Preprint of: Thinley, C., G. Palmer, J.K. Vanclay and M. Henson, 2005. Spiral and interlocking grain in *Eucalyptus dunnii*. *Holz als Roh- und Werkstoff* 63(5):372-379.

Spiral and interlocking grain in *Eucalyptus dunnii*

C THINLEY
Sustainable Forestry Program, Southern Cross University, PO Box 157, Lismore NSW 2480, Australia
Renewable Natural Resources Research Centre, Yusipang, P.O. Box 740, Thimphu, Bhutan

G PALMER
Sustainable Forestry Program, Southern Cross University, PO Box 157, Lismore NSW 2480, Australia

JK VANCLAY
Sustainable Forestry Program, Southern Cross University, PO Box 157, Lismore NSW 2480, Australia
Jvanclay@scu.edu.au Tel +61 2 6620 3147 Fax +61 2 6621 2669

M HENSON
Forestry NSW, PO Box J19, Coffs Harbour Jetty NSW 2450, Australia

Abstract

Spiral grain in 181 trees from a 9-year-old plantation-grown *Eucalyptus dunnii* was normally distributed with mean –0.33 degrees (to the left) and standard deviation 1.7 degrees, and was affected by family and by crown asymmetry. Interlocking grain was common, exhibiting a mean amplitude of 3.4 degrees (standard deviation 1.5°) and a mean wavelength of 39 mm (standard deviation 12 mm). The relatively large amplitude of interlocking grain means that most trees will have spiral grain that alternates between left and right during each year. The wavelength of interlocking grain is influenced by tree size, but amplitude of interlocking is under genetic control. Both spiral grain and the amplitude of any interlocking were heritable (h^2=0.99 and 0.63 respectively).

Key words: *Plantation Dunn's white gum spiral grain heritability*

Introduction

Eucalyptus dunnii Maiden (Dunn's white gum, Benson and Hager 1993) is a relatively new, but increasingly important plantation species in eastern Australia. Over 10,000 ha of *E. dunnii* plantation have been established during the last decade, and it remains one of the favoured species for planting, with some 40% of current plantings in eastern Australia (south-east Queensland and north-east NSW) using this species. Although it forms a crucial component of the long-term supply to the sawlog industry, this emerging resource remains relatively unknown to industry. The object of this study is to document the extent and nature of spiral grain in an *E. dunnii* progeny trial, to provide guidance for further tree breeding efforts and to provide an early indication of the nature of the emerging plantation resource.

Spiral grain is one of several wood characteristics that may influence the utility and acceptability of plantation-grown *E. dunnii* in the market place. Spiral grain is the phenomenon where tracheids in the stem systematically have the same inclination, forming a spiral and causing twisting in dried sawn timber through anisotropic shrinkage (Harris 1989). The resulting twist may result in the downgrading or rejection of large proportions of sawn boards (Balodis 1972, Johansson et al. 2001, Kliger 2001). Spiral grain is recognised as one of the key properties determining the suitability of wood for use as sawn timber (Raymond 2002).

Interlocking grain occurs when spiral grain varies systematically, usually cycling between a left and right deviation. While spiral grain is considered an undesirable trait, interlocking grain may be desirable, as interlocking grain can increase stability, and contribute to beautiful figure (e.g., ribbon stripe).

Literature

Few studies of spiral grain in eucalypts and other broadleaved species have been published, so comparisons have been made with studies in conifers. Viitaniemi (1988) reported that spiral grain in Scots pine (*Pinus silvestris*) was typical of that in many conifers, and tended to change from near vertical in seedings, increased gradually to a maximum left spiral at about 15-20 years after which it gradually reverted towards the right, reaching a maximum right spiral at about age 60-80 years. Cown et al. (1991) found a similar trend in *Pinus radiata*, with the greatest deviation from vertical in the innermost 10 growth rings, where the grain angle averaged 4.7 degrees to the left. In a study of 19-year-old Norway spruce (*Picea abies*) clonal trials, Hannrup et al. (2002) found that mean grain angle reached a maximum inclination to the left at ring number four. Pape (1999) reported a similar pattern for Norway spruce, but noted that the formation of spiral grain appeared to be under genetic control, while the expression of spiral grain could be influenced by silviculture and growth rate. These widely-held views were challenged recently by Skatter and Kucera (1997, 1998) and Eklund and Säll (2000) who argued that spiral grain formed in response to wind torque, and that the direction of the spirals depended on crown asymmetry and prevailing winds.

Cown et al. (1991) found that measurements of spiral grain taken from individual rings did not provide a reliable indication of whole-tree values. This is not surprising, and implies that spiral grain varied with age in the study material. In contrast, Hansen (1999) found that estimates of spiral grain in sitka spruce (*Picea sitchensis)* were repeatable when made in annual rings 6-16 (from the pith).

Hansen (1999) found that the correlations between means of within-ring spiral-grain at different heights were better than 0.70, and that measurements of spiral grain in ring 10 provided good predictors of overall spiral grain in sitka spruce. Danborg (1994, with *Picea abies*) and Dumbrell and McGrath (2000, with *Pinus radiata*) found that spiral grain did not vary with within-tree height, and was unaffected by growth rate. In contrast, Rodríguez et al. (2000) reported that spiral grain in *Pinus pinaster* followed a similar pattern in the nine trees they studied, decreasing from pith to cortex, and increasing with stem height, especially within the crown.

Spiral grain is heritable. Mikami and Nagasaka (1975) reported that heritability of spiral grain in *Larix leptolepis* was 0.4. Hansen and Roulund (1998) found that the individual narrow-sense heritability of the spiral grain in sitka spruce was 0.7. Mean grain angle in Norway spruce has been reported to have a broad-sense heritability (H^2) of 0.42 (Hannrup et al. 2002), and a narrow-sense heritability (h^2)

between 0.29 and 0.47 (Silva et al. 2000). Heritability in Scots pine has been found to be 0.4 (Hannrup et al. 2003).

Study Site

The study was conducted in a 9-year-old progeny trial (Johnson and Arnold 1998) at Boambee State Forest (30°18'S, 153°03'E, 60 m asl), south-west of Coffs Harbour (coastal NSW, Australia). Boambee experiences a mild temperate climate (average daily temperature 14-23°C), with a median rainfall of 1585 mm. The soils are yellow podsolics over shale bedrock.

The trial contained seedlings raised from 219 open–pollinated (family) seedlots collected from individual *E. dunnii* trees in wild populations throughout most of the species' natural range (Benson and Hager 1993). These seedlots were collected by the CSIRO Australian Tree Seed Centre between 1986 and 1991, and represent 21 different provenances, numbered from north to south. Each seedlot was represented by six replicates of 4-tree row plots arranged as incomplete block designs with one-dimensional blocking within replicates. Trees were spaced at 3.0 m (between rows) x 2.4 m (within rows).

The study site was previously an *E. grandis* plantation, which was clearfelled at age 40. Logging debris was pushed into wind-rows and burnt in the spring of 1994. A winged ripper pulled by a crawler tractor ripped planting lines to a 50-60 cm depth between the stumps. Regrowth of woody weeds was sprayed with glyphosate herbicide in December 1994. The trials were hand-planted in February 1995 with sun-hardened seedlings in Hiko V93 cells. Within a month of planting, each seedling received one 20 g Langley Tree Tablet (N 20%: P 4.4%: K 8.2%: S 6.0%), buried 10 cm deep about 15 cm away from the seedling. Thinning at age 4 removed the poorest 2 trees from each 4-tree row plot, based on a subjective estimate of tree volume and stem form (Johnson and Arnold 1998). At the time of last measure in late 2003, trees averaged 23 cm dbh (diameter over bark at breast height, 1.3 m) and 28 m in height.

Samples for the present study were obtained during a thinning of the plantation. Three to four stems of each of 47 selected genotypes, totaling 181 stems, were removed (and thus became part of this study), leaving the best individual of each genotype to grow on. The site has been the focus for a number of previous studies of growth and wood quality, which provided data on dbh, tree heights, crown dimensions and other tree parameters (Johnson and Arnold 1998, Murphy et al. 2005).

Method

Spiral grain was measured on a flitch sawn from a short log taken from a height of about 3 m above ground. The flitch was sawn in a plane parallel to any end-splitting, and the bark was removed to expose the cambium. The flitch was placed on trestles, with the cut surface downwards. The grain direction at the cambium was marked with a scribe incorporated in a free-swinging arm (like a phonogram arm), by drawing the arm smoothly along the length of the flitch. Divergence between the grain direction and the longitudinal axis of the flitch (marked with a chalked stringline) was measured in millimetres over a standard half-metre length, and converted to degrees using the formula $\alpha = \sin^{-1}(d/500)$, where α is the angle in degrees and *d* is the measured divergence (in millimetres). In a small number of cases where the grain angle was particularly large, divergence was measured over a length of 250 mm and converted to degrees using the formula $\alpha = \sin^{-1}(d/250)$.

The usual convention for recording spiral grain as left- or right-handed can be ambiguous, depending on the viewpoint. For instance, the grain depicted in Figure 1 may be considered right-handed, because the grain tends to diverge toward the right as it approaches the observer, or equivalently, because it tends in a clockwise direction when viewed at the end of the log (irrespective of the orientation of the log). Alternatively, this same spiral can be considered left-handed, because it spirals to the left as it proceeds up the tree. We adopt the former convention, and record the grain as a right-handed or positive spiral if the grain spirals clockwise when viewed from the end of a log.

As crown asymmetry may be correlated with spiral grain (Skatter and Kucera 1997, 1998; Eklund and Säll 2000), we used existing measurements of crown width in each of the cardinal directions (N, E, S, W) to derive two estimates of crown asymmetry, the horizontal displacement and orientation of the crown centroid relative to the stump.

A series of 25 mm discs were cut from felled stems at about 2.5 m above ground level. One of these discs was randomly selected to assess interlocking grain. These discs were split with a hydraulic splitter (a Super-Axe WS400 made by Whitlands Engineering), adjusted to force a straight edge 2 mm evenly into the 25 mm discs, which were then allowed to split without further force. Discs were spilt twice in perpendicular orientations, dividing each disc into quarters, and exposing eight edges for inspection.

Visual inspection revealed that interlocking grain varies greatly between and within trees – it can be cyclical, constant, or steadily increasing (Figure 2). The images in Figure 1 are not from a camera, but from a flat-bed scanner. The split edge in straight grained samples should be perpendicular to the flat-bed glass, and thus not visible on this image.

Figure 1

After inspecting a number of discs, we elected to choose two examples with edges that maintained a clean straight line on the “cut” side, one with the most pronounced interlocking grain, and one with the least interlocking, to span the extremes represented within each disc. For each of these faces (hence two records per disc), we recorded the thickness of the disc, and the wavelength and amplitude (all in mm) of up to five cycles of interlocking grain. The core (20 mm) was not assessed for interlocking grain. To enable comparison with spiral grain data, the measurements of the amplitude of interlocking grain were converted to degrees using the formula $\alpha = \tan^{-1}(\text{amplitude/thickness})$.

In some cases, the selected split surface exhibited no visible evidence of interlocking grain (e.g., Figure 2d). Such cases require a default value to be supplied for the wavelength and amplitude of interlocking grain. These data are not “missing values”, as samples were inspected and assessed to be free of interlocking grain. A “true” absence of interlocking grain would imply a wavelength approaching infinity and/or an amplitude of zero, but such defaults create problems in statistical analysis. It is unlikely that interlocking grain can be reliably detected if the wavelength is less than the radius of the disc, or if the amplitude is less than 1 mm, and these thresholds were chosen as the defaults to be used when no interlocking was visible.

Results and Discussion

Variation within discs

Observations on paired grain measurements within each disc were sufficiently similar to provide reassurance about the method. The correlation between paired observations (within discs) were 0.70 for amplitude, and 0.45 for wavelength ($n=181$, $P<0.0001$ in both cases). In further analyses, we used the mean of the two readings taken from each disc, as recommended by Miyaki et al. (1983). The wavelength of any interlocking grain tended to increase with disc radius ($r=0.26$, $P=0.0002$), but amplitude was not correlated with radius in this way ($r=0.01$, $P=0.45$). In discs that were eccentric, variation in both amplitude and wavelength increased with eccentricity ($r=0.23$, $P=0.003$), but there was no evidence that eccentric discs had more interlocking. These observations provided reassurance that spiral grain could be measured on sawn flitches and discs without controlling for stem orientation.

Variation within trees

We examined the within-tree pattern of interlocking grain in ten trees (67, 1304, 1368, 1608, 2237, 2265, 2811, 3304, 4153, 4168), using three discs, using one disc cut at breast height, and a pair of discs cut at about 2.5 metres above the ground. The wavelength and amplitude of interlocking grain observed in the paired adjacent discs exhibited correlations of 0.56 and 0.84 respectively. The correlations between these adjacent pairs and estimates from breast-height discs were 0.58 and 0.80 for wavelength, and 0.85 and 0.93 for amplitude ($P<0.05$ in all cases). These correlations suggest that estimates from the sample discs are representative of the trees under study.

Spiral grain

Spiral grain in 9-year-old *E. dunnii* was normally distributed with mean –0.33 degrees (to the left) and standard deviation 1.7 degrees (Figure 2). Regression analysis revealed that provenance ($P=0.006$), family ($P=0.0002$) and crown eccentricity (both displacement, $P=0.002$, and direction, $P=0.03$) all influenced spiral grain (Table 1). Spiral grain tends to be more negative in trees with eccentric crowns, especially if any crown eccentricity is towards the south-west. Conversely, trees with a north-easterly eccentricity tend to have spiral grain that is less negative.

Figure 2

Table 1

Skatter and Kucera (1997, 1998) and Eklund and Säll (2000) argued that the direction of spiral grain can be attributed to the torsion effect of the prevailing wind, but this view was not supported in the present study. At Boambee, light winds (7-30 km/ha, 32% of the time year-round) tend to come from the south-west quarter, but strong winds tend to come from the north-east (>30km/hr, 15% of afternoons during September-February). Analysis of our data showed that the most informative transformation of crown asymmetry was a cosine transformation of the departure from 45° (i.e., north-east; eight points of the compass were considered). This was positively correlated with spiral grain, implying that the effect of crown asymmetry tends to be greatest (most negative) when asymmetry is towards the south-west, and least when asymmetry is towards the north-east. This observation is inconsistent with a causal effect of wind torsion, because the informative transformation of crown asymmetry is parallel to, and not perpendicular to the prevailing winds.

Although statistical analyses suggest that provenance is a significant determinant of spiral grain, the ranking of provenances changes substantially if crown asymmetry is also taken into account. Thus, although provenance may have a strong influence on the incidence of spiral grain, the present data do not provide a reliable basis for selecting preferred provenances. In contrast to the provenance data, the ranking of families was not greatly influenced by any adjustment for crown asymmetry, and several families exhibit mean family values significantly different from zero (Figure 3). Most of the significant mean family values were negative (spiralling to the left).

Figure 3

Amplitude of interlocking grain

The amplitude of interlocking grain was normally distributed with mean 3.4 degrees and standard deviation 1.5 degrees, and was well-correlated with the incidence of spiral grain (with absolute value of spiral grain, $r=0.28$, $P=0.0001$). There was a weak correlation between spiral grain and amplitude of interlocking ($r=-0.22$, $P=0.002$). This tendency is stronger in trees with negative (left) spiral grain. However, because spiral grain is itself under genetic control, this effect disappeared once family affiliation was taken into account (Table 2, Figure 4). Provenance had no detectable effect on interlocking grain ($P=0.34$).

Table 2
Figure 4

The absolute value of spiral grain ($P=0.04$) remained a significant predictor once family affiliation had been taken into account. There was also a tendency for slow-growing trees to have interlocking grain of larger amplitude ($P=0.1$). Other tree (dbh and crown asymmetry) and site factors (replication and block) were not significant predictors of interlocking grain (all $P>0.5$).

The correlation between amplitude of interlocking and spiral grain, coupled with the magnitude of interlocking, means that many trees may exhibit both a negative and a positive spiral grain during any year. This suggests that twist will not be a problem in the *E. dunnii* plantation material, and that much of the sawn material may exhibit interlocking grain.

Figure 5

Figure 5 shows the family mean estimates of spiral grain and amplitude of interlocking, and contrasts these with data from the samples illustrated in Figure 2. It is clear that the samples in Figure 2 were deliberately chosen to illustrate the extremes evident in the data. Families near the top of Figure 5 (with large amplitudes) are likely to develop pronounced interlocking grain which may confer stability and may contribute to attractive figure in wood products. Similarly, families near the right of Figure 5 (with spiral grain close to zero), are less likely to twist due to anisotropic shrinkage. The lower-left corner of Figure 5 indicates wood properties that are likely to be problematic during processing; no families in the current study were observed to display these properties (large negative spiral and low amplitude of interlocking).

Wavelength of interlocking grain

Interlocking grain exhibited a near-normal distribution with mean 3.9 cm and standard deviation of 1.2 cm. A square-root transformation was used to stabilize the variance. Regression analyses indicated that the wavelength of interlocking grain is not affected by provenance, family, or site (Table 3), but is affected by tree size (diameter at 1.3 m, $r=0.55$, $P<0.0001$) and is negatively correlated with the amplitude of any interlocking grain ($P=0.06$). Larger trees have larger wavelengths (Figure 6), and larger wavelengths tend to be associated with smaller amplitudes in interlocking grain. Since all trees in the study were the same age (9 years), it may be that wavelength is determined by season. In a few samples, the full wavelength (~) appeared to correspond to a full year of growth. This tendency was most evident during years 5-9, in trees where the interlocking grain exhibited a large amplitude (see Figure 2, e-f), but was not evident in all trees. This is consistent with observations of Detienne (1979), who observed an annual cycle in the interlocking grain of *Daniella* species in west Africa.

Table 3
Figure 6

Heritability

Heritabilities and genetic correlations were calculated using an individual tree model in ASReml (Gilmour et al. 2000), with provenance excluded from the model. The heritability calculations assumed that the open pollinated progeny are unrelated. The estimated heritability (h^2) for spiral grain was 0.999, and for the amplitude of interlocking grain was 0.63 (s.e.=0.31, P=0.02). The wavelength of interlocking is not inherited (h^2=0.0). This suggests that there is ample scope for conventional tree breeding to modify spiral grain in future plantation material.

Conclusion

Conclusions drawn from this study need to be tempered by the young nature of the material available. The study was based on 9-year-old material which had not reached commercial dimensions (mean 23 cm dbh; maximum 34 cm dbh). However, it is the only material available to gauge the nature of this emerging resource, and is the only quantitative basis currently available to guide further tree breeding efforts.

Spiral grain in 9-year-old *E. dunnii* varied between -6 and +6 degrees with mean -0.33 degrees, and tended to increase in trees with asymmetric crowns. The tendency to form spiral grain is heritable (h^2=0.99), and is correlated with the amplitude of interlocking grain, which typically cycles three or four degrees around the average spiral grain. The amplitude of interlocking is heritable (h^2=0.63). The wavelength of any interlocking grain is correlated with tree size, suggesting that it may be an annual or seasonal phenomenon. The correlation between spiral grain and amplitude of interlocking observed in this study means that *E. dunnii* trees tend not to exhibit pronounced spiral grain without interlocking which may be problematic in timber processing.

Forest managers undertaking thinnings in *E. dunnii* plantations should be aware that trees with asymmetric crowns tend to have spiral grain that is more pronounced, and should assess this characteristic amongst other selection criteria used for thinning.

Acknowledgements

This work funded by State Forests of NSW and Southern Cross University through Collaborative Research Grant 50415-30535. Many students and staff from Southern Cross University were involved in this work, and thanks are due to Peter Bligh-Jones, Martin Davies, Alex Jay and Tim Murphy for their assistance. Paul Fuller and Dr Shakti Chauhan of the University of Canterbury also made valuable contributions to this work.

References

Balodis V (1972) Influence of grain angle on twist in seasoned boards. Wood Science 5:44-50

Benson JS, Hager TC (1993) The distribution, abundance and habitat of *Eucalyptus dunnii* (Myrtaceae) (Dunn's white gum) in New South Wales. Cunninghamia 3:123-145

Cown DJ, Young GD, Kimberley MO (1991) Spiral grain patterns in plantation-grown *Pinus radiata*. NZ Journal Forest Science 21(2-3):206-216

Danborg F (1994) Spiral grain in plantation trees of *Picea abies*. Canadian Journal of Forest Research 24(8):1662-1671

Detienne P (1979) Contrefil a rythme annuel dans les Faro, *Daniella* sp. pl. (Annually recurring interlocked-grain in Faro, *Daniella* spp.) Bois et Forets des Tropiques 183:67-71

Dumbrell IC, McGrath JF (2000) Effect of fertiliser and growth rate on angle of spiral grain in young *Pinus radiata* in Western Australia. Australian Forestry 63:142-146

Eklund L, Säll H (2000) The influence of wind on spiral grain formation in conifer trees. Trees: Structure and Function 14(6):324-328

Gilmour AR, Cullis BS, Welham SJ, Thompson R (2000) ASREML Reference Manual. NSW Agriculture, Orange Agric. Inst. Orange, Australia.
Hannrup B, Grabner M, Karlsson B, Müller U, Rosner S, Wilhelmsson L, Wimmer R (2002) Genetic parameters for spiral-grain angle in two 19-year-old clonal Norway spruce trials. Annals of Forest Science 59(5/6):551-556
Hannrup B, Säll H, Jansson G (2003) Genetic parameters for spiral grain in Scots pine and Norway spruce. Silvae Genetica 52:215-220
Harris JM (1989) Spiral grain and wave phenomena in wood formation. Springer, New York Berlin Heidelberg
Hansen JK (1999) Genetic variation of spiral grain in Sitka spruce growing in Denmark: Multiple-trait selection for improved timber quality. Ph.D. Thesis, Royal Veterinary and Agricultural University, Denmark.
Hansen JK, Roulund H (1998) Genetic parameters for spiral grain in two 18-year-old progeny trials with Sitka spruce in Denmark. Canadian Journal of Forest Research 28(6):920-931
Johansson M, Perstorper M, Kliger R, Johansson G (2001) Distortion of Norway spruce timber, Part 2: Modelling twist. Holz als Roh- und Werkstoff 59(3):155-162
Johnson IG, Arnold RJ (1998) *Eucalyptus dunnii* provenance-family trials in northern New South Wales – age three-year assessment. State Forests of NSW Research Paper 37, 28 p.
Kliger IR (2001) Spiral grain on logs under bark reveals twist-prone raw material. Forest Products Journal 51(6):67-73.
Mikami S, Nagasaka K (1975) Selection for minimizing spiral grain in *Larix leptolepis* Gord. Bulletin of the Government Forest Experiment Station, Meguro 276:1-22
Miyaki M, Hatakeyama S, Goshu K (1983) Relationship between grain inclination and axis of pith when using the splitting method. Journal of the Japanese Forestry Society 65(5):183-186
Murphy T, Henson M, Vanclay JK (2005) Growth stress in *Eucalyptus dunnii*. Australian Forestry, 68(2):144-149
Pape R (1999) Influence of thinning on spiral grain in Norway spruce grown on highly productive sites in southern Sweden. Silva Fennica 33(1): 3–12
Raymond CA (2002) Genetics of Eucalyptus wood properties. Annals of Forest Science 59:525–531
Rodríguez MR, Valenzuela HL, Espinosa BM (2000) Variacion radial y en el fuste de la fibra revirada presente en un rodal adulto de pino maritimo (*Pinus pinaster* Ait.,). (Radial and longitudinal variation of spiral grain in an adult stand of maritime pine). Maderas: Ciencia y Technologia 2(2):140-149
Silva JCC, Borralho NMG, Wellendorf H (2000) Genetic parameter estimates for diameter growth, pilodyn penetration and spiral grain in *Picea abies* (L.) Karst. Silvae Genetica 49:29-36
Skatter S, Kucera B (1997) Spiral grain - an adaptation of trees to withstand stem breakage caused by wind-induced torsion. Holz als Roh- und Werkstoff 55(4):207-213
Skatter S, Kucera B (1998) The cause of the prevalent directions of the spiral grain patterns in conifers. Trees: Structure and Function 12(5):265-273.
Viitaniemi P (1988) Puun kierteisyys ja sen mittaaminen (Spiral grain and its measurement), Tutkimuksia, Valtion Teknillinen Tutkimuskeskus 522

Figure 1. Six examples of grain in *E. dunnii*. (a & b) Two examples of typical interlocking grain (Trees 108 and 767). Notice that the pith (left) is devoid of interlocking grain. Both amplitude and wavelength of interlocking may increase (a) or decrease (b) near cambium (right). (c) Example of spiral grain gradually increasing, with minimal interlocking (Tree 2243). Grain is near zero (i.e. vertical, parallel to plane of view) near the pith (left), and deviates more from vertical (grain angle is becoming more positive) with increasing distance from the pith. (d) Example of straight grain, with no clear evidence of interlocking grain (tree 3075). (e & f) Two examples of pronounced interlocking grain (Trees 2237 and 2784 respectively).

Figure 2. Spiral grain at 9 years was normally distributed with mean –0.33 and standard deviation 1.7 degrees. The dashed line is the cumulative normal distribution, and open circles are data from the present study.

Figure 3. Mean spiral grain (degrees) by family, with error bars indicating ±1 standard error.

Figure 4. Mean amplitude (degrees) of interlocking grain by family, with error bars indicating ±1 standard error.

Figure 5. Family mean estimates of spiral grain and amplitude of interlocking (solid diamonds), with the corresponding data from the six individual tree data (open circles) illustrated in Figure 2. The dotted lines emphasise that for most families, variation in grain angle is greater then the currently-observed value.

Figure 6. Tree size (cm dbh) and wavelength (cm) of interlocking are correlated.

Table 1. Analysis of Variance of Spiral Grain

Table 2. Analysis of Variance of the Amplitude of Interlocking Grain

Table 3. Analysis of Variance of the Wavelength of Interlocking Grain

Table 1. Analysis of Variance of Spiral Grain

Source	df	SS	MS	F	P	Sig
Provenance	13	64.27	4.94	2.40	0.006	**
Family within provenance	33	164.30	4.98	2.41	0.0002	***
Crown displacement (m)	1	20.39	20.39	9.88	0.002	**
Cos(Crown displacement-45°)	1	10.06	10.06	4.88	0.029	*
Residual	130	268.30	2.06			
Other variables considered						
Dbh	1	2.62	2.62	1.28	0.26	
Dbh increment (2003-4)	1	2.45	2.45	1.19	0.28	
Sin(Crown displacement-45°)	1	0.62	0.62	0.30	0.59	
Block	10	15.52	1.55	0.74	0.68	
Replication	4	2.99	0.74	0.36	0.84	

Table 2. Analysis of Variance of the Amplitude of Interlocking Grain

Source	df	SS	MS	F	P	Sig
Family	46	156.2	3.395	1.855	0.003	**
Abs(Spiral)	1	7.704	7.704	4.209	0.042	*
Dbh increment (2003-4)	1	6.912	6.912	3.777	0.054	
Residual	130	237.92	1.8302			
Other variables considered						
Provenance	13	26.822	2.063	1.127	0.34	
Sin(Crown displacement-45°)	1	0.7911	0.791	0.432	0.51	
Block	10	13.709	1.370	0.749	0.68	
Replication	4	2.8944	0.724	0.395	0.81	
Crown displacement (m)	1	0.2883	0.288	0.157		
Dbh	1	0.0564	0.056	0.030		
Cos(Crown displacement-45°)	1	0.0339	0.034	0.018		

Table 3. Analysis of Variance of the Wavelength of Interlocking Grain.

Source	df	SS	MS	F	P	Sig
Amplitude of interlocking	1	3.74	3.74	3.54	0.061	
Dbh	1	89.69	89.69	84.83	<0.0001	***
Residual	178	188.18	1.06			
Crown displacement (m)	1	3.41	3.41	3.22	0.07	
Dbh increment (2003-4)	1	1.70	1.70	1.61	0.21	
Replication	4	5.91	1.48	1.40	0.24	
Cos(Crown displacement-45°)	1	0.51	0.51	0.49	0.49	
Provenance	13	13.03	1.00	0.95	0.51	
Block	10	9.71	0.97	0.92	0.52	
Family	46	45.48	0.99	0.94	0.59	
Sin(Crown displacement-45°)	1	0.01	0.01	0.01		
Abs(Spiral)	1	.00	0.00	0.00		

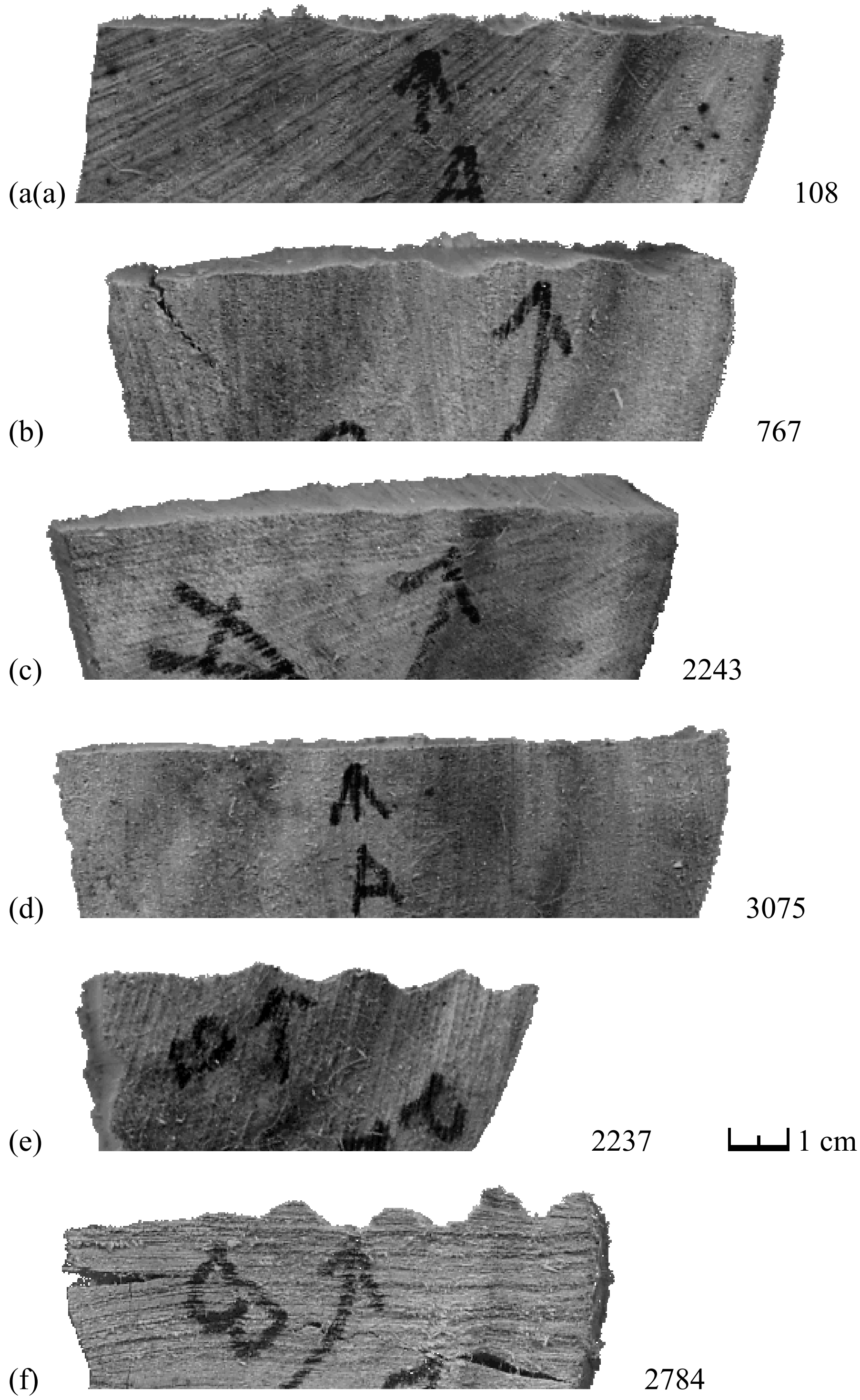

Figure 1. Six examples of grain in *E. dunnii*. (a & b) Two examples of typical interlocking grain (Trees 108 and 767). Notice that the pith (left) is devoid of interlocking grain. Both amplitude and wavelength of interlocking may increase (a) or decrease (b) near cambium (right). (c) Example of spiral grain gradually increasing, with minimal interlocking (Tree 2243). Grain is near zero (i.e. vertical, parallel to plane of view) near the pith (left), and deviates more from vertical (grain angle is becoming more positive) with increasing distance from the pith. (d) Example of straight grain, with no clear evidence of interlocking grain (tree 3075). (e & f) Two examples of pronounced interlocking grain (Trees 2237 and 2784 respectively).

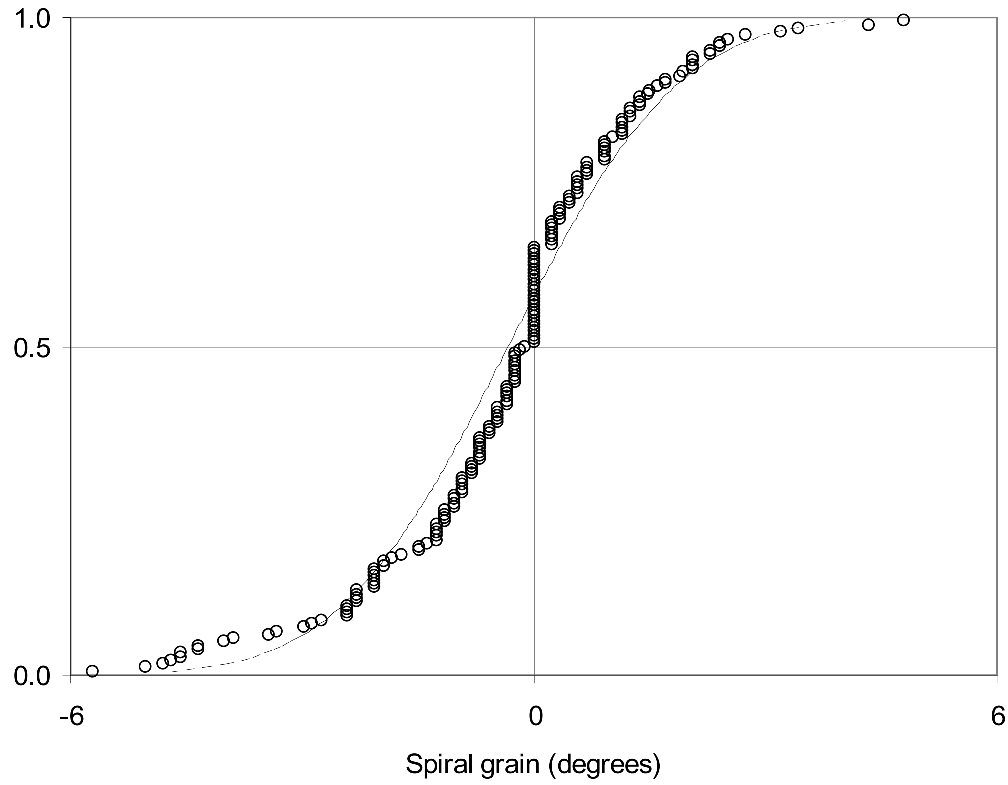

Figure 2. Spiral grain at 9 years was normally distributed with mean –0.33 and standard deviation 1.7 degrees. The dashed line is the cumulative normal distribution, and open circles are data from the present study.

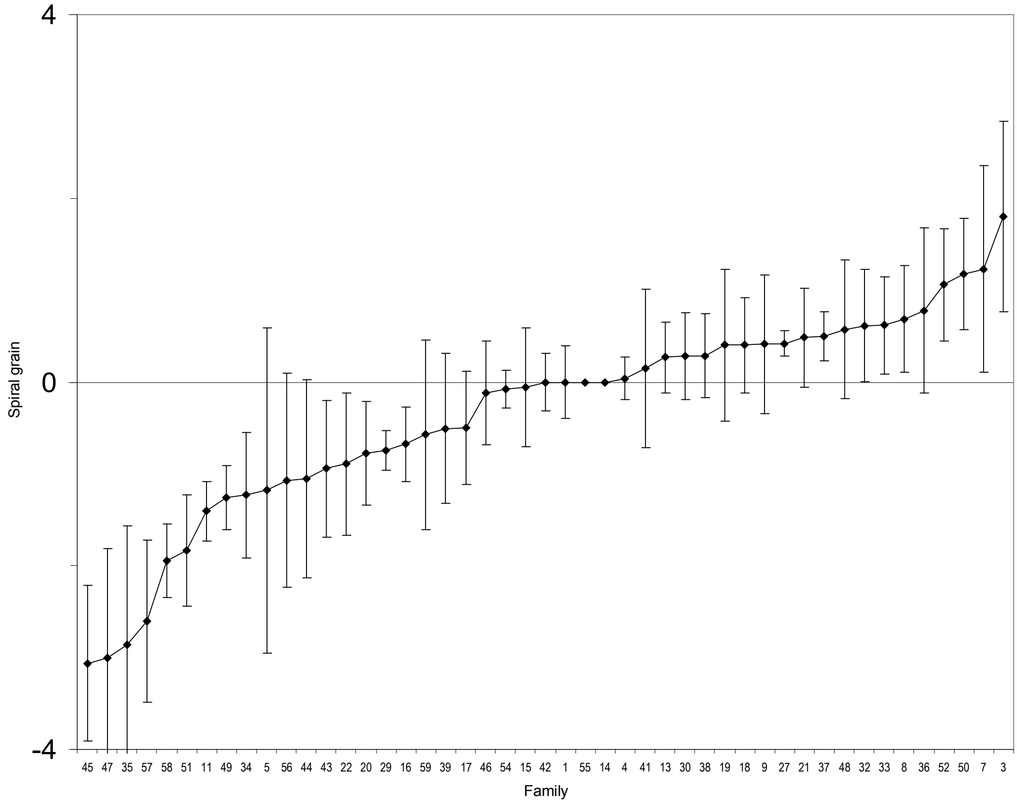

Figure 3. Mean spiral grain (degrees) by family, with error bars indicating ±1 standard error.

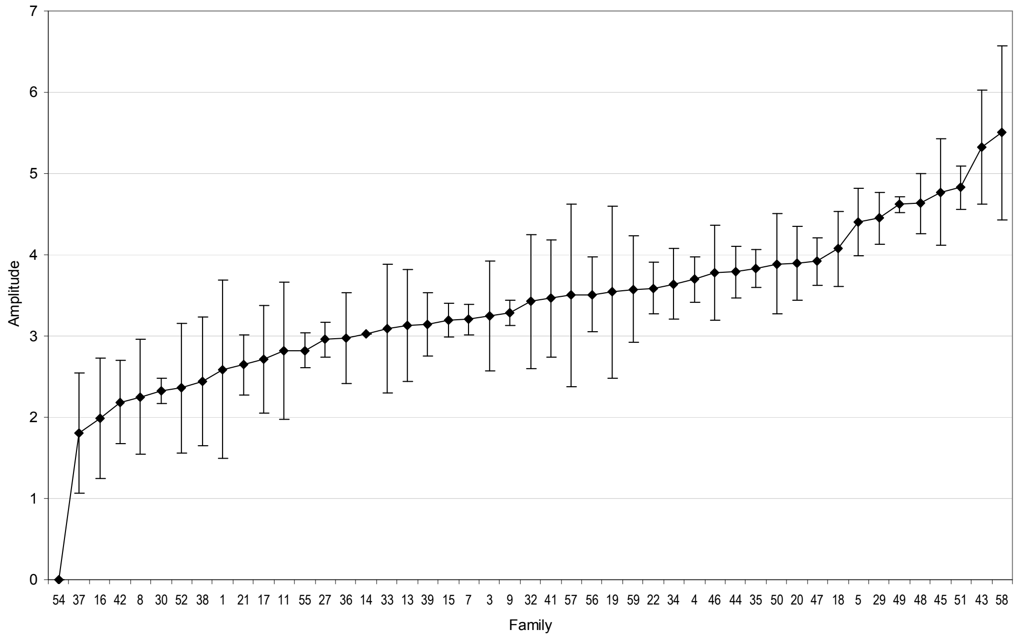

Figure 4. Mean amplitude (degrees) of interlocking grain by family, with error bars indicating ±1 standard error.

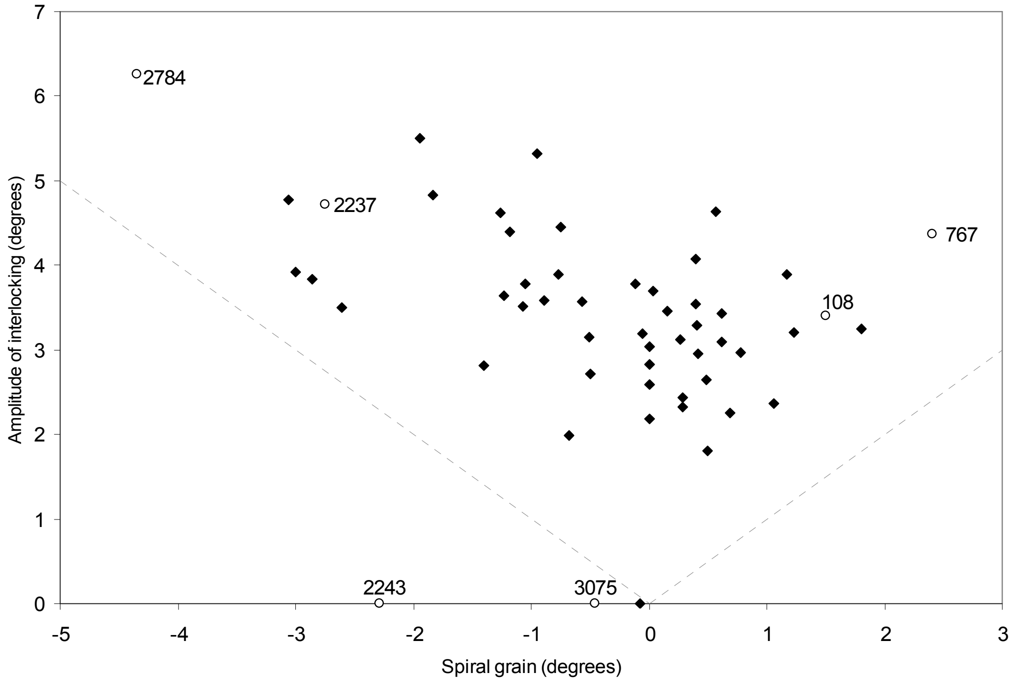

Figure 5. Family mean estimates of spiral grain and amplitude of interlocking (solid diamonds), with the corresponding data from the six individual tree data (open circles) illustrated in Figure 2. The dotted lines emphasise that for most families, variation in grain angle is greater then the currently-observed value.

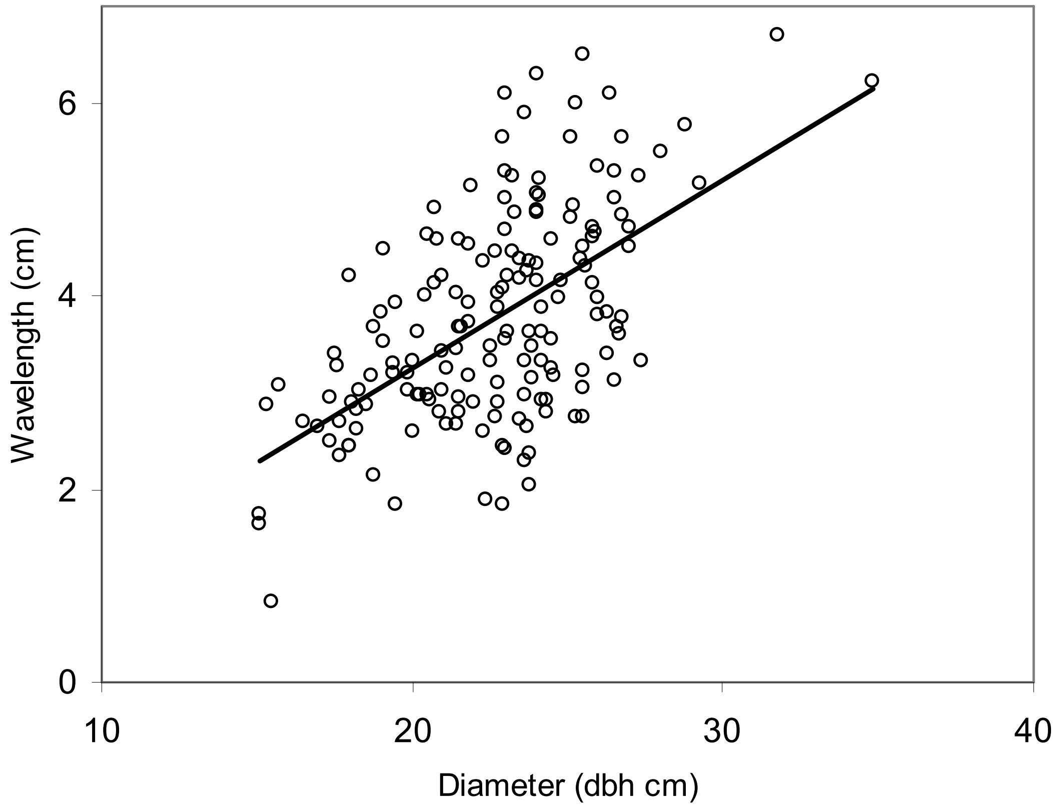

Figure 6. Tree size (cm dbh) and wavelength (cm) of interlocking are correlated.