

Flexural rigidity (EI)

The mean EI values are shown in Fig. 5. A three-way ANOVA indicated that there was a significant difference between the three species ($F_{2,162} = 33.415$, $p = 0.000$); post hoc Tukey tests showed that all three species were significantly different from each other ($p < 0.05$) with horse chestnut the most rigid and ash the least. The three-way ANOVA also indicated that there were significant differences in the mean EI values between branch and coppice shoots ($F_{1,162} = 156.53$, $p = 0.000$) but the different species showed quite different patterns. Overall, in horse chestnut, EI values in branches were approximately double that in coppices ($F_{1,58} = 9.28$, $p = 0.003$). Sycamore also showed bigger EI values in branches than coppices, around 1.6

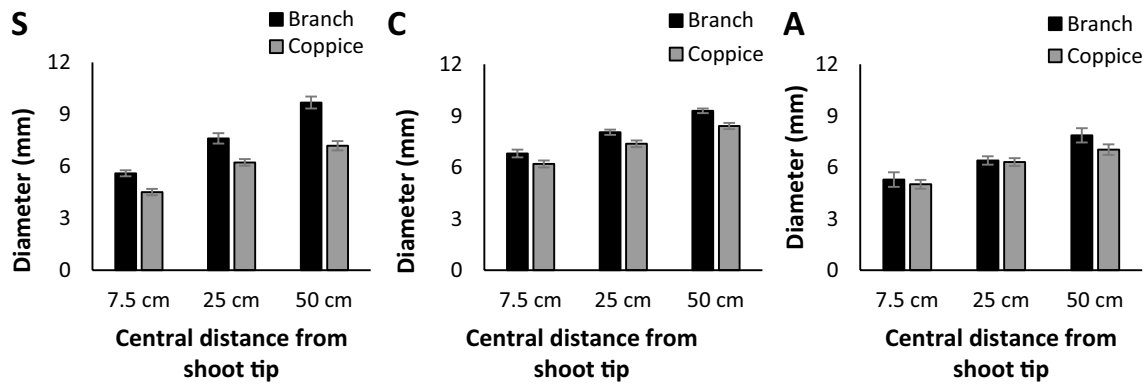


Fig. 3 The mean diameters of three species in two shoot types (branch vs. coppice) and three shoot locations from tips. (S) is sycamore, (C) is horse chestnut, and (A) is ash. A standard error is shown by the error bars

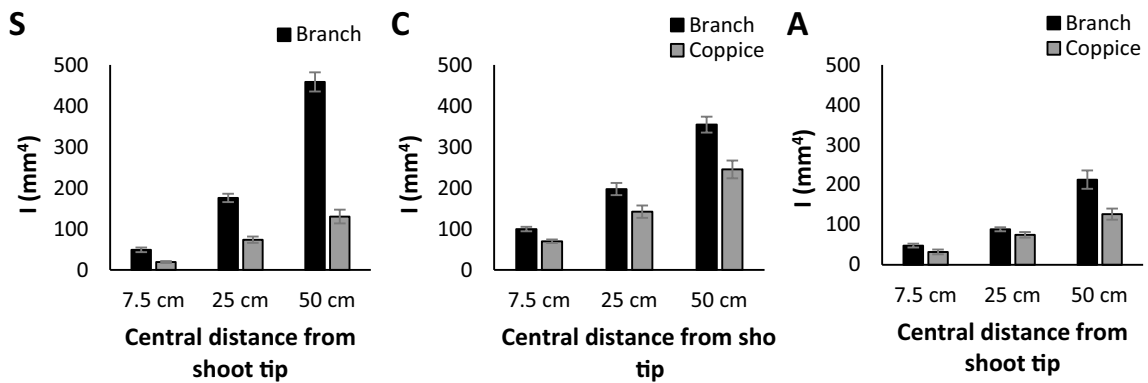


Fig. 4 The mean second moment of area (*I*) values (without pith) of three species in two shoot types (branch vs. coppice) and three shoot locations from tips. (S) is sycamore, (C) is horse chestnut, and (A) is ash. A standard error is shown by the error bars

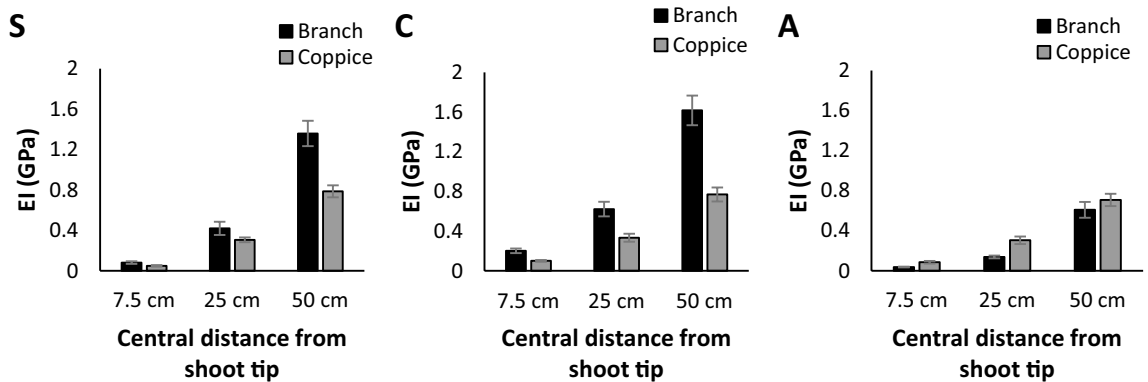


Fig. 5 The mean EI values of three species in two shoot types (branch vs. coppice) and three shoot locations from the tips. (S) is sycamore, (C) is horse chestnut, and (A) is ash. A standard error is shown by the error bars

times greater EI values in branches than coppices, though this difference was not statistically significant ($F_{1,58} = 3.55$, $p > 0.05$). In contrast, in ash EI values of branch shoots were slightly smaller than the coppice shoots, though

once again this difference was not statistically significant ($F_{1,58} = 1.97$, $p = 0.165$).

A significant difference was also found between the three shoot locations ($F_{2,162} = 312.188$, $p = 0.000$); a post

hoc Tukey test indicated that 50 cm from the tip specimens had a significantly larger EI than at the other two locations ($p < 0.05$) a pattern seen in all three tree species.

Flexural modulus (E)

Comparison of mean E values measured for three wood species in the branch and coppice shoots and three shoot locations are shown in Fig. 6. A three-way ANOVA analysis indicated that the mean E values of the three wood species were significantly different ($F_{2,162} = 10.879$, $p = 0.000$) with sycamore wood being stiffest. The three-way ANOVA also showed that overall there were significant differences between branch and coppice shoots ($F_{1,162} = 63.858$, $p = 0.000$), but in this case E was higher overall in the coppice shoots. The three species also showed quite different patterns. In both sycamore ($F_{1,58} = 24.33$, $p = 0.000$) and ash ($F_{1,58} = 31.93$, $p = 0.000$) the coppice shoots were around twice as stiff as the branches, whereas in horse chestnut E was 1.3 times greater in branches than coppices ($F_{1,58} = 10.71$, $p = 0.002$). Stiffness was also highest further

away from the tip ($F_{2,162} = 96.75$, $p = 0.000$), a pattern seen in all three species.

Flexural strength (M_{\max})

The results for M_{\max} in the three tree species between branch and coppice shoots and at the three shoot locations are presented in Fig. 7. A three-way ANOVA analysis indicated that the mean M_{\max} was significantly different between the three tree species ($F_{2,162} = 40.14$, $p = 0.000$). A post hoc Tukey test showed sycamore (1.47 N m) and horse chestnut (1.38 N m) had a significantly higher M_{\max} than ash (0.87 N m). However, no significant differences were found between sycamore and horse chestnut ($p > 0.05$). There were also overall differences between the two shoot types ($F_{1,162} = 57.363$, $p = 0.000$), branches being stronger than coppice shoots. This was especially true in sycamore, where branches were on average 1.5 times as strong ($F_{1,58} = 4.411$, $p = 0.040$), and horse chestnut, where branches were 1.6 times as strong ($F_{1,58} = 8.171$, $p = 0.006$), but in ash no significant difference was found in M_{\max} values between branch and coppice

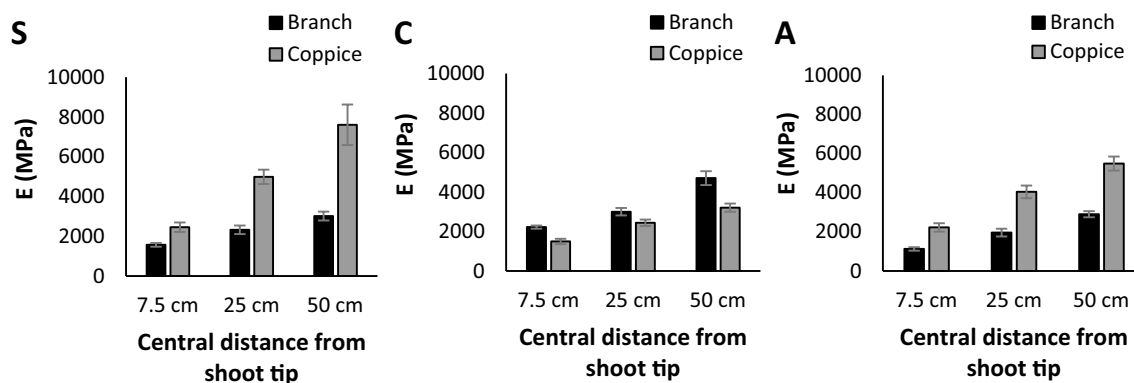


Fig. 6 The mean E values of three species in two shoot types (branch vs. coppice) and three shoot locations from the tips. (S) is sycamore, (C) is horse chestnut, and (A) is ash. A standard error is shown by the error bars

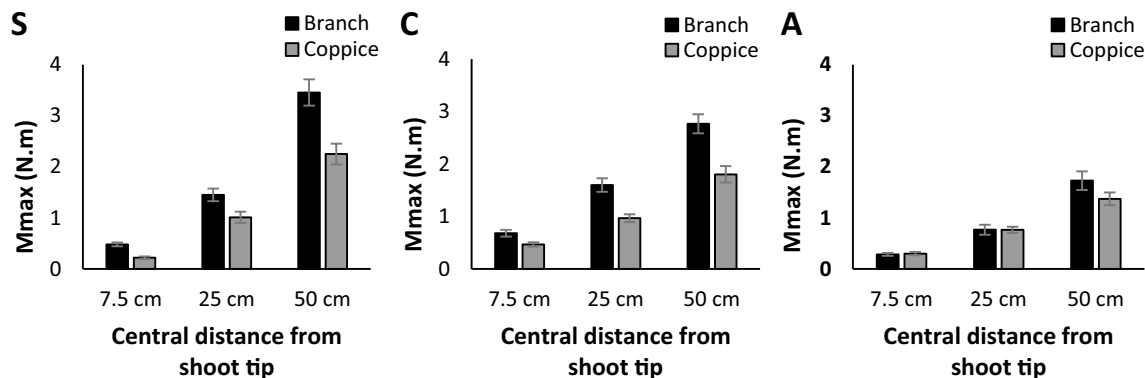


Fig. 7 The mean M_{\max} values of three species in two shoot types (branch vs. coppice) and three shoot locations from the tips. (S) is sycamore, (C) is horse chestnut, and (A) is ash. A standard error is shown by the error bars

shoots ($F_{1,58} = 0.497, p = 0.484$). The three-way ANOVA results also showed that M_{\max} differed significantly between the three shoot locations ($F_{2,162} = 319.627, p = 0.000$), branches becoming stronger away from the tip, a pattern that was seen in all three species.

Maximum longitudinal stress ($\sigma_{B_{\max}}$)

Figure 8 presents the mean $\sigma_{B_{\max}}$ values in the two different shoot types (branch vs. coppice) for the three species. The average values of $\sigma_{B_{\max}}$ differed significantly between the three species ($F_{2,162} = 20.341, p = 0.000$); Tukey’s tests showed that $\sigma_{B_{\max}}$ was higher in sycamore than ash and horse chestnut, but no significant difference was found between ash and horse chestnut. Overall, a three-way ANOVA analysis found no significant differences between branch and coppice shoots ($F_{1,162} = 2.261, p = 0.135$). However, in horse chestnut, the branches did have significantly higher $\sigma_{B_{\max}}$ ($F_{1,58} = 5.896, p = 0.018$), though this was not

the case in sycamore coppices ($F_{1,58} = 0.931, p = 0.339$) or ash ($F_{1,58} = 1.418, p = 0.239$).

A three-way ANOVA analysis also showed that the mean $\sigma_{B_{\max}}$ was significantly different in all shoot locations ($F_{2,162} = 55.126, p = 0.000$); a post hoc Tukey test found that 50 cm from the tip specimens had significantly higher $\sigma_{B_{\max}}$ values (0.043 GPa) ($p < 0.05$) than at the other two locations, something that was also true for all three species.

Density

Mean density values are shown in Fig. 9. A three-way ANOVA found a significant difference between the three species ($F_{2,162} = 44.23, p = 0.000$), with density being highest in sycamore, followed by ash and horse chestnut; a post hoc Tukey test showed all species were significantly different from each other ($p < 0.05$). Overall, mean densities also showed significant differences between branches and coppice shoots ($F_{1,162} = 44.85, p = 0.000$). A two-way ANOVA on each species showed that mean density values

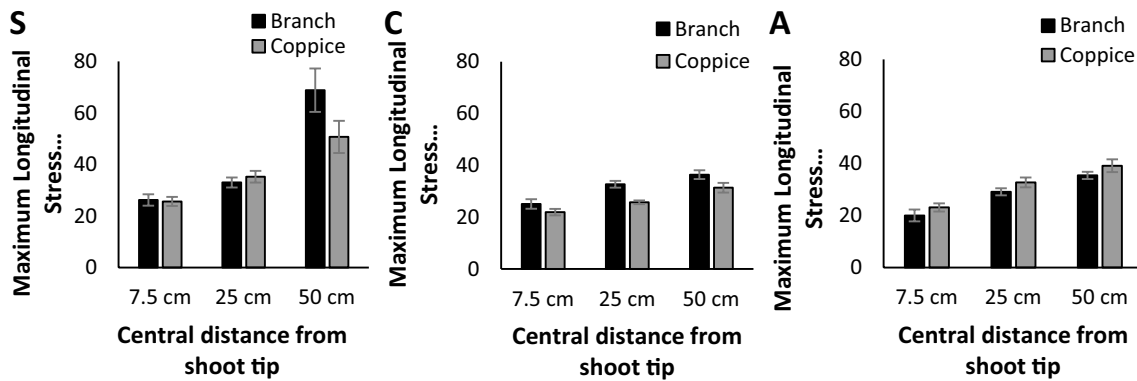


Fig. 8 The mean $\sigma_{B_{\max}}$ results of three species in two shoot types (branch vs. coppice) and three shoot locations from the tips. (S) is sycamore, (C) is horse chestnut, and (A) is ash. A standard error is shown by the error bars

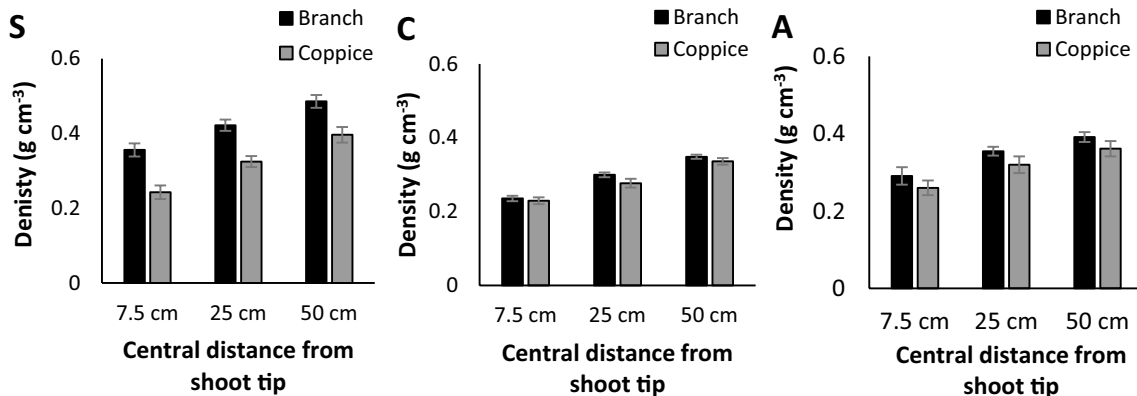


Fig. 9 The mean density results of three species in two shoot types (branch vs. coppice) and three shoot locations from the tips. (S) is sycamore, (C) is horse chestnut, and (A) is ash. A standard error is shown by the error bars

were significantly higher in branches than coppice in both sycamore (0.42 vs 0.32 g cm^{-3}) ($F_{1,54}=49.76$, $p=0.000$) and ash (0.35 vs. 0.31 g cm^{-3}) ($F_{1,54}=4.54$, $p=0.038$), but not between branches (0.29 g cm^{-3}) and coppice shoots (0.28 g cm^{-3}) of horse chestnut ($F_{1,54}=3.95$, $p>0.05$). The mean densities also differed significantly between the three shoot locations ($F_{2,162}=87.72$, $p=0.000$); a post hoc Tukey test indicated each location was significantly different from each other ($p<0.05$). In all three species, the mean densities were generally significantly higher in the base of branch than that of the other two locations.

Specific modulus (E/D)

The results for mean E/D values in the three tree species between branch and coppice shoots and at the three shoot locations are presented in Fig. 10. Overall, the average values of E/D differed significantly between three species ($F_{2,162}=13.39$, $p=0.000$); Tukey's tests showed that E/D was significantly greater in sycamore than horse chestnut and ash. Overall specific modulus of sycamore was around 1.2 times higher than the others. Overall, a three-way ANOVA analysis found significant difference in specific modulus values between branch and coppice shoots ($F_{1,162}=145.52$, $p=0.000$); coppice shoots were found to be 1.7 times higher E/D values than branch shoots. A two-way ANOVA on each species showed different patterns; sycamore and ash showed greater E/D values in their coppices than branches [$(F_{1,54}=122.38$, $p=0.000$) and $F_{1,54}=123.13$, $p=0.000$, respectively], however, branches of chestnut showed higher specific modulus values than its coppices ($F_{1,54}=66.02$, $p=0.000$). A three-way ANOVA also found that E/D differed significantly between three shoot locations ($F_{2,162}=67.27$, $p=0.000$); a post hoc Tukey test showed each location was significantly different from each other ($p<0.05$). The mean E/D values were

generally significantly higher in the base of branch than that of the other two locations in all three species.

Leaf node frequencies

The mean leaf node frequencies are shown in Fig. 11. A three-way ANOVA indicated that there were significant differences between the three species ($F_{2,162}=9.94$, $p=0.000$). Overall, it is apparent that horse chestnut had a significantly higher mean frequency than sycamore and ash ($p<0.05$). However, a post hoc Tukey test did not find significant differences between sycamore and ash ($p>0.05$). The three-way ANOVA also found significant differences between branches and coppice shoots ($F_{1,162}=31.64$, $p=0.000$). However, there were quite different patterns in the three species. Two-way ANOVA of sycamore showed significantly higher leaf node frequency in its branch shoots than coppice shoots ($F_{1,54}=22.02$, $p=0.000$), around 45% greater than coppices. An even greater difference was seen in ash ($F_{1,54}=33.19$, $p=0.000$), in which the branches had more than three times greater leaf node frequency than coppiced shoots. In contrast, in horse chestnut, coppice shoots had a significantly higher mean leaf node frequency than branch shoots ($F_{1,54}=33.22$, $p=0.000$). Coppice shoots had around 68% greater leaf node frequency than branch shoots.

The mean leaf node frequency also differed significantly between three internode lengths ($F_{2,162}=103.22$, $p=0.000$); there was a significantly higher leaf node frequency 7.5 cm from the tip than further down the branch ($p<0.05$). A post hoc Tukey test showed each length was significantly different from each other with higher frequencies nearer the tip. Though this pattern was not significant in horse chestnut ($p>0.05$).

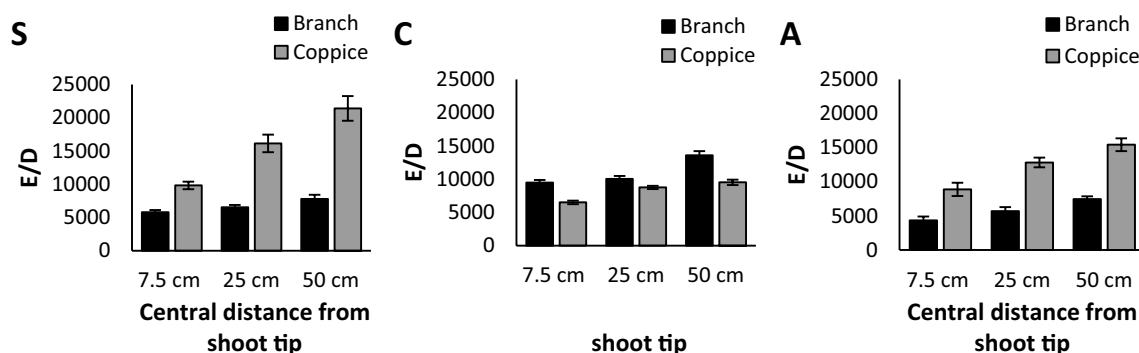


Fig. 10 The mean specific modulus (specific stiffness, E is modulus of elasticity and D is density) results of three species in two shoot types (branch vs. coppice) and three shoot locations from the tips. (S)

is sycamore, (C) is horse chestnut, and (A) is ash. A standard error is shown by the error bars

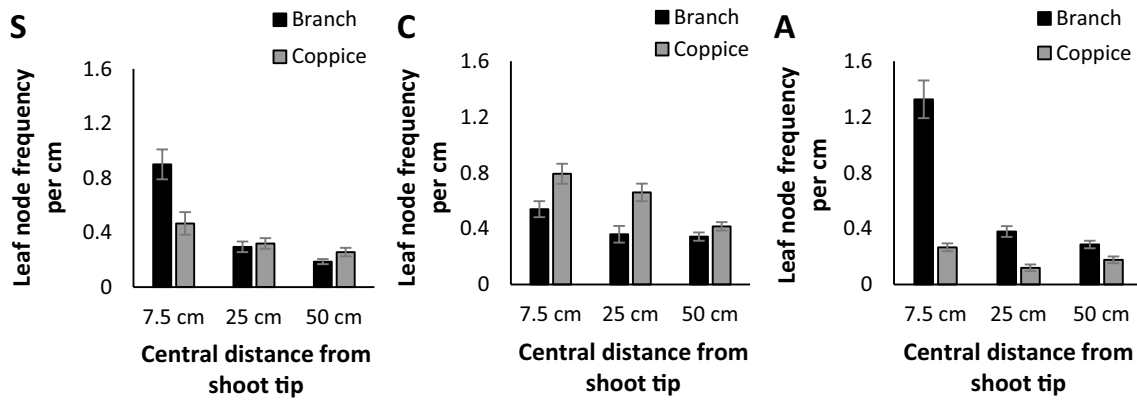


Fig. 11 The leaf node frequency per cm of (S) is sycamore, (C) is horse chestnut, and (A) is ash in two shoot types and three shoot locations from the tips. A standard error is shown by the error bars

Ages

Figure 12 shows an overview of the mean ages for each species. A two-way ANOVA showed that the mean ages (at base) showed significant differences between the three species ($F_{2,171} = 129.09, p = 0.000$); a post hoc Tukey test showed that horse chestnut was significantly younger at the base than sycamore and ash ($p < 0.05$). The mean ages of branches were also higher than coppice shoots ($F_{1,162} = 343.77, p = 0.000$). However, sycamore and ash showed a greater difference between branches and coppice; the mean age of the branch was around three and nearly six times higher than coppiced shoots, respectively, while there was no significant difference between the branches and coppices of horse chestnut.

Morphological characteristics (pith, xylem, bark)

Mean pith, xylem, and bark percentages for each three species are shown in Figs. 13, 14 and 15. A three-way ANOVA indicated the mean pith percentage differed between the

three species ($F_{2,162} = 67.49, p = 0.000$). A post hoc Tukey test showed that ash had significantly more pith than chestnut and sycamore ($p < 0.05$). Overall, the mean pith% also differed significantly between branches and coppice shoots ($F_{1,162} = 12.67, p = 0.000$); coppice shoots had 8.3% more pith than branches. A three-way ANOVA also showed that the mean ratio of pith was significantly different between the three shoot locations ($F_{2,162} = 101.58, p = 0.000$). A post hoc Tukey test showed all shoot locations had significantly different pith % from each other ($p < 0.05$); at 7.5 the shoots had significantly more pith than at 25 and 50 cm ones, respectively. A two-way ANOVA on each species also showed interesting results; branches of chestnut had significantly greater pith% than its coppice shoots ($F_{1,54} = 5.61, p = 0.021$), but both sycamore and ash showed more pith in their coppice shoots ($F_{1,54} = 27.49, p = 0.000$ and $F_{1,54} = 29.05, p = 0.000$, respectively).

Figure 14 shows the overall percentages of the xylem for the three species. A three-way ANOVA indicated a significant difference between the species ($F_{2,162} = 44.48, p = 0.000$); a post hoc Tukey test indicated that each

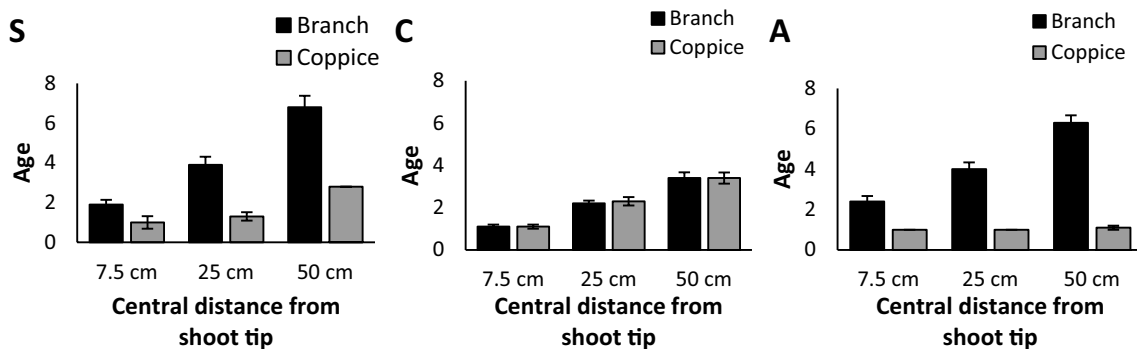


Fig. 12 The mean ages of three species in two shoot types (branch vs. coppice) (S) is sycamore, (C) is horse chestnut, and (A) is ash. A standard error is shown by the error bars

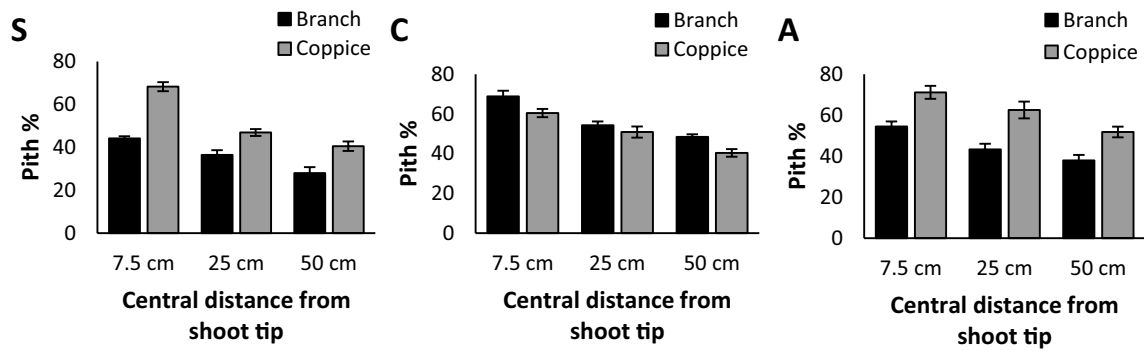


Fig. 13 The pith percentage results of three species in two shoot types (branch vs. coppice) and three shoot locations from the tips. (S) is sycamore, (C) is horse chestnut, and (A) is ash in two shoot types and three shoot locations from the tips. A standard error is shown by the error bars

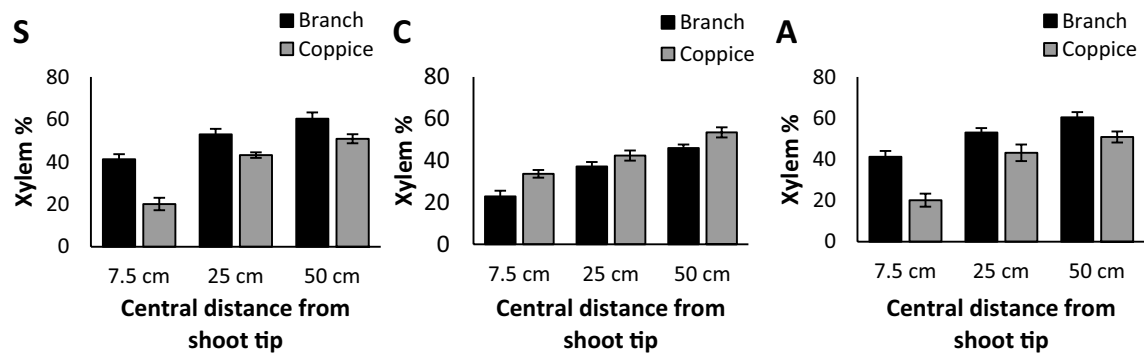


Fig. 14 The xylem percentage results of three species in two shoot types (branch vs. coppice) and three shoot locations from the tips. (S) is sycamore, (C) is horse chestnut, and (A) is ash in two shoot types and three shoot locations from the tips. A standard error is shown by the error bars

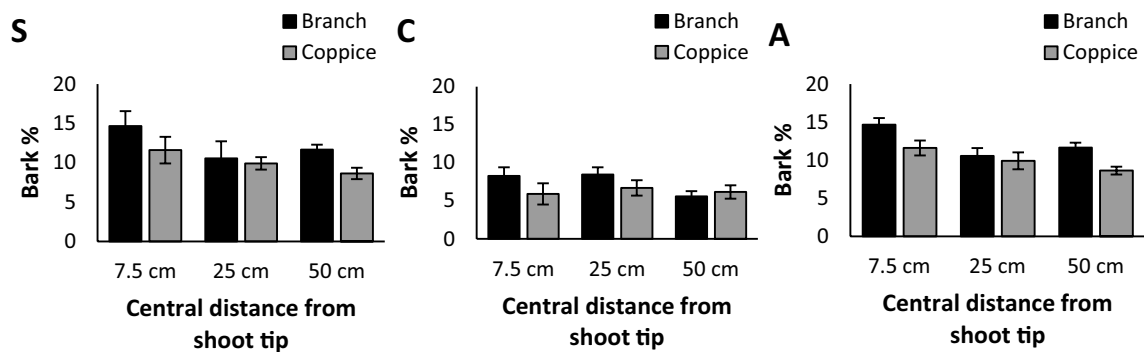


Fig. 15 The bark percentage results of three species in two shoot types (branch vs. coppice) and three shoot locations from the tips. (S) is sycamore, (C) is horse chestnut, and (A) is ash in two shoot types and three shoot locations from the tips. A standard error is shown by the error bars

species showed significantly different xylem % than each other; sycamore had more xylem than horse chestnut and ash ($p < 0.05$). Overall, a three-way ANOVA also found significant differences in the percentage of xylem between branches and coppice shoots ($F_{1,162} = 6.90$, $p = 0.009$). However, the percentage of xylem differed significantly in the three locations ($F_{2,162} = 115.01$, $p = 0.000$); a post hoc Tukey test showed that at 50 cm specimens had

significantly more xylem than at the other two locations ($p < 0.05$). A two-way ANOVA analysis showed again interesting results; sycamore and ash had more xylem in their branches ($F_{1,54} = 15.39$, $p = 0.000$ and $F_{1,54} = 8.19$, $p = 0.006$, respectively), while more xylem tissue was found to be in coppice shoots of chestnut ($F_{1,54} = 7.20$, $p = 0.009$).

Discussion

Our three point bending tests showed that the mechanical properties of branches and coppice shoots in the three species showed quite different patterns depending on their growth form. Though branches were thicker than coppice shoots in all three species, only horse chestnut and sycamore were more rigid, while calculations showed that especially in ash the coppice shoots were apparently composed of stiffer (higher E) material. A similar, though less-pronounced situation, was seen for strength parameters, in which horse chestnut branches were stronger and had higher breaking stress than coppice shoots, whereas in ash there was no difference between the two growth forms. Flexural stiffness (EI) is functionally more important than flexural modulus (E) since EI is a composite measure of the overall bending stiffness and is mainly influenced by the stem radius. EI is, therefore, more ecologically relevant parameter to determine how the stems show mechanical response to environmental loads. Overall horse chestnut was stiffer and stronger in its branch shoots than its coppices. Similarly sycamore was also stiffer and stronger in its branches, except higher E in its coppices. However, the branches of sycamore and ash have smaller diameter, so the smaller diameters resulting in lower values of I and lower values of E . Therefore, EI is lower as a result of lower values of both I and E . It could show that ecologically the branch of horse chestnut is well adapted to environmental loading and horse chestnut branches could better suit to facilitate damping and absorb more bending energy when exposed to wind. In comparing of coppice of horse chestnut vs. sycamore and ash, horse chestnut had a low E value (greater flexibility) but more than two times higher I values than sycamore and ash. However, sycamore and ash ecologically should be more able to absorb bending energy and function better at damping than horse chestnut. This study also investigated the specific modulus (E divided by density) of branches and coppice shoots for each tree species to determine how branches and coppice stems resist deformation. The specific modulus results followed the same pattern in branches and coppices; specific modulus was found to be higher in coppices shoots of the sycamore and ash trees, while the inverse pattern was observed in horse chestnut which showed higher specific modulus in its branches. Overall, these results could suggest that the branches of ash tree develop higher flexibility (low E) than coppice shoots, however, its coppice shoots were stiffer (higher E) which could provide more structural and mechanical support to grow and survive.

Overall, the growth patterns and mechanics of the branch and coppice shoots helps explain how the three different tree species we investigated are managed and

exploited. In horse chestnut, the coppice shoots grow just as slowly and have weaker mechanical properties than the branches. This explains why this tree is not exploited for coppicing. Although sycamore coppice shoots in contrast grew faster and had good material property (higher E), its branch shoots were stiffer (EI) and stronger (maximum longitudinal stress) than the coppices. It shows that sycamore should not balance two important functions (higher structural E and higher EI) at the same time in their coppice shoots. Therefore, sycamore coppices would not be useful, so once again coppicing is not a common form of management for this tree species, especially as it has sympodial branching and so it does not coppice well. The growth rate of ash is the dominant factor in selecting this species over the other for poles and tool handles. Ash was the only species which shows rapid stem elongation; that is although the age of ash coppices were around 3 times and 2.6 times lower than horse chestnut and sycamore, respectively, ash produced reasonably longer coppice shoots than the other species. The coppice shoots of ash also showed higher material properties (higher structural E) than its branches. Ash also had few leaf nodes with monopodial growth, which gave straight shoots, and wood with good material properties. It is no surprise; therefore, that ash has long been subjected to coppicing as a form of management, producing straight, rigid poles which are widely used for the handles of tools (Bealer 1996). We did statistical analysis to determine whether the differences come mainly from type (coppice vs. branch) or from age. Our analysis showed that differences between both E and EI are mainly affected by the shoot types (branch vs. coppice) for each three tree species. We also investigated the effect of age since some species (sycamore and ash) showed greater differences in their branches and coppice shoots, however, there was no relationship between mechanical properties and age.

As seen in previous studies, flexural stiffness is mainly affected by wood density, microfibril angle (MFA), latewood percentage, presence of reaction wood, arrangement of cell wall layers and tracheid/fibre length and inclination angle (Niklas 1997b; Dahle and Grabosky 2010; Niklas and Spatz 2012). It is well known that higher latewood percentage, higher density, thicker cell walls, higher proportion of cell wall material and longer fibre length could make mechanical properties better. In this study, however, this is despite the lack of a major difference in the pattern of wood density. Overall, though wood density was found to be highest in the branches than the coppice shoots, horse chestnut and ash trees did not show any difference in their densities between branch and coppice shoots. In this study, linear regression analysis did not find any relationship between mechanical properties and density. Here, we did not examine the branches and coppice shoots anatomy. Study of wider range

of anatomical and morphological properties (e.g., cell size, cell diameters, cell shape, latewood percentages) could help to determine why wood mechanics differ between branches and coppice shoots. Instead, it seems more likely that the relative mechanical properties of the branches and coppice shoots in the three species examined in this study were related to the leaf node frequency. We hypothesised that horse chestnut branches are stiffer and stronger than coppice shoots because the leaf node frequency is lower. In contrast, the reverse is true in sycamore and especially ash, where the leaf node frequency is lower in the coppiced shoots.

To test this suggestion, we performed a log-linear regression analysis fitting log-transformed data to determine the effect of leaf node frequency on the mechanical properties. Linear regression analyses showed that there was a significant negative relationship between $\log_{10}[E]$ and $\log_{10}[\text{Leaf node frequency}]$, though the relationship was weak ($R^2 = 0.32$, $p = 0.000$). A linear regression analysis also showed that there was a significant negative relationship between $\log_{10}[\sigma_{Bmax}]$ and $\log_{10}[\text{Leaf node frequency}]$ ($R^2 = 0.17$, $p = 0.000$).

These results suggest, therefore, that it is the differences in leaf node frequency that explain the differences in mechanical properties both between shoot types and between species. The present findings are in agreement with the results of previous studies, which concluded that there was an inverse relationship between E and leaf nodes (Bergman et al. 2009; Caringella et al. 2014). These previous authors suggest that the nodes act as “springs”, allowing localised flexion of the branches at the nodal points.

In the branches, the higher flexibility at the nodal points could be related to both the orientation of fibres and gaps around the branching. At the nodal region, the fibres could be oriented radially and this arrangement may probably result in greater flexibility in the parallel plane. On the other hand, there is gap in the nodal region, since the vascular cylinder of stem is interrupted. However, parenchyma cells occupies the gap (Dahiya et al. 2005). These cells might tend to be only concentrated to parts of the vascular supply for the growth of lateral buds and flowers (Gunning et al. 1970). Thus, the main role of cells in the nodal region is to facilitate vascular network, not mechanical support. Mechanical support might be provided by the cells which produce in the internodal region. Therefore, the gap in nodal region could cause weakness at this point. However, the nodal region should be investigated in detail as to determine how fibres are oriented around the nodes.

However, our results also suggest why there are differences between the frequency of leaf nodes in the two forms of shoot. The lower frequency of leaf nodes in ash and sycamore coppice shoots seems to be related to the comparative growth rates of the shoots as shown by their relative ages. In both sycamore and especially ash, the coppiced shoots were

far younger, showing that they had grown faster, at least in extension growth, than the branch tips, and though they produced similar numbers of leaves, these were further apart. In horse chestnut this was not the case and the slow-growing coppice shoots had more leaves per unit length.

Branch and coppice shoots also showed a different failure mechanism; coppice shoots exhibited more buckling, whereas there was mainly clean fracture in the branches. Overall, there was also more buckling than clean fracture. In our study, particularly ash showed more buckling failure pattern in both its branch and coppice shoots. However, previous study by van Casteren et al. (2012) investigated the greenwood properties of different coppice shoots. In their study, ash more likely failed by clean fracture mode in which the fracture went straight and longitudinal crack occurred along the mid-point of the stem. They suggested that failure could run easily through the centre of the stem because they probably would not cross any ray cells at this point. The difference between these two studies could be related to difference between relative bending span. However, we conducted logistic regression to estimate the likelihood of occurrence of buckling modes in relation to a series of predictor variables (diameter, density, relative pith diameter, the ratios of pith, bark and xylem, leaf node frequency and age). There was no overall effect on failure mode with leaf node frequency, but diameter did have a significant effect. Overall, there was a negative relationship between buckling and diameter: the greater the thickness the higher the likelihood of clean fracture occurrence ($\chi^2_1 = 9.56$, $p = 0.003$). This may not have been because of any differences between the wood in branches of different diameter; it may have just been because the relative span in our bending tests would have been lower in thicker branches, so stresses would have been more concentrated at the points on contact, resulting in more frequent fractures. Furthermore, especially in ash, the greater the pith percentage the higher the likelihood of transverse buckling occurrence ($\chi^2_1 = 5.34$, $p = 0.021$). However, there was no relationship between buckling and pith percentage in both horse chestnut and sycamore ($p > 0.05$).

We also found that mechanical properties were greater at the base of branches and coppice shoots than their tips. The present study also agrees relatively with that from previous studies (Dahle and Grabosky 2010). Regions near the base of the branches were relatively denser, stiffer and thicker than that of two shoot locations. All these would help branches to reduce oscillation from the bending loads of wind and provide self-support (Bertram 1989; Niklas 1994, 1997a, b, c; Suzuki and; Hiura 2000; Spatz et al. 2007).

We also surprisingly found that relative mechanical properties (E and EI) of the branch and coppice shoots in three species in this study were also related to relative diameter of pith. In this study, it can be clearly seen that, sycamore and ash had more pith (pith %) in their coppices,

but percentage of pith was higher in branches of horse chestnut. To determine the effect of pith %, we performed a log-linear regression analysis fitting log-transformed data. Linear regression analyses found positive relationship between $\log_{10}[E]$ and $\log_{10}[\text{pith}\%]$, though the relationship was too weak ($R^2 = 0.07$, $p = 0.000$). We can suggest sycamore and ash is more flexible in their branches because pith percentage is lower; but horse chestnut is more flexible in its coppices due to its lower pith percentage. Ash particularly showed better material property (higher E) in its coppice shoots, this could be related its pith percentage. Ash had significantly higher percentage of pith in its coppices than the coppices of chestnut and sycamore. The higher percentage of pith in ash may provide some advantages: rapid extension growth and mechanical support for the skeleton of shoot (Mosbrugger 1990; Niklas 1992; Briand et al. 1999). Ash coppices show rapid stem elongation which may allow the stems to quickly erect. The large diameter of pith could help rapid elongation growth, particularly in coppices, that is less energy is needed during stem elongation since source of soils (e.g., moisture and nutrients) could be converted to only structural purposes like elongation growth (Briand et al. 1999). Coppice stems are more likely aligned vertically and these stems are close to the soil (ground) than the branches so it could use the source of soils directly. (Briand et al. 1999). Pith percentage may be dominant factor for E values in greenwood. Therefore, further studies should be carried out to support this suggestion and the stems could be compared between green and dry conditions to understand the mechanical role of pith in detail.

Author contribution statement SO designed and performed experiments, analysed data and wrote the manuscript and ARE provided sample collection and edited manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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