



Assessing wood grain and twist in a 2-year-old *Eucalyptus bosistoana* breeding population

Monika Sharma¹ · Stephanie M. Dijkstra^{1,2} · Ashley Garrill² · David A. Collings^{2,3} · Clemens M. Altaner¹

Received: 27 March 2024 / Accepted: 13 September 2024 / Published online: 24 September 2024
© The Author(s) 2024

Abstract

Key message Radial grain patterns in young *E. bosistoana* trees are not random but are under genetic control and are correlated to other properties. Detailed high-resolution grain assessments match results from economical larger resolution techniques.

Abstract Interlocked grain affects stem properties and timber value. *Eucalyptus bosistoana* is an emerging plantation species that is supported by a breeding programme, and which shows prominent interlocked grain. Grain assessments are difficult, either restricted in their spatial resolution or resource demanding. Comparative analysis of flexible and high-resolution X-ray microtomography grain measurements were shown to match the economical splitting test. Splitting demonstrated that, on average, grain in the 2-year-old *E. bosistoana* trees was straight close to the pith becoming slightly left-handed over the first 4 mm, but then developing a strong right-handed twist reaching an average of almost 5° by 12 mm. There was, however, a large degree of variability. Further, grain measures obtained from splitting tests correlated to the observed twisting of the stems. Lastly, twisting of timber was under genetic control. The combination of a heritability (h^2) value of 0.34 and a coefficient of genetic variation value (r_g) of 44% means that our assessment techniques for young trees could be incorporated into a breeding programme.

Keywords Heritability · Interlocked grain · Splitting · Twist · X-ray computed microtomography

Introduction

Grain patterns, the orientation of the main cell axis with respect to the stem axis, affect the value of timber. Spiral grain occurs when grain winds around the stem axis in one consistent direction, and can either be left- or right-handed, referring to the direction of the spiral as it ascends the tree. This pattern causes timber to twist during drying due to the anisotropic shrinkage of wood (Harris 1989), diminishing the value of sawn timber (Haslett et al. 1991; Kliger 2001). Interlocked grain, however, is present when the main cell axis alternates between a left-hand and a right-hand spiral along the radial axis of the tree. Interlocked grain can be characterised by the amplitude and period of the grain in radial direction as well as its regularity (Thinley et al. 2005). Regular interlocked grain can add value to timber due to its attractive appearance when quartersawn (Scheiber 1973). Wood with interlocked grain does not twist as drying stresses cancel out. Nevertheless, interlocked grain can induce problems in peeled veneers where the grain is unidirectional due to being thinner than the interlocked grain period (Brouse

✉ Clemens M. Altaner
clemens.altaner@canterbury.ac.nz

Monika Sharma
monika.sharma@canterbury.ac.nz

Stephanie M. Dijkstra
stephanie.sillars@gmail.com

Ashley Garrill
ashley.garrill@canterbury.ac.nz

David A. Collings
david.collings@anu.edu.au

¹ School of Forestry, The University of Canterbury, Christchurch 8140, New Zealand

² School of Biological Sciences, University of Canterbury, Christchurch 8140, New Zealand

³ Research School of Biology, The Australian National University, Canberra, ACT 2601, Australia

1966; Webb 1969). In contrast to spiral grain, which is common to softwoods, regular interlocked grain appears to be unique to hardwoods (Harris 1989). The evolutionary advantage of trees expressing interlocked grain has been debated. Whilst it was proposed that interlocked grain increases security in water supply to all sectors of the crown (Rudinski 1959, cited in Webb 1969), more recent research has focussed on biomechanical advantages. Interlocked grain has been found to reduce the modulus of elasticity and modulus of rupture of wood, whilst it increases tenacity, that is the energy needed to split timber along the grain (Bossu et al. 2018; Hernández and Almeida 2003). This appears to be particularly relevant for trees which develop large growth stresses (Cabrol et al. 2009; França et al. 2020).

It is the consensus opinion that changes in cell orientation in trees occur during cambial divisions (Harris 1989; Schulgasser and Witzum 2007), but how grain patterns emerge is not well understood. Microscopic studies have found some correlation between grain direction and the direction of cell formation in the cambium (as summarised by Harris 1989). Asymmetric boundary conditions for the maturing xylem cells in combination with their tendency to twist has been proposed to cause their reorientation (Schulgasser and Witzum 2007). However, the implied link to the cellulose microfibril orientation is weak (Bremaud et al. 2010). Studies have reported strong genetic control of spiral grain in gymnosperms (Harris 1989). For example, heritability (h^2) values of > 0.3 were reported for Norway spruce (Costa e Silva et al. 2000; Hallingbäck et al. 2008) and radiata pine (Gapare et al. 2007). Not many reports on the genetic control of interlocked grain features have been published. Thinley et al. (2005) reported that whilst the amplitude of interlocked grain was under genetic control in 9-year-old *Eucalyptus dunnii*, the period was controlled by diameter growth. A similar finding was reported for 4-year-old *Eucalyptus camaldulensis* (Ishiguri et al. 2017). Significant differences in interlocked grain amplitude were also reported between *Eucalyptus gaudis* × *Eucalyptus urophylla* hybrid clones (França et al. 2020). Harris (1989) commented that there has been a “serious dearth of research into heritability of wavy and interlocked grain” despite warranting high priority as a key trait of high-value decorative timber species.

Eucalyptus bosistoana is a tall eucalypt species native to the moister regions of SE Australia. It grows well in New Zealand’s warmer regions (Salekin et al. 2021) and provides a Class 1 ground-durable timber (Australia Standard 5604 (2005)) with exceptionally high stiffness and strength (Bootle 2005). *E. bosistoana* usually features interlocked grain (Bootle 2005). It is one of the species that has been identified by New Zealand Dryland Forests Innovation (NDZFI) to support a hardwood plantation forest industry (Millen et al. 2018) supplying ground-durable posts for agricultural industries (Altaner and Palmer 2021),

high-performance engineered wood products and sawn timber (Millen et al. 2020). It further has the potential to support an essential oil by-product from the foliage (Rajapaksha et al. 2023). NZDFI has invested in an *E. bosistoana* breeding programme since 2008 (Millen et al. 2018) and seedlings with improved growth and wood characteristics (Davies et al. 2017; Li et al. 2018) have been commercially deployed since 2021 to establish a sustainable plantation resource in New Zealand (Altaner and Palmer 2021). To accelerate the NZDFI breeding programme, early-screening methods have been adopted (Apiolaza 2009) and *E. bosistoana* seedlings were destructively tested at the age of less than 2 years for growth strain, acoustic velocity, density and shrinkage (Altaner 2019).

In this study, we investigated *E. bosistoana* seedlings that were less than 2 years old and that were part of a larger breeding trial of more than 4000 trees to determine whether interlocked grain is a heritable phenotype, and to assess whether rapid screening for interlocked grain is possible with a large population. A range of methods to quantify interlocked grain in wood have been developed (Harris 1989) and of these, quantifying the shape of longitudinal fracture planes is a comparatively efficient method to obtain low resolution data from a large number of samples. Whilst the recent development of X-ray computed microtomography (μ CT) has simplified the generation of three-dimensional anatomical detail associated with grain development and has provided high-resolution measurements of grain (Cipta et al. 2022; Collings et al. 2021), these μ CT measurements have not been so far correlated with measurements made by wood splitting. Thus, in completing our first objective, we demonstrated that high-resolution μ CT measurements matched wood splitting data, although the high variability of the grain was a limiting factor. We further investigated whether simple measurements of physical twist of the timber after drying might be linked to interlocked grain.

Materials and methods

Plant material

A total of 4,033 trees of *Eucalyptus bosistoana* F. Muell. from 81 separate families were grown in a trial conducted at Murray’s Nursery (Woodville, North Island, New Zealand; 40° 19′ 44″S, 175° 52′ 49″E) (Altaner 2019). Seedlings were planted in February 2015 and harvested between September and October 2017, and were assessed prior to harvest for height and form (Class 1: multiple forking; 2: major fork in first log (2 m); 3: high fork above 2 m; 4: breakout above 2 m; 5: large ramification; 6: small ramification; 7: no malformation). The bottom 500 mm of the stems were cut, labelled and packed on ice for transport to the University

of Canterbury, ensuring that they arrived with minimal degradation. Following the detailed description of Davies et al. (2017), all samples were measured within 1 week of arrival for diameter, growth strain, green and dry densities, acoustic velocity and twist. The measurements also allowed to calculate volumetric shrinkage and the modulus of elasticity (MoE).

Wood splitting and grain measurements

A random subset of 140 whole wood discs 40 mm in thickness were cut from the samples and kiln dried at 103 °C before being stored at 20 °C and 65% relative humidity. No warping or uneven shrinkage was observed in the discs. Discs were then trimmed to 20 mm in thickness with cut faces perpendicular to the stem axis. The pith at each end of the disc was marked with white ink that was visible during subsequent image analysis. Using a hammer and chisel, discs were then split in half. The split was an even, straight edge through the upper face, but the edges of the split were irregular on the reverse face because of the presence of interlocked grain. Following splitting, the halved wood discs were held together with elastic band and the reverse face was digitally imaged. For imaging, the discs were oriented so that the straight edge from which the split propagated was aligned horizontally to provide a reference for grain deflection values (Supplementary Information 1A, C, D). Photoshop (version 11.0.1, Adobe Systems, San Jose, CA USA) and ImageJ (FIJI version 1.53f, NIH, Bethesda, MD USA, Schneider et al. (2012)) were used to quantify splitting patterns. A grid with vertical lines spaced every 4 pixels was superimposed in a layer above the images and small coloured dots manually applied at locations where the grid overlapped with the fracture edges and to mark the central pith (Supplementary Information 1D). The coordinates of these dots were then identified using a macroscript in ImageJ (Supplementary Information 1E–I) and the locations of the fracture edges and central pith used to calculate grain angles. Right-handed grain, which resulted from an upwards deflection of the split to the right of the pith (Supplementary Information 1B), was defined as a positive angle, whilst left-handed grain as a negative angle.

Two radial profiles were available for each of the 140 trees. To quantify grain, two measurements were extracted from each radial profile: the average grain angle in a radial profile and the magnitude of grain change, defined as the difference between the maximum grain angles in the left- and right-handed directions.

Twisting measurements in dried stem halves

The 500-mm-long stem sections were debarked and cut lengthwise through the pith with a bandsaw, with the paired

stems assessed for growth strain using a previously published method (Chauhan and Entwistle 2010; Davies et al. 2017; Entwistle et al. 2014). Paired 150-mm-long sections were then cut from the longer sections, with these shorter sections used for measurements of densities, acoustic velocity, and shrinkage (water displacement before and after drying). Twist was measured on the, at 20 °C and 65% relative humidity, equilibrated stem halves with a cell phone (Xperia Z5 Compact, Sony) running the Bubble Level Android application (version 3.23, NixGames), which determines the angle at which the phone is held. The application was calibrated by holding the phone vertically against the vertical edge of a measurement rig with this defined as 0° (Supplementary Information 2). The butt end of the sample was then placed so that the radial face was flat against the vertical section of the measurement rig and the edge of the cell phone was placed along the radial face of the free end. This deflection angle provided a measure of the twisting caused by drying. Twist to the left was defined as a negative angle, whilst twist to the right was defined as a positive angle.

X-ray imaging and grain measurements

Four samples previously imaged after splitting were selected for X-ray micro-computed tomography (μ CT) analysis. Because of size constraints, only a quarter of the original wood disc could be analysed, but this still allowed direct comparisons between the splitting and μ CT data. Using procedures developed for other wood samples (Collings et al. 2021; Thomas et al. 2022), the quartered discs were analysed using a Bruker μ CT Skyscan 1172 system (Kontich, Belgium) and were scanned at 40 kV with a current of 250 μ A, with a resolution of 4.33 μ m/pixel. Whilst imaging, the samples were rotated 180° through the beam with a rotation step size of 0.39°. Tomography images were reconstructed using the NRecon programme (version 1.7.3.0, Bruker). Image pre-processing was done in Adobe Photoshop, and ImageJ was used to vertically align the samples and to create two stacks of 500 images, each corresponding to ~2 mm in depth, from either end of the ~7 mm-thick original image stack. The data stacks were then smoothed using a 3D Gaussian blur (values, 1, 1 and 5), and brightness and contrast were optimised. After this, the pith was blacked out and the stem centre marked with a 10 pixel-wide white circle providing a reference point for grain angle calculation. The data stack was then rotated through 10° increments to 90°, and 1-mm wide strips were selected. These strips corresponded to between 7 and 9 different strips, separated by 10°, through the quartered wood disc. These strips, however, needed to avoid gaps as these compromised the quantification of grain (Supplementary Information 1D). The ImageJ *RESLICE* function then recalculated tangential longitudinal sections through these slices, and the grain angle calculated

for each image in the stacks using the *DIRECTIONALITY* plugin which uses a Fast Fourier Transform (FFT) to determine the dominant direction in the sample. An Excel spreadsheet converted these measurements to grain angles as a function from the centre of the wood disc. The final grain output averaged the two 2 mm deep image stacks, and pooled data into 10 μm intervals.

Statistical analysis

Data were analysed using R software (R CoreTeam 2022). The linear mixed model below was fitted with the Asreml-R package (Butler et al. 2009) to obtain the variances needed to calculate narrow sense half-sib (relatedness coefficient $r_c=0.25$) heritability (h^2). Confidence intervals were calculated by bootstrapping.

$$y = \mu + b + f + e$$

where y represents the phenotypic observations, μ the overall mean, and b , f and e the random block, family and residual effects, respectively.

Results and discussion

Comparing wood splitting and X-ray microtomography for wood grain measurements

X-ray computed microtomography (μCT) can measure wood grain with higher resolution than established methods such as wood splitting (Harris 1989; Hernández and Almeida 2003). Cipta et al. (2022) analysed μCT data using a FFT of cross-sections to analyse vessel orientation in interlocked grain of camphor laurel wood. In a different approach, FFT analysis of tangential longitudinal sections was used to directly measure cell orientation of tracheids in pine (Thomas et al. 2022) and fibres in mahogany (Collings et al. 2021). In combination with separately measured vessel orientation in cross-sections using image analysis, systematic differences in vessel and fibre orientations with respect to the locations in which interlocked grain reversed were revealed (Collings et al. 2021). Vessel orientation was not, however, measured in this current study. As wood splitting and μCT methods have not been previously compared, we analysed four trees with both approaches (Fig. 1). To provide sufficient resolution to directly measure grain using FFT, imaging was limited to quartered wood discs and to only ~ 7 mm along the grain of the 20-mm-thick discs, and even within this image volume, we quantified grain in two ~ 2 mm-stem lengths. Therefore, resulting cross-sections, in which the presence of xylem vessels was evident

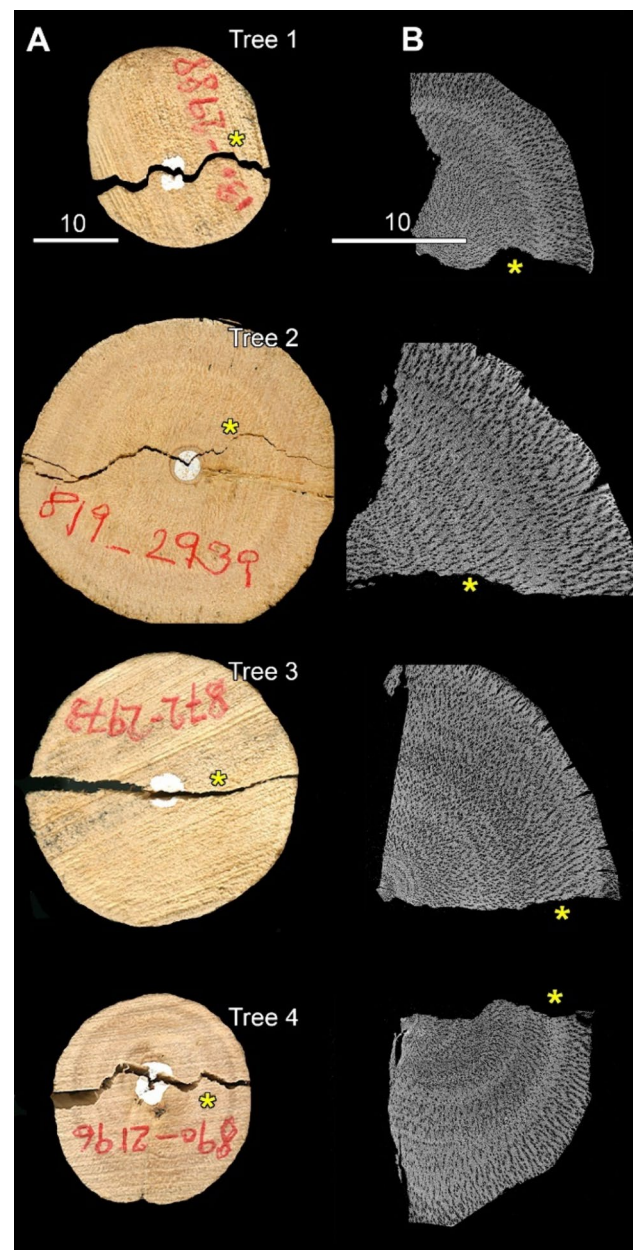


Fig. 1 Observations of interlocked grain using two different methods in four separate trees. **A** Split wood discs. 20-mm-thick wood discs were split with a hammer and chisel, with the split propagating through the disc following the grain so that the straight split on one side of the disc became a jagged split on the opposite face. **B** X-ray computed microtomography images of quartered wood discs. Because the plane shown does not correspond to the face of the halved disc shown in **A**, the shape of the quarter discs can vary. Yellow asterisks indicate the split face that corresponds to the wood splitting measurements. Bars in **A** and **B** = 10 mm

as dark circles (Fig. 1B), represent different planes to the scanned images of the ends of the wood discs.

Wood grain varied in radial direction between -4° left-handed to 12° right-handed within the first ~ 10 mm of tree

growth (Fig. 2). The μ CT and splitting data showed correlations with r values between 0.55 and 0.97 for the four trees (Fig. 2C) when comparing measurements on the same radius. Sections collected at 10° rotational intervals from the split face showed the same pattern (grey lines), resulting in an average curve (black line) that was very similar to the grain measured at the split face (Fig. 2B). The imperfect correlations between μ CT and splitting at the same radii included local variation on the mm scale along the grain in axial direction, as μ CT only measured grain in a relatively short stretch of ~ 2 mm, whereas splitting was over 20 mm. Correlations dropped to r values between 0.18 and 0.84 when comparing the averaged values for μ CT (over a quarter section) and splitting (over 2 opposing diameter) (Fig. 2D). We also investigated grain across the stem by comparing the opposite sides of the split wood. The calculated Pearson

coefficients varied between 0.78 for tree 1, to as low as -0.72 for tree 3 (Fig. 2A) demonstrating large variability in wood grain across the stems.

Two conclusions can be drawn. First, the two methods give comparable results when assessing the same tissue. Second, wood grain is variable, both, locally within a tree on the mm scale in tangential, radial, and longitudinal direction as well as between trees. The two approaches are complimentary, with the more resource demanding μ CT providing finer detail of wood grain on a localised spot than the more economical splitting method allowing larger scale assessments. Furthermore, because μ CT can be reprocessed to generate different image planes, it was possible to assess grain along stem lengths as well as in radial and tangential planes, something not possible by splitting (Supplementary Information 3). Our observations are, therefore, different

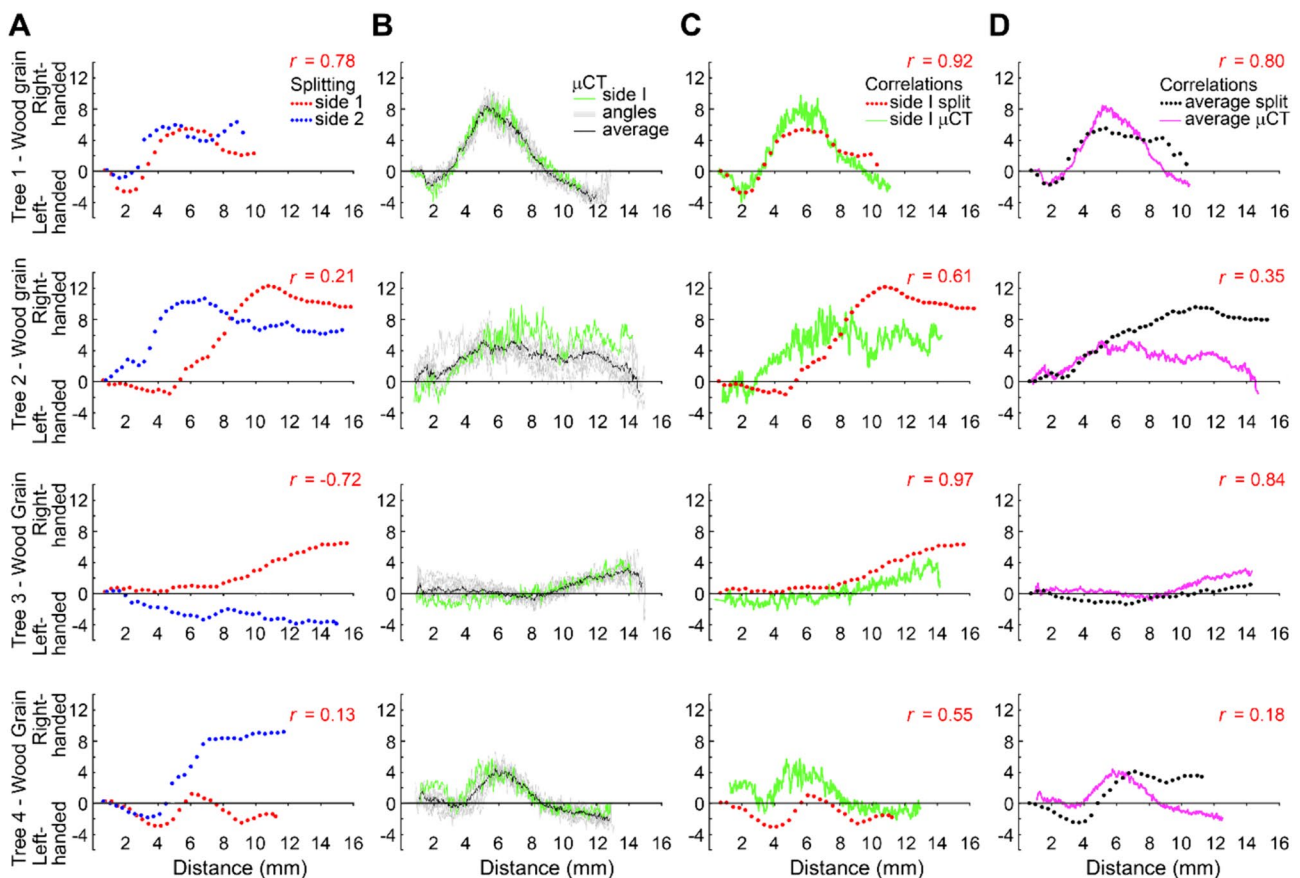


Fig. 2 Measurements of wood grain by splitting and X-ray computed microtomography in four separate trees (rows 1 through 4). **A** Grain measurements made by splitting. Side 1 (red dots) corresponds to the face subsequently used for μ CT measurements. Positive grain angles indicate right-handed grain, whilst negative grain angles indicate left-handed grain. Pearson correlation coefficients (r) were calculated between plots of side 2 and side 1, with a value of 1 indicating perfect correlation between the two sides. **B** Grain measured by X-ray computed microtomography. The green line indicates measurements adja-

cent to the fracture face used for splitting, whilst the different grey lines represent 7 or 8 grain profiles collected at 10° intervals. The average grain for the different rotation angles is shown by the black line. **C**, **D** Correlations between measurements approaches: comparison of grain measured along the fracture face by splitting (red dots) and μ CT (green line) (**C**), average grain of the two sides by splitting (black dots) and different angles by μ CT (purple line) (**D**). Pearson correlation coefficients (r) were calculated from plots of the splitting data against pooled μ CT data

from those of Thinley et al. (2005) who reported that good correlations for the average amplitude and wavelength of paired measurements within *E. dunnii* stem discs, although this might be accounted for by the small sample size of four trees in our study.

Comparing wood grain assessments by splitting to twist measurements

We measured wood grain by splitting and the amount of twist of half-rounds for 140 young *E. bosistoana* trees to determine whether links exist between grain pattern and twisting. For each of the 140 trees, 2 measurements were extracted from each splitting test, the average grain angle, and the maximum difference in grain (the difference between the maximum left- and right-handed grain measurements).

The average grain in the 140 young trees was right-handed (2.43°) (Fig. 3) and the average twist for the trees was also right-handed (13.78°) (Table 1). The twisting of stem halves was significantly correlated to the maximum difference in grain assessed via splitting ($r=0.35$; CI_{95} 0.19–0.49; values represent the correlation coefficient, and the 95% confidence interval) (Supplementary Information 4). The positive correlation indicated that timber with large changes in grain are likely also to physically twist. The relationship is complex as left- and right-handed grain within a sample can cancel (Harris 1989) and this is reflected by the imperfect correlation. However, a

correlation between surface grain and twist in timber has been reported for other eucalypts (Wessels et al. 2016).

The variation of grain and twist around the stem could be analysed by comparing the grain metrics in opposing radii of the tree discs and the twist of the opposing stem halves. The maximum difference in grain values from the opposing radial profiles of the splitting test was significantly correlated ($r=0.34$; CI_{95} 0.18; 0.48). This accounted for the variation seen in the high-resolution μ CT assessment, whilst confirming that some consistency of grain is present within a stem. The twist of opposing half-rounds was more strongly correlated with $r=0.75$ (CI_{95} 0.67; 0.82). Similar results have been reported for other features of interlocked grain. The amplitude ($r=0.70$) and period ($r=0.45$) of interlocked grain were found to be correlated between opposing radii in *E. dunnii* stem discs (Thinley et al. 2005). It should be noted that it was not possible to assess period and amplitude in the young *E. bosistoana* stem sections as interlocked grain had not developed sufficiently across the young stem (Fig. 3).

Two conclusions can be drawn. First, grain variations assessed by splitting are correlated to twist observed in solid wood of young trees. Second, whilst not perfect, twist measurements on half or radius of a stem are representative of the whole cross-section because of the strong correlation between twist on one side of the stem with the other (Supplementary Information 4A).

Fig. 3 Average wood grain (with standard errors) measured from splitting patterns varied with distance from the pith in a total of 140 *E. bosistoana* trees

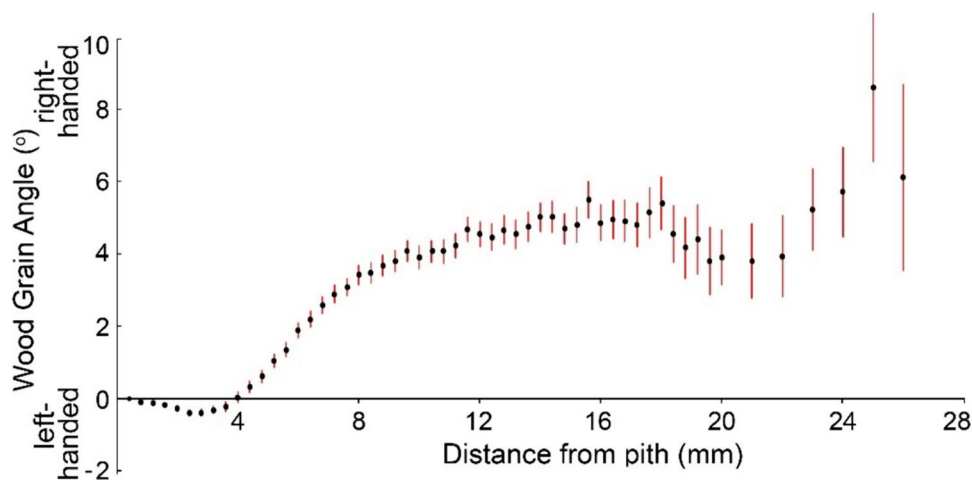


Table 1 Twist and grain metrics for 140 *E. bosistoana* trees that were 2 years old

Trait	Mean	Standard deviation	Min	Max	CPV (%)
Twist ($^\circ$)	13.78	9.76	− 6.75	45.55	70.9
Average grain angle ($^\circ$)	2.43	2.14	− 2.60	9.84	88.1
Maximum difference in grain ($^\circ$)	8.12	3.67	1.20	20.94	29.8

CPV coefficient of phenotypic variation

Genetic control of twist in young *E. bosistoana*

The quick measurement of twist on half-rounds of young trees allowed the assessment of a larger breeding population including 2,686 trees representing 81 families. In addition to the twist measurement, data for other traits were available for these trees, namely tree height and diameter, tree form, growth strain, densities, modulus of elasticity (MoE), and volumetric shrinkage. Descriptive statistics and heritabilities are given in Table 2.

Twist in the 2-year-old *E. bosistoana* trees was under similar genetic control ($h^2=0.34$, CI_{95} 0.20, 0.46) as tree diameter and tree form, the two most common traits considered in tree breeding programmes (Table 2). Combined with the larger genetic variation (coefficient of genetic variation (CGV) > 40% compared to < 20%), more genetic gain could be achieved selecting for twist. Breeding values for twist can be found in Supplementary Information 5. Genetic and phenotypic correlations between the twist measurements of the individual half-rounds and their averages were strong ($r_g=0.998$) (Table 3). This implies that the measurement of one half-round has the potential to significantly reduce the effort required for phenotyping without compromising accuracy.

The availability of phenotypic data for the same trees for other traits allowed exploration of further correlations (Table 3). Twist was genetically positively ($r_g=0.46$) correlated to tree form, implying that wood from trees with better form expressed more twist. Taller trees ($r_g=0.35$) and trees with denser wood ($r_g=0.24$; 0.36) also tended to express more twist. The causalities for these correlations is unclear.

Table 3 Genetic and phenotypic correlations between twist and other traits of 2-year-old *E. bosistoana* (95% CI in brackets). Correlations with 95% confidence interval included 0 are in bold. The analysis included 2,686 individuals from 81 families

	Twist	
	Phenotypic correlation (r_p)	Genetic correlation (r_g)
Diameter	0.04 (0.00, 0.08)	0.24 (− 0.02, 0.51)
Tree height	0.00 (− 0.04, 0.04)	0.35 (0.12, 0.59)
Tree form	− 0.05 (− 0.09, − 0.01)	0.46 (0.22, 0.72)
Microstrain ^a	0.03 (− 0.01, 0.07)	− 0.02 (− 0.33, 0.28)
Basic density	0.05 (0.01, 0.08)	0.24 (− 0.01, 0.49)
Dry density ^b	0.14 (0.10, 0.17)	0.36 (0.13, 0.60)
MoE (GPa) ^b	− 0.18 (− 0.22, − 0.14)	− 0.22 (− 0.45, 0.04)
Volumetric shrinkage	0.05 (0.01, 0.09)	− 0.11 (− 0.37, 0.15)
Twist side A	0.94 (0.94, 0.95)	0.998 (NA)
Twist side B	0.94 (0.94, 0.95)	0.998 (NA)

^aGrowth strain measured according to Davies et al. (2017)

^bmeasured at 12% moisture content

Thinley et al. (2005) reported a larger amplitude of interlocked grain for slower growing *E. dunnii* trees. It should be noted that no correlations between growth strain and twist (Table 3) or grain angle measurements from splitting tests (data not shown) were found. Therefore, this study did not support the thought that interlocked grain aids trees to cope with large growth stresses in stems (Harris 1989; Hernández and Almeida 2003).

Table 2 Descriptive statistics and heritability (h^2) for various traits of 2-year-old *E. bosistoana* trees. The analysis included 2,686 individuals from 81 families

Trait	Mean	Standard deviation	Min	Max	CPV ^a (%)	CGV ^a (%)	h^{2*b}
Diameter (mm)	36.55	8.65	10.64	63.47	23.66	16.32	0.44 (0.28, 0.62)
Tree height (m)	2.39	5.94	0.1	3.9	24.86	22.35	0.80 (0.58, 1.01)
Form	4.50	2.29	1	6	57.62	17.98	0.26 (0.16, 0.36)
Microstrain ^c	378.7	149.6	118.3	2554	39.50	16.35	0.17 (0.09, 0.24)
Basic density (g/cm ³)	0.649	0.04	0.522	0.793	5.85	6.42	1.21 (0.88, 1.48)
Air-dried density ^d (g/cm ³)	0.898	0.03	0.789	1.154	3.75	3.10	0.67 (0.45, 0.88)
Modulus of elasticity ^d (GPa)	12.31	1.97	6.76	19.71	16.04	18.66	1.32 (0.96, 1.60)
Volumetric shrinkage (%)	27.79	3.45	12.7	41.87	12.42	10.94	0.78 (0.55, 0.98)
Average twist (°)	14.87	11.21	− 66.35	106.85	75.39	44.26	0.34 (0.20, 0.46)
Twist side A (°)	14.77	11.91	− 72.7	106.3	80.58	46.30	0.33 (0.20, 0.46)
Twist side B (°)	14.97	11.94	− 60	107.4	79.76	42.33	0.28 (0.17, 0.40)

^aCPV coefficient of phenotypic variation; CGV coefficient of genetic variation

^bRelatedness coefficient $r_c=0.25$. Values in brackets indicate 95% confidence intervals

^cGrowth strain measured according to Davies et al. (2017)

^dmeasured at 12% moisture content

The relationship between the twist of a half-log and the radial grain pattern is complex. For example, half-logs with interlocked grain, that is grain periodically switching from left-hand to right-hand, do not twist (Scheiber 1973). Consequently, it is difficult to quantify twist in sawn timber from the radial grain pattern, with both magnitude of the grain as well as its local distribution having an effect. Considering wood quality, trees with either straight or regular interlocked grain can be desirable. Interlocked grain cannot be assessed by measuring twist. Furthermore, as interlocked grain is expressed at a larger scale, in the range of centimetres to tens of centimetres, assessment of the presence and regularity would need larger diameter, i.e. older, trees than those available for this study. Straight-grained trees could be identified at young age if a consistent radial grain pattern is expressed. This, however, needs to be confirmed with larger trees.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00468-024-02567-w>.

Acknowledgements We acknowledge the facilities and the scientific and technical assistance of the Australian Centre for Microscopy & Microanalysis at the University of Sydney, notably the work of Dr Matthew Foley. SD was a recipient of a scholarship from Ngāi Tahu whilst DC thanks Chris Grof (University of Newcastle) for his support.

Author contribution statement CA, AG, DC, and SD planned and designed the research. SD, MS, and DC conducted the experiments. Image analysis was conducted by SD and DC. Statistical analysis was done by CA and MS. The manuscript was drafted by DC and CA. All authors edited and approved the final version of the manuscript.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. The work was partially funded by New Zealand's Ministry of Primary Industries' Sustainable Farming Fund (SFF407602).

Data availability The data that support the findings of this study are available on reasonable request from the corresponding author.

Declarations

Conflict of interest The authors have no relevant financial interests to disclose. Clemens Altaner is Science Team Leader of the New Zealand Dryland Forests Innovation (NZDFI).

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Altaner C (2019) Minimising growth-strain in eucalypts to transform processing. University of Canterbury, Christchurch, New Zealand
- Altaner C, Palmer H (2021) Producing posts and veneer from durable eucalypt timber. NZ Tree Grow November: 33–37
- Apiolaza LA (2009) Very early selection for solid wood quality: screening for early winners. Ann for Sci 66:10. <https://doi.org/10.1051/Forest/2009047>
- Australia Standard 5604 (2005) Timber—natural durability ratings
- Bootle KR (2005) Wood in Australia. Types, properties, and uses. McGraw-Hill, Australia
- Bossu J, Lehnbach R, Corn S, Regazzi A, Beauchêne J, Clair B (2018) Interlocked grain and density patterns in *Bagassa guianensis*: changes with ontogeny and mechanical consequences for trees. Trees—Struct Funct 32:1643–1655. <https://doi.org/10.1007/s00468-018-1740-x>
- Bremaud I, Minato K, Langbour P, Thibaut B (2010) Physico-chemical indicators of inter-specific variability in vibration damping of wood. Ann for Sci. <https://doi.org/10.1051/forest/2010032>
- Brouse (1966) Some causes of warping in plywood and veneered products. USDA forest products laboratory, Madison, US. <https://www.fpl.fs.usda.gov/documnts/fplrn/fplrn0136.pdf>. Accessed 20 Sept 2024
- Butler D, Cullis B, Gilmour A, Gogel B (2009) ASReml R package version 30. VSN International Ltd., Hemel Hempstead, UK
- Cabrolier P, Beauchêne J, Thibaut B (2009) Is interlocked grain an adaptive trait for tropical tree species in rainforest ? 6th Plant Biomechanics Conference, Cayenne
- Chauhan S, Entwistle K (2010) Measurement of surface growth stress in *Eucalyptus nitens* Maiden by splitting a log along its axis. Holzforsch 64:267–272. <https://doi.org/10.1515/hf.2010.022>
- Cipta H, Kobayashi K, Chen S, Sugiyama J (2022) Examination of *Cinnamomum camphora* interlocked grain adopting X-ray computed tomography combined with particle image velocimetry. J Wood Sci 68:56. <https://doi.org/10.1186/s10086-022-02064-z>
- Collings DA, Thomas J, Dijkstra SM, Harrington JJ (2021) The formation of interlocked grain in African mahogany (*Khaya* spp.) analysed by X-ray computed microtomography. Tree Physiol 41:1542–1557. <https://doi.org/10.1093/treephys/tpab020>
- Costa e Silva J, Borralho NMG, Wellendorf H, (2000) Genetic parameter estimates for diameter growth, pilodyn penetration and spiral grain in *Picea abies* (L.) Karst. Silvae Genet 49:29–36
- Davies NT, Apiolaza LA, Sharma M (2017) Heritability of growth strain in *Eucalyptus bosistoana*: a Bayesian approach with left-censored data. NZ J for Sci 47:1–5
- Entwistle K, Chauhan S, Sharma M, Walker J (2014) The effect of saw kerf width on the value of the axial growth stress measured by slitting a log along its axis. Wood Mater Sci Eng. <https://doi.org/10.1080/17480272.2014.929176>
- França FJN, França TSFA, Vidaurre GB (2020) Effect of growth stress and interlocked grain on splitting of seven different hybrid clones of *Eucalyptus grandis* × *Eucalyptus urophylla* wood. Holzforsch 74:917–926. <https://doi.org/10.1515/hf-2019-0209>
- Gapare W, Hathorn A, Kain D, Matheson C, Wu H (2007) Inheritance of spiral grain in the juvenile core of *Pinus radiata*. Can J for Res 37:116–127. <https://doi.org/10.1139/x06-202>
- Hallingbäck HR, Jansson G, Hannrup B (2008) Genetic parameters for grain angle in 28-year-old Norway spruce progeny trials and their parent seed orchard. Ann for Sci 65:301–301. <https://doi.org/10.1051/forest:2008005>
- Harris JM (1989) Spiral grain and wave phenomena in wood formation. Springer Verlag, Berlin

- Haslett AN, Simpson IG, Kimberley MO (1991) Utilisation of 25-year-old *Pinus radiata*. Part 2: warp of structural timber in drying. NZ J for Sci 21:228–234
- Hernández RE, Almeida G (2003) Effects of wood density and interlocked grain on the shear strength of three Amazonian tropical hardwoods. Wood Fiber Sci 35:154–166
- Ishiguri F, Diloksumpun S, Tanabe J, Ohshima J, Iizuka K, Yokota S (2017) Among-family variations of solid wood properties in 4-year-old *Eucalyptus camaldulensis* trees selected for pulpwood production in Thailand. Int Wood Prod J 8:36–40. <https://doi.org/10.1080/20426445.2016.1261528>
- Kliger R (2001) Spiral grain on logs under bark reveals twist-prone raw material. For Prod J 51:67–73
- Li Y, Apiolaza LA, Altaner C (2018) Genetic variation in heartwood properties and growth traits of *Eucalyptus bosistoana*. Eur J for Res 137:565–572. <https://doi.org/10.1007/s10342-018-1125-0>
- Millen P, van Ballekom S, Altaner C, Apiolaza L, Mason E, McConnochie R, Morgenroth J, Murray T (2018) Durable eucalypt forests—a multi-regional opportunity for investment in New Zealand drylands. NZ J for 63:11–23
- Millen P, Altaner C, Palmer H (2020) Durable hardwood peeler pole plantations. A new growing regime for eucalypts. NZ Tree Grow 41:8–13
- R CoreTeam (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rajapaksha C, Greaves P, Altaner CM (2023) Economic potential of essential oil production from New Zealand-grown *Eucalyptus bosistoana*. Sci Rep 13:9. <https://doi.org/10.1038/s41598-023-40632-5>
- Salekin S, Mason EG, Morgenroth J, Bloomberg M, Meason DF (2021) Hybrid height growth and survival model for juvenile *Eucalyptus globoides* (Blakely) and *E. bosistoana* (F. Muell) in New Zealand. For Ecol Manage 490:119074. <https://doi.org/10.1016/j.foreco.2021.119074>
- Scheiber C (1973) Phänomen Wechseldrehwuchs Holzind 26:151–155
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675. <https://doi.org/10.1038/nmeth.2089>
- Schulgasser K, Witzum A (2007) The mechanism of spiral grain formation in trees. Wood Sci Technol 41:133–156. <https://doi.org/10.1007/s00226-006-0100-y>
- Thinley C, Palmer G, Vanclay JK, Henson M (2005) Spiral and interlocking grain in *Eucalyptus dunnii*. Holz Roh Werkst 63:372–379. <https://doi.org/10.1007/s00107-005-0011-x>
- Thomas J, Dijkstra SM, Harrington JJ, Collings DA (2022) Induction of compression wood inhibits development of spiral grain in radiata pine. IAWA J 44:36–62. <https://doi.org/10.1163/22941932-bja10088>
- Webb CD (1969) Variation of interlocked grain in sweetgum. Fort Prod J 19:45–48
- Wessels CB, Crafford PL, Du Toit B, Grahn T, Johansson M, Lundqvist SO, Sall H, Seifert T (2016) Variation in physical and mechanical properties from three drought tolerant *Eucalyptus* species grown on the dry west coast of Southern Africa. Eur J Wood Prod 74:563–575. <https://doi.org/10.1007/s00107-016-1016-3>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.