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Comparison of wood, fibre and vessel properties of drought-tolerant eucalypts in South Africa[§]

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Three drought-tolerant eucalypt genotypes have been investigated for a broad spectrum of properties to provide a basis for comparison on their suitability for various end-uses. The genotypes included were a *Eucalyptus grandis* × *E. camaldulensis* hybrid, *E. gomphocephala* and *E. cladocalyx*, selected based on previous studies that indicated good potential to tolerate arid conditions, reasonably good volume growth and straightness of stems. In this study, information was added on differences between species and parts of stems in growth (volume and biomass) and properties of wood (density and stiffness), fibres (dimensions and microfibril angle) and vessels (size and numbers). We found high wood densities and stiffness values for *E. cladocalyx* and *E. gomphcephala*, making them suitable for construction wood. Logs from the mid-part of the stem had the best timber properties, as the butt logs showed the highest microfibril angle and lowest wood stiffness due to longitudinal juvenility. Such juvenility was also to some degree observed for wood density and fibre length. The information gained will be especially helpful for selecting species and processing options for small farm and community plantations for producing higher-value products that may be sold to generate much-needed income as well as for local uses, such as fuelwood and charcoal.

Keywords: density, *Eucalyptus*, fibre dimensions, fibre length, fibre wall thickness, fibre width, microfibril angle, vessel fraction, vessel size, wood stiffness

Introduction

According to FAO (1989) a land area of 45 million km², one-third of the total land area on Earth, is prone to arid and semi-arid conditions, with serious consequences for plant production. Aridity in substantial areas of a country typically leads to a concentration of agricultural and forestry production on the remaining suitable land. In the past the commercial forest industry often managed to select sites with sufficient water supply for production. With ongoing population growth in many developing countries together with climatic changes, which might reduce available soil water, the pressure on land will increase. Thus a closer appraisal of drought-tolerant tree genotypes is warranted, which are able to produce timber and fibre in very dry conditions, where forestry has been deemed previously to be economically unsustainable. The introduction of drought-hardy, non-invasive species, which can perform on marginal land, could help to create income from woodlots in environmentally disadvantaged regions for communities and farmers and render plantation forestry also more resilient to climatic change.

Promising results in this direction have been obtained in South Africa, where different *Eucalyptus* genotypes were tested for their performance in low-rainfall environments with mean annual precipitation of 200–450 mm (Ellis 1995; Ellis and van Laar 1999; van Wyk et al. 2001). After a 20-year testing phase, the genotypes with the best volume growth (van Wyk et al. 2001; du Toit et al. 2017) were evaluated for biomass production (Phiri et al. 2015) and timber quality (Wessels et al. 2016). This article provides additional information on wood and fibre quality and vessel variables.

The investigation was based on a framework of methods developed by Innventia, Sweden, and applied to different wood sources worldwide for benchmarking properties of forest resources and materials thereof (Lundqvist et al. 2010a). Related data are produced for properties of trees, parts of stems, wood, fibres, vessels and productrelated properties, and are compiled in a benchmarking database (Johansson et al. 2013; Lundqvist et al. 2013a, 2013b). Compatibility among species and projects is secured through use of standardised routines all along the chain from sampling, via measurements to database structures, allowing investigation of property differences among species, genotypes and parts of stems, as well as influences of wood on products. The concept was first applied in 2005 on Picea abies and Pinus sylvestris, then on Picea mariana, Pinus sylvestris, Pinus taeda and Pinus maximinoii, birch (Betula spp.) and four types of eucalypts from plantations in Brazil and Uruguay, and within this study also on the three genotypes of eucalypts grown in South Africa.

[§] This article is based on a paper presented at the Symposium on Silviculture and Management of Dryland Forests, Stellenbosch University, South Africa, 16–19 March 2015, jointly organised by IUFRO unit 1.02.05 and the Department of Forest and Wood Science, Stellenbosch University

In this study, the resulting data have been used to investigate variations within stems and differences among the genotypes regarding:

- (1) growth and biomass
- (2) properties of wood, fibres and vessels
- (3) solid wood from product perspectives
- (4) wood and fibres from pulp and paper perspectives (not reported here).

The aim of this study was to provide information about differences in a wide range of properties among the three selected species as a basis for judgement on their best uses in alternative products in small-scale forestry.

Materials and methods

Genotypes

The eucalypts compared were a hybrid of *E. grandis* and *E. camaldulensis*, and the species *E. gomphocephala* and *E. cladocalyx*. These genotypes were selected based on their superior performance in terms of volume growth on dry sites in a winter rainfall area on the South African west coast (van Wyk et al. 2001; du Toit et al. 2017). The genotypes planted in these growth trials had been partly pre-selected in other countries, such as Israel and Morocco for their drought tolerance (van Wyk et al. 2001).

The *E. grandis* \times *E. camaldulensis* hybrid formed fairly straight stems. However, Wessels et al. (2016) highlighted that the cream- to pink-coloured wood tends to split and is prone to significant shrinkage and collapse with an adverse effect on sawn timber production. The parental species were hybridised to combine the drought hardiness and high density of *E. camaldulensis* with the favourable stem form and good growth of *E. grandis*.

The sugar gum, *E. cladocalyx*, is a species from southern Australia around Adelaide and southern Victoria, where it is planted for firewood and windbreaks (Boland et al. 2006). It has been introduced to South Africa as a tree for wind breaks and is also grown for honey production and fuelwood. It forms straight stems with strong apical dominance but also tends to produce thick branches if grown without sufficient competition. As an adult tree it shows good fire tolerance due to a thick bark layer (Odhiambo et al. 2014). The yellowish-brown wood is heavy and has a high natural resistance to decay (Cookson 2004). It is thus used for poles and also in marine environments. However, it also produces interlocked grain and high levels of twist of sawn boards (Wessels et al. 2016).

Tuart, *E. gomphocephala*, originates from the southern parts of Western Australia around Perth (Boland et al. 2006) and is also found around Adelaide. The species is well known for its good growth performance in winter rainfall areas with dry summer conditions (National Academy of Sciences 1980) where it outperforms other species such as *E. camaldulensis* on sites with highly alkaline soils. The mean annual precipitation in its natural habitat is about 600–1 000 mm (National Academy of Sciences 1980). However, it is very drought tolerant and in South Africa it is frequently grown as a shade tree along roads under harsh conditions. Wessels et al. (2016) found that the light brown, almost oak-coloured wood of *E. gomphocephala* also had high levels of spiral

grain, which led to substantial twist of boards. *Eucalyptus gomphocephala* was also the genotype with the worst stem form amongst the three tested species.

Sampled sites

Twenty-year-old trees were sampled at two trial sites on the west coast of South Africa:

- (1) Site 1: a semi-dry site at Pampoenvlei about 50 km north of Cape Town. It is a flat dune area with mean annual precipitation of 423 mm (Ellis and van Laar 1999; van Wyk et al. 2001; du Toit et al. 2017). The arid conditions of this site is somewhat ameliorated by cool sea mists and an underground water table approximately 2–3 m from the surface in the winter months.
- (2) Site 2: a very-dry site with even more harsh conditions at Chemfos situated further from the coast, close to Hopetown about 80 km north of Cape Town, also on deep sandy soil with a mean annual precipitation of 256 mm (du Toit et al. 2017).

More information on the species and sites can be found in du Toit et al. (2017).

Sampling and measurements

At each site, all trees of the selected genotypes were characterised for breast-height diameter, health, previous damage and stem form, and four trees representing different growth rates were selected from each genotype and site: one large tree, one small tree and two mediumsized trees. Bolts were cut at four heights along each stem: at breast height (1.3 m), at 25% and 60% of the total tree height, and at a diameter of 7 cm (close to the top). The positions were adjusted to avoid sampling at

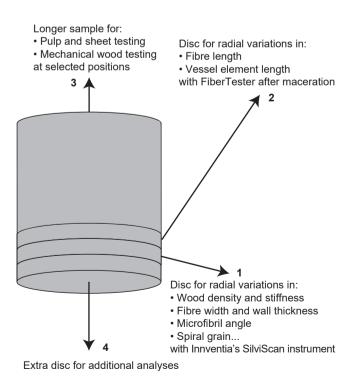


Figure 1: Division of sample bolts into subsample discs for different measurements

whorls or other disturbing features. The resulting bolts were divided into subsamples in the form of discs for measurement of radial variations in different properties (Figure 1).

The results presented in this article are based on measurements of radial variations of different wood properties, determined on different samples as seen in Figure 1. Properties of wood, fibres and vessels were determined with SilviScan on material from Disc 1. Fibre lengths were measured on material from Disc 2.

SilviScan is an instrument for measurement on the same sample of radial variations in growth and properties of wood (density and stiffness [modulus of elasticity; MOE]), fibres (microfibril angle [MFA], width and wall thickness) and vessels (fraction, number and size) through integrated use of different measurement techniques: image analysis for wood anatomical properties, X-ray transmission for wood density and X-ray diffraction for microfibril angle determination (Evans 1994, 1999; Chen and Evans 2010; Lundqvist et al. 2010c). Data from other features of the diffractograms are combined with density data to estimate MOE (Evans 2006). The measurements were performed on 2 mm thick wood strips extending from pith to bark. In this article, the variations are presented with averages for consecutive radial 2 mm intervals.

For fibre length data at each sampling position, a radial bar was cut from pith to bark, in the same direction as the SilviScan sample strip. One-centimetre-broad radial intervals were analysed: one at radial distance 1–2 cm from the pith, one close to the bark and, for the lower positions with a sufficiently large stem diameter, one at 3–4 cm from the pith. The measurements were performed with a FiberTester (Karlsson 2006), analysing images of fibres obtained from laboratory kraft cooking.

Results

The outcome regarding tree form (size and taper) of the sampled trees is shown in Figure 2.

Radial and longitudinal variations in wood density are illustrated in Figure 3. It should be noted that the densities shown were determined from samples with moisture content (u = 8%) in equilibrium with the atmosphere of the conditioned laboratory (conditioned weight/conditioned volume), providing higher values than a basic density analysis (oven-dried weight/green volume). The three upper plots show the density variations from pith to bark at breast height for each genotype. The thin lines represent variations in individual trees, the thicker lines their average variations from the pith to a radius of 100 mm. Further out, data were only available for large trees and averages would be less reliable. The lower plots of Figure 3 illustrate the density variations along the stem axis, presented with area-weighted averages for all sampled cross-sections for the two sites. (The density for the top position of one large tree of the hybrid was missing, making the tree appear shorter than it is.)

For *E. gomphocephala* and *E. cladocalyx*, the fastergrowing trees of Site 1 showed a slight increase for the average density of the cross-sections from breast height to the sample location above it. This is an indication of a transition from juvenility towards maturity of wood not only radially but also in the longitudinal direction of the stem. It occurs also for other wood and fibre properties, to different extents among properties and species, and will be commented on further below.

Averages for stems were calculated as well as volumeweighted averages for sites and genotypes (Figure 4). The hybrid showed a much lower wood density than the other

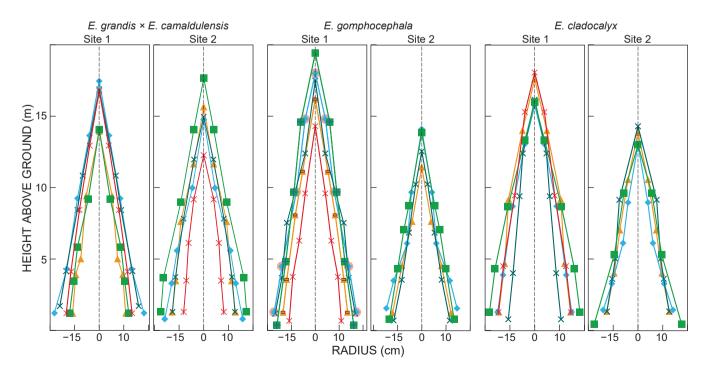


Figure 2: Graphic illustration of the size and taper of the individual trees sampled from each genotype and site

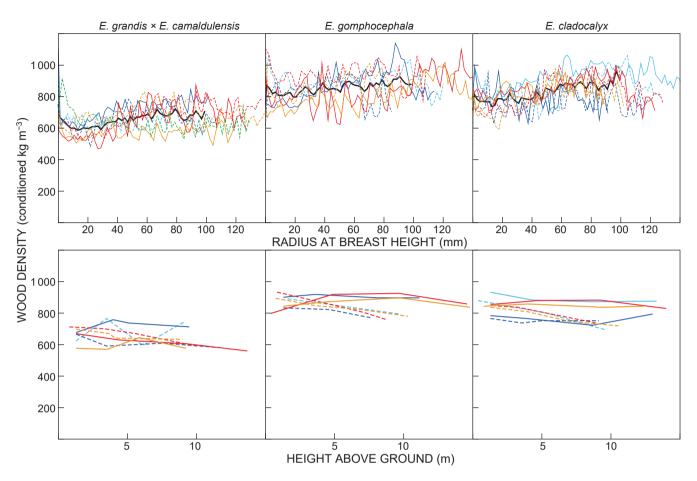


Figure 3: Upper graphs, radial variations of wood density (conditioned wood) at breast height. Lower graphs, longitudinal variations along the stems. Solid lines for Site 1, dashed lines for Site 2

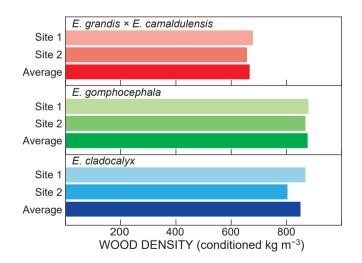


Figure 4: Averages for wood density of full stems of the different genotype and sites

genotypes. Interestingly, the density was lower on the more arid Site 2, and especially so for *E. cladocalyx*.

Growth and stem biomass

In Figure 5, four variables related to growth and biomass were compared among the genotypes: stem volume at age

20 years, vessel fraction (as proportion of wood volume), wood density (conditioned), which is influenced by vessel fraction and fibre dimensions, and stem biomass without bark at age 20 years, calculated from stem shape and density variations.

Comparison of the genotypes for the variables showed:

- E. grandis × E. camaldulensis had the largest stem volume, but also the largest vessel fraction, resulting in the lowest density and biomass.
- *E. gomphocephala* showed a similarly large stem volume, but the lowest vessel fraction. Therefore, it had the highest density and largest biomass.
- E. cladocalyx had the smallest stem volume and a moderate vessel fraction. This resulted in high density and an average biomass.

Wood properties

In Figure 6 the relations between three major wood properties of importance for solid wood products are presented: Wood density (again), microfibril angle (MFA) and wood stiffness (MOE), which is strongly correlated with density (positively) and MFA (negatively). Data shown are volume-weighted averages:

- E. grandis × E. camaldulensis had the lowest wood density and high MFA, and therefore the lowest MOE
- · E. gomphocephala had the highest wood density but also

the highest MFA, and therefore medium MOE values

• *E. cladocalyx* had high wood density and the lowest MFA, which yielded the highest MOE.

For MOE and MFA, it is important to consider also variations along the stem. All the genotypes investigated showed pronounced longitudinal juvenility for MFA. This is illustrated in Figure 7, showing the radial variation of MFA at the four heights for *E. gomphocephala*, averaged among the four trees of Site 1. At breast height these trees had a

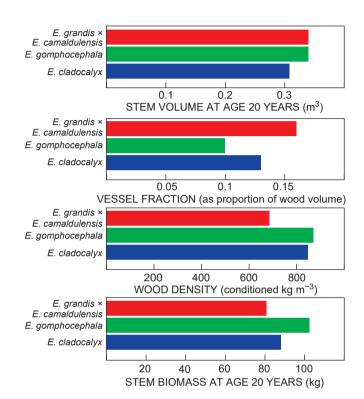


Figure 5: Average stem volume, vessel fraction, wood density and stem biomass per genotype at age 20 years

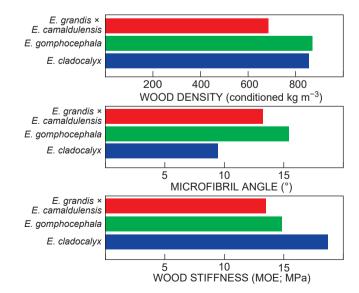


Figure 6: Averages wood density, microfibril angle and wood stiffness (modulus of elasticity; MOE) per genotype at age 20 years

wide juvenile core of diameter about 10 cm indicated by MFAs higher than 20°. Already at 25% of the tree height, this juvenile core had decreased to about 4 cm, and its diameter decreased further upwards along the stem, meaning that the MFA of wood at the same radius and cambial age decreases longitudinally. As the wood density did not vary substantially (see Figure 3), these patterns of variation in MFA were directly reflected in the variation in MOE (see Figure 8). A consequence of this is that the logs with the highest wood stiffness are not those with the largest diameter, but those higher up the stem (Wessels et al. 2016).

Fibre properties

In Figure 9, the radial variations at breast height and the variations along the stem are shown for fibre length. Solid lines represent samples from Site 1 and dashed lines samples from Site 2. The fibres were clearly shorter in a core with a diameter of 6–8 cm around the pith. Within this core, there was a quite steep length development, with a gradually smaller increase with radius further towards the bark. The total increase in fibre length from pith to bark was 25–35%. The levels differed among the genotypes,

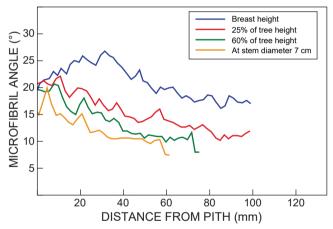


Figure 7: Average radial variations in microfibril angle at the four heights sampled for *E. gomphocephala* at Site 1

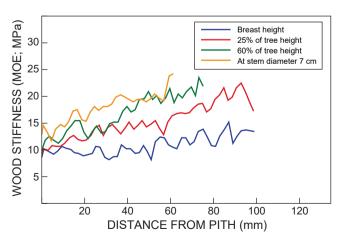


Figure 8: Average radial variations in wood stiffness (modulus of elasticity; MOE) at the four heights sampled for *E. gomphocephala* at Site 1

and for the hybrid the fibres were longer in the slow-grown trees from Site 2. The longitudinal development of fibre length along the stem, expressed with cross-sectional stem averages, showed that the logs at the mid part of the stem had the longest fibres, which indicates that fibres at the same radius tend to be shorter close to the base of the tree, again an effect of longitudinal juvenility.

For fibre width, the within-stem variations of individual trees were much smaller than that for fibre length, only up to about $\pm 6\%$ of the mean value for the most variable trees (data not shown). There were, however, significant but small differences among the genotypes.

The radial variations in fibre wall thickness expressed as averages for genotypes showed steady increases from radius 1 cm to the bark, with about the same order of size as was observed for fibre length, and with clear differences among the genotypes (Figure 10). The cross-sectional averages of fibre wall thickness varied only slightly in the longitudinal direction for two of the genotypes, indicating a slight increase upwards along the stem. This indicates increasing wall thickness at the same radius further up the tree. As the relative variation in fibre wall thickness is much larger than that of the fibre width, the wall thickness will, together with the vessel fraction, be the major determinant of wood density.

A comparison of volume-weighted averages for the stems of all trees of each genotype showed that:

 E. grandis × E. camaldulensis showed the longest fibres and the thinnest fibre walls

E. grandis × E. camaldulensis

 E. cladocalyx had the shortest fibres and very thick fibre walls.

The fibre widths were similar for all of the genotypes.

Vessels

The radial and longitudinal variations for three properties related to vessels are presented in Figure 11, as well as differences among the phenotypes, similar to fibre dimensions in Figure 10. The radial variations in vessel fraction at breast height showed different levels between the genotypes with a general slight increase with radius across all genotypes. Each genotype showed relatively large increases in vessel size with radius, following a similar radial pattern as fibre length: a core with a large increase, and smaller increases nearer the bark. This was accompanied by reduction in the vessel number per unit area but to a slightly lesser degree. These two developments in combination explained the slight increase in the vessel fraction with increasing radius. All of these vessel-related properties increased upwards in the stem.

Discussion

Growth

E. gomphocephala

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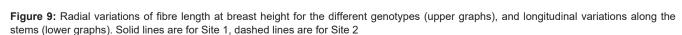
Growth is often characterised by different aspects: (1) the physical extensions of the stem, such as diameter, which is important for sawing, (2) the volume, and (3) the

E. cladocalyx

0.2 FIBRE LENGTH (mm) 0.1 120 120 20 40 60 80 100 20 40 60 80 100 120 20 40 60 80 100 RADIUS AT BREAST HEIGHT (mm) 0.9 0.8 0.7 0.6 0.5 0.4 0.3 0.2 0.1 10 10 5 10 5 5 HEIGHT ABOVE GROUND (m)

0.9

0.8 0.7 0.6 0.5 0.4 0.3



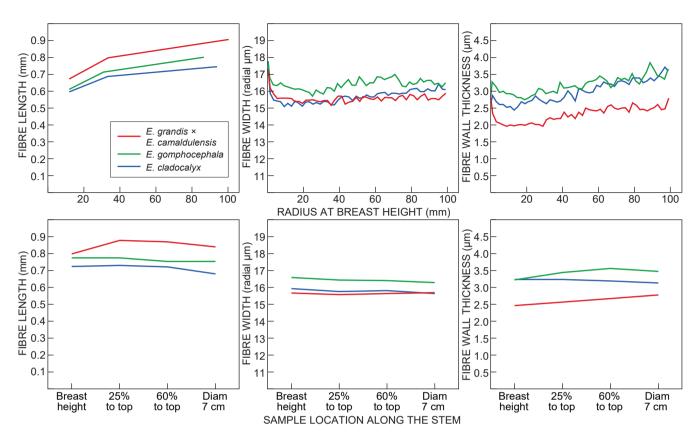


Figure 10: Differences among the genotypes in radial variations of fibre dimensions at breast height (upper graphs) and in longitudinal variations along the stem (lower graphs)

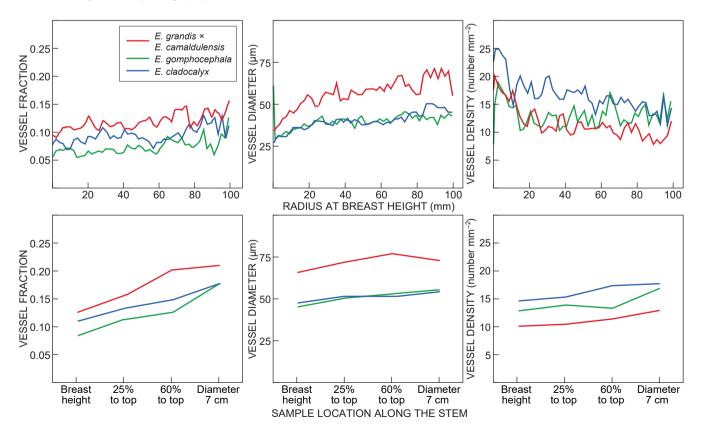


Figure 11: Differences among genotypes in radial variations of properties related to vessels at breast height (upper graphs) and in longitudinal variations along the stem (lower graphs)

amount of dry biomass produced. Results on the biomass based on data from the genotypes have been published by Phiri et al. (2015). In this article, we have elucidated the importance of the volume fraction of vessels in this context and how it determines the density of wood to a large extent.

The hybrid *E. grandis* \times *E. camaldulensis* showed the highest individual tree volume, but still the lowest production of biomass per tree, due to its large vessel fraction and low wood densities. Vessels are of crucial importance for water conductance in trees (Tyree and Zimmermann 2003; Nikolova et al. 2009). With regard to wood utilisation, they may influence impregnation and natural durability, in paper they may create problems on printing by vessel picking, especially the large diameter vessels (Haygreen and Bowyer 1989; Lundqvist 2002), and they add to the raw material transportation work per unit of dry biomass as a void volume.

Radial variation

Radial variation is typical for many wood properties and our genotypes follow the typical patterns with regard to wood density, MFA and stiffness. A general increase in wood density from pith to bark was postulated for eucalypts by Downes and Raymond (1997). We have observed the same pattern for the trees in this study. It was also observed for several other *Eucalyptus* species (e.g. Nicholls and Pederick 1979; Malan and Gerischer 1987; Evans et al 2000).

It is well known that the MFA is high in a core of inner wood around the pith (Evans et al. 2000). This was also observed for the genotypes investigated, but at different levels, and with different sizes of the cores. The narrowest cores were observed for *E. cladocalyx*. In addition, a longitudinal juvenility was evident.

Also for fibre properties, the drought-tolerant genotypes followed previously reported general patterns of variation in eucalypts: in relative terms, large increases with radius in fibre length and wall thickness, and a small radial increase in fibre width. These patterns have also been observed for other eucalypts previously tested with the same benchmarking concept. Miranda and Pereira (2002) reported radial fibre length variations for *E. globulus* in a similar range. Given the small relative variation in fibre width with radius, the radial variation in fibre wall thickness will be closely associated with the radial variation in wood density.

The radial variations observed for properties of vessels of the three genotypes were also in line with previous observations: an increase in average diameter and crosssectional area of the vessels (mm²) with radius, and a decrease in vessel density (number mm⁻²), which led in combination to a slight increase in vessel fraction (volume proportion) with radius. Such increased vessel conductive area with increasing stem size resembles previous findings for eucalypts by Downes et al. (1997), and matches observations for other eucalypts in benchmarking projects (Lundqvist et al. 2010b), poplars and birch (Lundqvist et al. 2010c). According to Hagen–Poisson's law conductance is related to the fourth power of the vessel diameters (Nikolova et al. 2009), hence the local conductance of

Longitudinal variation

The longitudinal variations in cross-sectional averages for all properties were influenced by the increasing content of juvenile wood when approaching the top of the tree, and for most species and properties the logs with on average the most mature wood were found close to the base. However, for some genotypes and properties showing pronounced longitudinal juvenility close to the base of the tree, the logs with the most mature average wood and fibre properties were found towards the mid-part of the stem.

In this study, longitudinal juvenility was observed for MFA in all three of the genotypes. The highest cross-sectional averages for MFA were observed at breast height, despite its wood being of highest average cambial age. The crosssectional average MFA was clearly lower at the sampling position above. The effect was observed also by Evans et al. (2000) in a detailed study of variations in MFA and wood density of *E. nitens* in Australia, and has been described for other *Eucalyptus* species investigated in industrial projects with the benchmarking concept (Lundqvist et al. 2010b). Similar effects have also been observed in conifers such as *Pinus taeda* and *Pinus radiata* (Burdon et al. 2004), *Pinus taeda* and *Pinus sylvestris* (Lundqvist et al. 2013b) and *Picea sitchensis* (Reynolds 2010).

Another illustration of longitudinal juvenility, but weaker in magnitude, was observed for density (Figure 3). This was also reported by Evans et al. (2000) for different eucalypts. For the hybrid, the fastest-growing genotype, the density increased slightly with height in the lower part of the stem, indicating increased maturity upwards in the longitudinal direction. This pattern has been observed for density in other *Eucalyptus* species on highly productive sites (Lundqvist et al. 2013b).

As MFA was lowest and density highest or relatively constant along the mid-part of the stem, this part of the stem will supply logs with on average higher MOE than at breast height. Thus, it cannot be naturally assumed that the butt log is the most valuable part of the stem for structural timber. Such longitudinal variations in MOE have been observed also in Sitka spruce (*Picea sitchensis*) accounting for low wood stiffness in butt logs (Reynolds 2010).

A similar pattern was observed for fibre length for the hybrid *E. grandis* \times *E. camaldulensis*, the fastest-growing genotype investigated (Figure 9). Logs from the mid-part of its stems showed the highest average fibre length. Similar results were reported for *E. globulus*, *E. nitens* and *E. regnans* by Downes et al. (1997), and observed for properties in eucalypts and other hardwoods (Evans et al. 2000; Lundqvist et al. 2010b). For Norway spruce, Scots pine and loblolly pine, models for within stem variations in fibre length, with shorter fibres close to ground level, have been presented (Lundqvist et al. 2005).

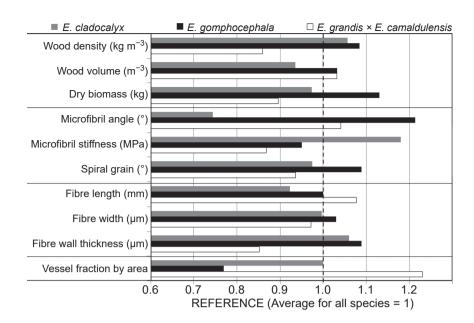


Figure 12: Comparison of the properties studied among the three eucalypts, with the overall average for each property as the reference (= 1)

Genetic and site effects

The volume growth of the stems was larger for all genotypes at Site 1, which receives higher precipitation, as expected. The difference was less pronounced for the hybrid. The wood density was higher for the trees on the less arid Site 1 for the hybrid and for *E. cladocalyx*, and slightly higher also for *E. gomphocephala*. The same pattern was observed for fibre wall thickness. All genotypes showed higher wood stiffness at Site 1. These correlations are not surprising, because fibre wall thickness is a strong determinant for wood density, which in turn has a strong effect on wood stiffness.

Thus, the hybrid showed the least difference among the genotypes in growth between the dry and very dry sites. This is not evidence for less overall sensitivity to drought. It is probably the genotype, among the three genotypes studied, that has been most subjected to genetic modification and may have been sensitive already to the low precipitation at Site 1. This shows that a study for general information on genotype \times environment effects must include a wider set of sites. The number of trees sampled per genotype and site was limited. The observations thus should be seen as indicative and largescale application of the results should be under-pinned with further tests.

Comparison of the three investigated genotypes and possible utilisation

In Figure 12, averages for the properties studied with the largest impacts on products and economic return are compared among the genotypes, in relative terms with the overall averages as the reference (= 1).

The hybrid *E. grandis* \times *E. camaldulensis* had the longest fibres and *E. cladocalyx* the shortest. The hybrid had the thinnest fibre walls and the largest volume proportion of vessels in the stem. Consequently, it had by far the lowest wood density and the lowest biomass. Its low wood density combined with a higher-than-average MFA gave it also the

lowest MOE. The study indicated that the hybrid was the least suitable among the genotypes for structural timber, but the best for common pulp and paper grades, albeit probably not competitive compared with other eucalypts developed for such use, and especially not if considering also its low yield on pulping (comparison based on data from previous studies).

The *E. gomphocephala* trees showed the thickest fibre walls and smallest vessel fraction, resulting in the highest wood density. It had, however, also by far the highest MFA, so the MOE was still clearly below that of *E. cladocalyx*.

The *E. cladocalyx* trees combined higher-than-average fibre wall thickness with an average fraction of vessels, resulting in higher-than-average wood density. It had also by far the lowest MFA, resulting in superior MOE values. The study indicated that, with regard to the properties studied, *E. cladocalyx* would be the most suitable species for structural timber, but the least suitable for common pulp and paper grades.

Conclusions

- Eucalyptus cladocalyx showed the greatest potential for timber production given the low MFA and high wood density, leading to a high microfibril stiffness.
- The hybrid *E. grandis* × *E. camaldulensis* was rated the least suitable genotype for timber production and the best source for pulp and paper, but still not competitive with other commercial species.
- Eucalyptus gomphocephala was slightly inferior for structural timber compared with *E. cladocalyx*, mainly because of its high MFA and bad stem form.
- The MFA and MOE values were highest in the middle section of the stem, because of the effects of longitudinal juvenility close to the base, and of radial/cambial juvenility at the top.
- Some effects from longitudinal juvenility were observed also for wood density and fibre length.

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