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Meta-analysis of racial variation in *Eucalyptus nitens* and *E. denticulata*

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Abstract

Eucalyptus nitens (Deane & Maiden) Maiden is widely planted in temperate regions of the southern hemisphere, principally for pulpwood production. *Eucalyptus denticulata* I.O. Cook & P.Y. Ladiges was previously recognised as an informal variant of *E. nitens* and, accordingly, was included in many '*E. nitens*' field trials. We reviewed data from 85 *E. nitens*/*E. denticulata* field trials, located in Australia, Chile, China, Italy, Lesotho, New Zealand, South Africa and Zimbabwe and ranging in age from less than one year to 14 years, to investigate racial (among population groups) genetic variation in growth, wood-property, tree-architecture, fitness and morphological/developmental traits. Meta-analyses were undertaken on these data to gauge the significance of differences among races across trials. Race × rainfall zone interaction was also investigated by categorising field trials as summer-rainfall, winter-rainfall or nursery-based. Race × rainfall zone interaction was significant for growth traits only. In general, Central Victorian *E. nitens* populations outperformed New South Wales *E. nitens* populations in winter-rainfall zones, but this ranking was reversed in summer-rainfall zones. On average, *E. denticulata* grew less rapidly than the best-performing *E. nitens* races, particularly in winter-rainfall zones. Differences among races were detected in basic density, a commercially important trait, but these differences were small in magnitude. Significant differences among races were also evident in branch size and stem form (straightness). *Eucalyptus denticulata* races had significantly thinner branches than all *E. nitens* races except Southern Central Victorian, and Central Victorian *E. nitens* races generally had the straightest stems. The small number of trials represented for most traits limited the power of meta-analyses but significant differences among races detected in our study are likely to represent consistent and robust differences across a broad range of environments.

Keywords: fitness; genetic variation; genotype × environment interaction; growth; morphology; population; provenance; race; tree architecture; wood properties.

Introduction

This study reviews both the published and unpublished literature pertaining to population-level genetic variation in *Eucalyptus nitens* (Deane & Maiden) Maiden and *E. denticulata* I.O. Cook & P.Y. Ladiges. *Eucalyptus nitens* and *E. denticulata* were recognised as separate taxa by Cook and Ladiges (1991) but were previously referred to variants of *E. nitens*: var. *nitens* and var. *errinundra* (Pederick, 1977; Pederick, 1979; Pederick & Lennox, 1979). *Eucalyptus nitens* has

a scattered natural distribution in south-eastern Australia, which extends from central Victoria to the Dorrigo area of northern New South Wales (Figure 1). The main populations of *E. denticulata* are in eastern Victoria on the Errinundra Plateau but the species is also present in central Victoria (Hamilton et al., 2008), where it is co-occurring and hybridises with *E. nitens* (Cook & Ladiges, 1991, 1998; Pederick, 1979). Together, the species are sometimes referred to as the '*E. nitens*/*E. denticulata* complex' (Dutkowski et al., 2001).

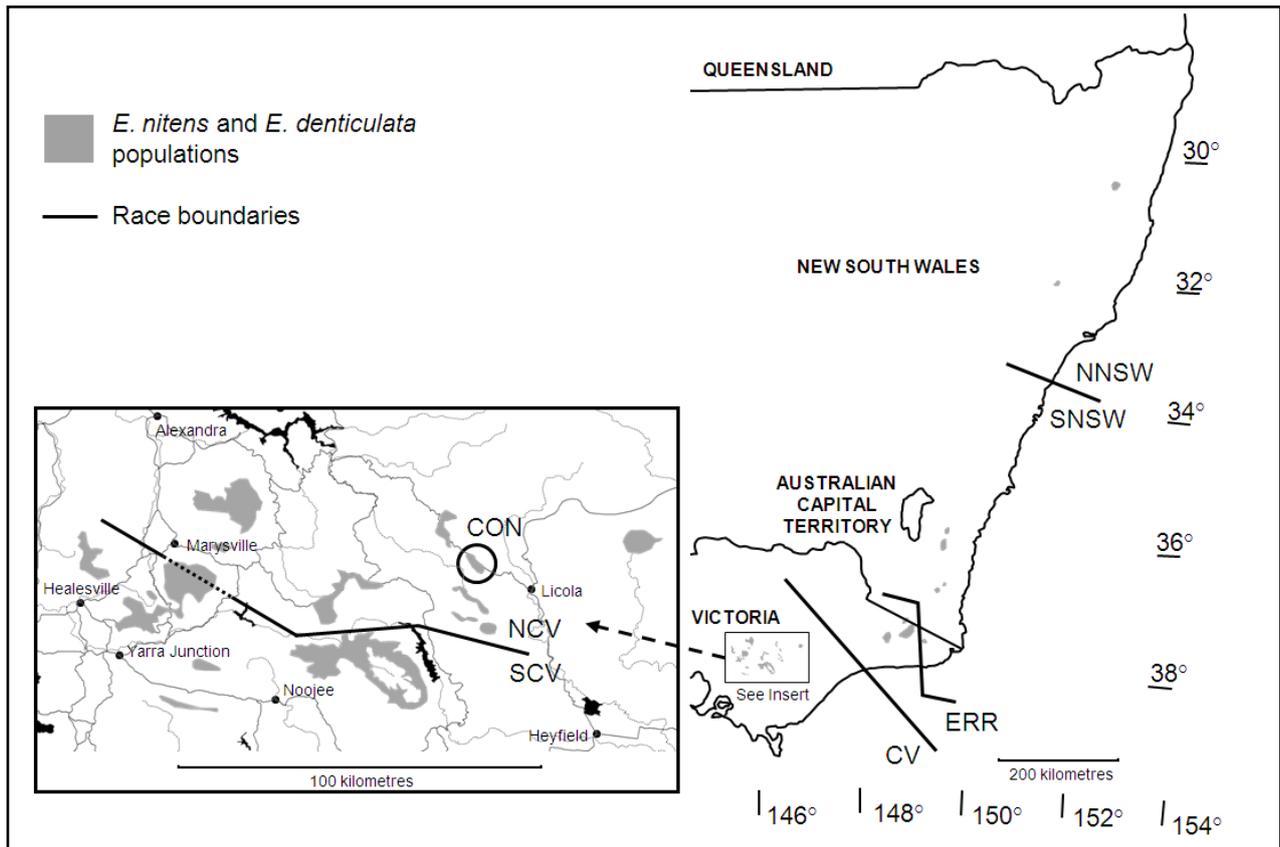


FIGURE 1: Main map: natural distribution and race boundaries of *Eucalyptus nitens* (Central Victoria, CV; Northern New South Wales, NNSW; and Southern New South Wales, SNSW) and *E. denticulata* (Errinundra, ERR). *Eucalyptus denticulata* and inter-species hybrid/intermediate genotypes are also interspersed within predominantly *E. nitens* populations in Central Victoria (CV). Insert: natural distribution and race boundaries of *Eucalyptus nitens* within central Victoria, (Connor's Plain, CON; Northern Central Victoria, NCV; and Southern Central Victoria, SCV). Map modified from Hamilton et al. (2008).

Eucalyptus nitens is widely planted in high-rainfall temperate regions of the southern hemisphere, particularly in Australia (approximately 235 000 ha; Gavran & Parsons, 2011) and Chile (approximately 185 000 ha; Instituto Forestal (INFOR), 2010) but also in New Zealand and southern Africa (Hamilton et al., 2008). The species is principally grown for kraft pulpwood, although substantial areas of plantation are now managed under solid-wood silvicultural regimes (Wood et al., 2009). *Eucalyptus denticulata* is not planted on a large scale. However, many *E. nitens* genetics trials were established before the recognition of *E. denticulata* as a separate species. Accordingly, *E. denticulata* genotypes are present in some '*E. nitens*' breeding populations.

Genetic variation at the population level can be exploited in breeding programmes, but an understanding of population \times environment interaction is required to maximise genetic gains in plantations (Costa e Silva et al., 2006). A meta-analysis of field-trial data in the published and unpublished literature was undertaken to examine genetic differences among populations (races) of *E. nitens* and *E. denticulata*, and test for

race \times environment interaction across summer- and winter-rainfall environments. A number of independent studies have investigated genetic variation among *E. nitens*/*E. denticulata* populations (Appendix A: Tables 1 to 5). However, with advances in understanding of the geographically structured genetic variation in the species (refer to Hamilton et al., 2008 for an overview) and the large number of studies undertaken for some traits (e.g. growth), a meta-analysis of all available data to identify robust trends and test hypotheses regarding genotype \times environment interaction is timely. Within-population genetic variation in *E. nitens* has previously been reviewed by Hamilton and Potts (2008) and is not addressed in this study.

Materials and Methods

The racial (population-group) structure outlined in Hamilton et al. (2008), which is based on studies by Cook and Ladiges (1991), Dutkowski et al. (2001) and Pederick (1985) was adopted. This population structure divides *E. denticulata* into two (Errinundra, ERR; and Central Victoria, CV) and *E. nitens* into five

(Northern New South Wales, NNSW; Southern New South Wales, SNSW; Northern Central Victoria, NCV; Southern Central Victoria, SCV and Connor's Plain, CON) geographically and genetically distinct races (Figure 1). However, in the literature, populations are commonly defined by sampling localities. A sampling locality represents a small area of native forest within racial boundaries, generally incorporating a single physiographic feature and minimal altitudinal range (Cook & Ladiges, 1991; Dutkowski et al., 2001; Pederick, 1979), from which open-pollinated seed was collected either as a bulk collection or as single-tree seedlots.

Estimated sampling locality and race means were recorded for growth (e.g. stem diameter and height), wood property (e.g. basic density, pulping and solid wood properties), tree architecture (e.g. bark thickness, branch size and stem form), fitness (e.g. frost damage and survival), and morphological/developmental (e.g. leaf characteristics and phase change) traits from published and unpublished studies of *Eucalyptus nitens*/*E. denticulata* base-population genetics trials. In total, data from 85 trials in eight countries (Australia, Chile, China, Italy, Lesotho, New Zealand, South Africa and Zimbabwe) were collated, including data collected at less than one year to 14 years of age. Means were recorded for each trait, trial and assessment age. Where analogous characteristics were deemed to have been assessed across studies, common trait names and indicative units of measurement were allocated. Where repeated estimates of a trait from the same trial were available, only one was retained (generally from the most recent assessment). Data for leaf oil traits were not reported as they were almost exclusively derived from one study (Li et al., 1994). Similarly, data for a number of solid-wood (Blackburn et al., 2010, 2011; McKimm, 1985a, 1985b; Nicholls & Pederick, 1979; Purnell, 1988; White et al., 1999) and wood-fibre/vessel properties (Clarke, 2000; McKimm, 1985; Nicholls & Pederick, 1979) were excluded as they were each reported in a single study only.

Locality-level seedlot data that could not be allocated to a race, due to uncertain genetic affinities, were excluded from the current study (e.g. Mt. Kaye near Errinundra; Hamilton et al. (2008)). Furthermore, in several of the reviewed studies, populations that exhibited *Eucalyptus denticulata* morphology/ontogeny (e.g. early phase change from juvenile to adult foliage) were excluded from *E. nitens* trials (e.g. Dutkowski et al., 2001). The exclusion of seedlots likely to contain hybrid/intermediate genotypes almost certainly inflated differences between Victorian populations of *E. nitens* and *E. denticulata*, compared with differences that would have been observed if these seedlots had been allocated to one or the other species. That is, differences reported in this study are assumed to reflect differences among races of 'pure' species within the *E. nitens*/*E. denticulata* complex. However,

it is possible that some central Victorian localities that were allocated to *E. nitens* races may have included *E. denticulata* or hybrid/intermediate genotypes, as the species co-occur in central Victoria and not all studies noted the presence or absence of *E. denticulata* in trials. Similarly, the possibility that some seedlots allocated to *E. denticulata* in the reviewed literature included *E. nitens* or hybrid/intermediate genotypes cannot be dismissed.

Data relating to seedlots derived from landraces, seed orchards, and routine plantations were excluded from analyses, along with those relating to central-Victorian 'Pederick' provenances (i.e. Macalister, Rubicon and Toorongo; Pederick, 1979), as provenance boundaries (Dutkowski et al., 2001; Hamilton et al., 2008) do not correspond with those of Central-Victorian races (for a meta-analysis based on Pederick provenances, refer to Hamilton, 2007). Pooled multiple-site estimates of locality or race means were also excluded from analyses. Where locality-level data were recorded, race means were estimated for the purposes of meta-analysis, by averaging locality values for each trait and trial.

Each trial was allocated to a rainfall zone: 'summer rainfall' (for trials in southern China, Lesotho, South Africa and Zimbabwe), 'winter rainfall' (for trials in south-eastern Australia, Chile, Italy and New Zealand), or else 'nursery-based'. These rainfall zones represented a coarse description of the continuum of rainfall patterns that occurred across *Eucalyptus nitens*/*E. denticulata* trials and, although all Chilean and New Zealand trials were allocated to the winter-rainfall zone, some trial locations in these countries receive substantial summer rainfall and/or a relatively even distribution of rainfall across seasons. Data from winter-rainfall zones was more prevalent than data from summer-rainfall zones.

Analyses

General trends in the data were examined by performing analyses on the log-transformed race means for all traits and trials. Values were log transformed to account for differences in scale across trials and assessment ages, which were particularly evident in growth traits. In those cases where a trait was assessed at only one site in a rainfall zone, no meta-analyses were undertaken. Where a trait was assessed in more than one trial in both rainfall zones, the following linear model was fitted:

$$Y = \mu + \text{RACE} + \text{ZONE} + \text{RACE} \times \text{ZONE} + \text{TRIAL}(\text{ZONE}) + \text{RESIDUAL}$$

where Y is the observation for the trait (i.e. the log-transformed race mean from a trial), μ is the trait mean, RACE is the fixed race effect; ZONE is the fixed rainfall-zone effect, RACE \times ZONE is the fixed race \times rainfall zone interaction effect, *TRIAL*(ZONE)

is the random trial (which encompasses the effects of environment, silviculture, and assessment age) within rainfall zone effect and *RESIDUAL* is the unexplained residual of observed race means. The significance of the RACE × ZONE term was tested with an F-test using the residual as the denominator, to determine if log-transformed differences among the races significantly varied across rainfall zones. For those traits where the race × rainfall zone interaction effect was not significant, data from both rainfall zones were combined and analysed by fitting a reduced model:

$$Y = \mu + \text{RACE} + \text{TRIAL} + \text{RESIDUAL}$$

In all other cases, and for those traits where a significant race × rainfall zone interaction was identified, this reduced model was fitted separately for each trait and rainfall zone.

The significance of the RACE term was tested with an F-test using the error as the denominator and race least-squares means were estimated. For traits for which the race effect was significant, the Tukey-Kramer multiple comparisons procedure was used to identify which races differed significantly from each other. Race means were then back-transformed. Alternative models fitting species as a fixed effect and race within species as a random effect were not used, as data from only one *Eucalyptus denticulata* race was available for most traits. The Proc Mixed procedure of SAS™ (SAS Institute Inc, Version 9.2) was used for analyses.

Results and Discussion

Given the paucity of data available for some traits and inherent difficulties associated with collating information from different sources with different approaches to trial management, trait assessment and genetic nomenclature/classification, it was not possible to fully quantify or account for differences in the precision of race means, imbalance in racial representation across trials or genotype × site interaction within rainfall zones. However, for traits assessed across a large number of trials, meta-analyses revealed consistent trends (e.g. the relative performance of races for different growth traits within rainfall zones; Appendix A: Table 1). Furthermore, in the current study, race means from individual trials were log transformed to account for differences in scale across trials and assessment ages. However, when analyses were undertaken on untransformed data, across-trial race means were not substantively altered for traits where significant differences were identified among races (Appendix A: Tables 1 to 5) and the significance of differences among races ($P < 0.05$) changed in very few traits (i.e. mean annual increment, $P = 0.013$; burst strength of pulp, $P = 0.049$; and juvenile leaf area, $P = 0.103$), arguing that the findings of the current study were robust.

Growth traits

The race × rainfall zone interaction was highly significant for all growth traits for which it was possible to test this effect (Appendix A: Table 1). Significant differences for all growth traits were observed among races in both rainfall zones. In winter-rainfall zones, Central Victorian *E. nitens* races outperformed the New South Wales races but the opposite was true for summer-rainfall zones, possibly due to the greater exposure and adaptation to fungal disease in summer-rainfall zones (e.g. *Teratosphaeria*, previously known as *Mycosphaerella*, species) (Eldridge et al., 1993; Purnell, 1988; Quaile & Mullin, 1983; Wang et al., 1994) and/or physiological adaptations to summer rainfall (Warren et al., 2005) in the New South Wales populations. Differences in growth among races were large when compared with most other traits (Appendix A: Tables 1 to 5). For instance, as a percentage of the overall trait mean, the diameter of races ranged from 82% (Errinundra, *E. denticulata*) to 114% (Connor's Plain, *E. nitens*) in winter-rainfall zones (Table 1). *Eucalyptus denticulata* races grew, on average, more slowly than the best-performing *E. nitens* races, particularly in winter-rainfall zones (Figures 2 and 3; Table 1). Indeed, some breeders have excluded *E. denticulata* genotypes from '*E. nitens*' breeding populations due to poor growth in trials (Dutkowski et al., 2001; Hamilton et al., 2008). However, multiple-trait breeding objectives, and a desire to maintain genetic diversity and/or investigate non-additive genetic effects expressed in inter-species/inter-race crosses, may see highly-ranked *E. denticulata* genotypes retained in other advanced-generation breeding populations.

In the current study, the Tukey-Kramer adjustment for multiple comparisons within summer- and winter-rainfall trial zones did not reveal significant differences among races for any growth trait within *E. denticulata* (CV and ERR), within Central Victorian *E. nitens* (CON, SCV and NCV) or within New South Wales *E. nitens* (NSW and SNSW). However, significant differences among races within these seed-collection regions were observed in many of the individual trials reviewed in Table 1 (Appendix A). This inconsistency may reflect race × environment interaction within winter- and summer-rainfall zones.

Wood property traits

With the exception of basic density, data from only one or two trials for each trait and rainfall zone were available and only small racial deviations from trait means were observed in most wood property traits (Appendix A: Table 2). The lack of data for these traits reflects, in some cases, their limited commercial importance and, in other cases, the expense of their assessment and consequent reluctance to publish results in the public domain (e.g. for the economically important trait of pulp yield). With the development of cheap assessment methods, such as those based on near infrared reflectance spectroscopy (NIR) for pulp

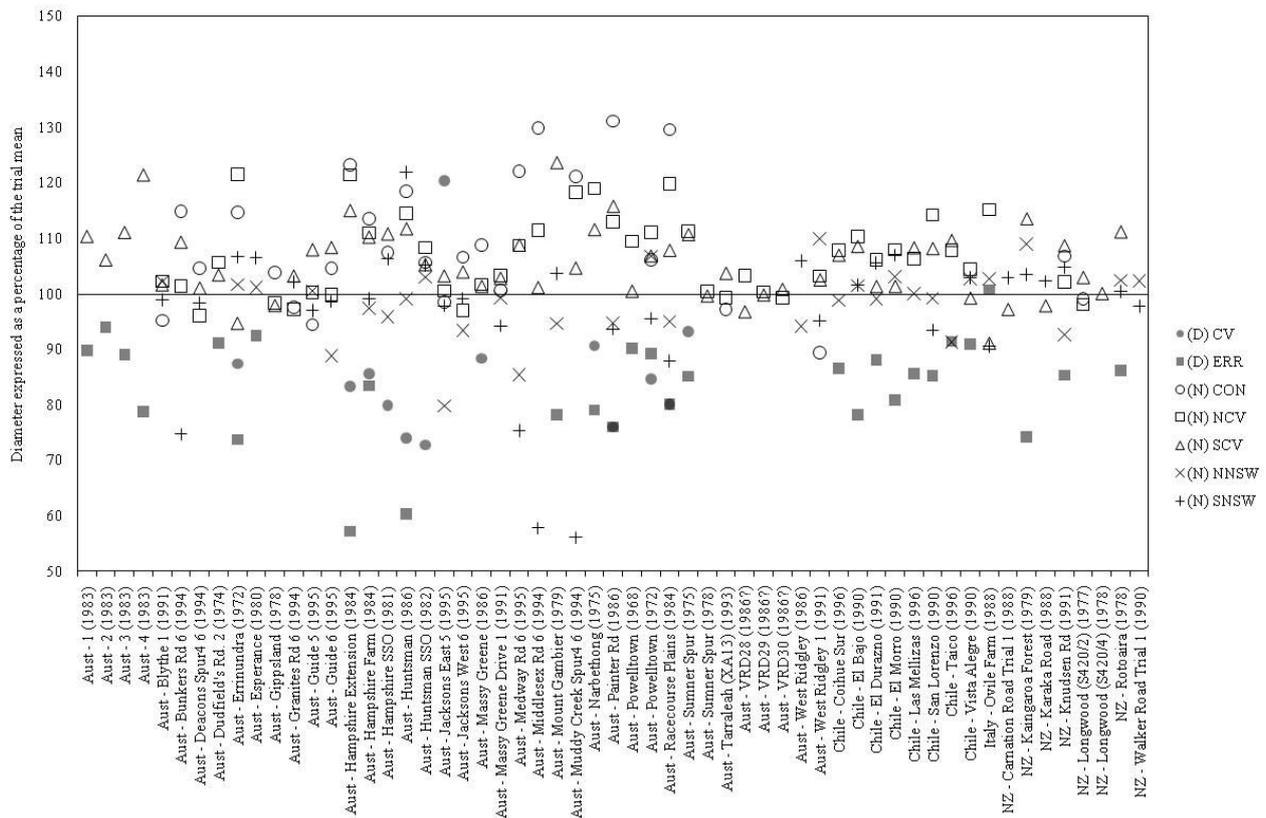


FIGURE 2: Untransformed mean diameters (expressed as a percentage of the trial mean) in winter-rainfall zone trials for *Eucalyptus denticulata* (D) (Central Victoria, CV; Errinundra, ERR) and *E. nitens* (N) (Connor's Plain, CON; Northern Central Victoria, NCV; Southern Central Victoria, SCV; Northern New South Wales, NNSW; and Southern New South Wales, SNSW) races. Trial country (Australia, Aust; Chile; Italy and New Zealand, NZ), name and year of planting (in parentheses) are presented.

yield and cellulose content (Schimleck et al., 2000), it is anticipated that additional race-level data for commercially important traits will become available in coming years.

Race \times rainfall zone interaction for basic density was not significant, but a highly significant ($P < 0.001$) overall difference among races was observed in this commercially important trait (Appendix A: Table 2). However, racial differences were small in magnitude compared with growth traits (Appendix A: Table 1), with the southern (98% of the overall trait mean) and northern (103%) races in NSW representing extremes of the racial variation. A significant difference in cellulose content among the three central Victorian *E. nitens* races was also detected, based on results from only two trials.

Tree-architecture traits

Significant differences between races were observed in branch size and stem form (straightness) (Appendix A: Table 3). Both *Eucalyptus denticulata* races had significantly thinner branches than both the NSW *E. nitens* races. Although not significantly different in most cases, Central Victorian *E. nitens*

races exhibited straighter stems than NSW *E. nitens* and *E. denticulata* races. Straight stems with fine branches are favoured for solid-wood production and may also reduce harvesting costs in pulpwood plantations, although the economic importance of tree-architecture traits in pulpwood operations is not well understood.

Fitness traits

Data from very few trials were available for fitness traits and evidence of a significant difference among races was detected for 'health' only (Appendix A: Table 4). However, Tukey-Kramer adjustment for multiple comparisons did not reveal significant differences among races in this trait, indicating that it was, in reality, on the border-line of statistical significance.

Although differences among races in frost (field trial) damage were not statistically significant ($P = 0.21$), (Appendix A: Table 4), the central Victorian races (CON, NCV and SCV) appeared to exhibit less frost damage than *Eucalyptus denticulata* and the NSW races. Of the central Victorian races, Connor's Plain showed the least damage, consistent with the observations of Pederick (1985) and Dutkowski et al.

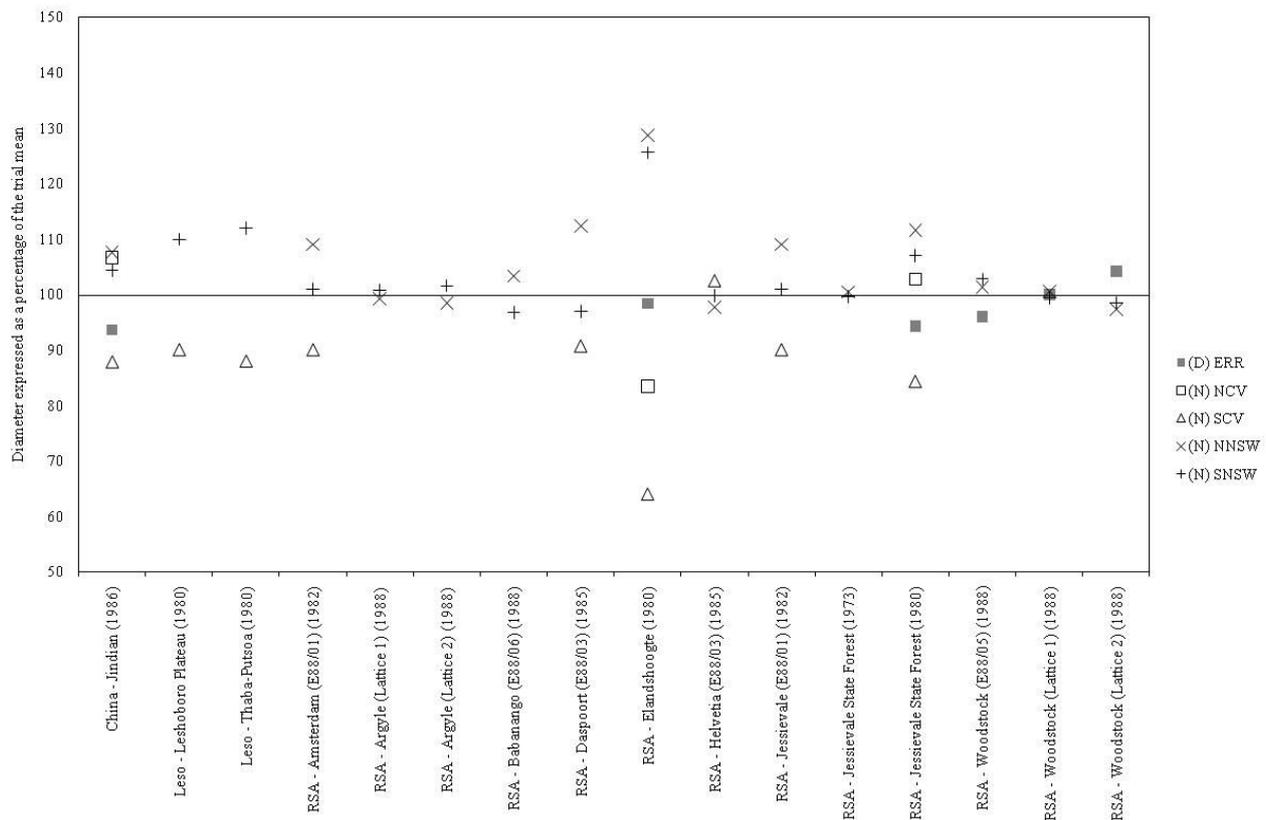


FIGURE 3: Untransformed mean diameters (expressed as a percentage of the trial mean) in summer-rainfall zone trials for *Eucalyptus denticulata* (D) (Errinundra, ERR) and *E. nitens* (N) (Northern Central Victoria, NCV; Southern Central Victoria, SCV; Northern New South Wales, NNSW; and Southern New South Wales, SNSW) races. Trial country (China, Lesotho, Leso; and South Africa, RSA), name and year of planting (in parentheses) are presented.

(2001). This possibly reflects adaptation to frost. The area from which this race originates, Connor's Plain, is at high elevation (~1200 m) and relatively flat, which may inhibit the drainage of cold air (Dutkowski et al., 2001). Further field trials are required to verify the hypothesis that the Connor's Plain race exhibits superior cold tolerance to that of other races.

The drivers of survival can be very different across trials and the lack of a consistent and robust pattern of survival among races across 23 trials was not unexpected (Appendix A: Table 4). The extent to which individual trials were exposed to stressors such as drought, frost, insects or disease was not indicated in a consistent and comparable manner in the literature, making more detailed meta-analysis of survival data impractical.

Morphological and developmental traits

Eucalyptus nitens is heteroblastic and a significant difference among races in the height of transition from juvenile to adult leaves (height to phase change) was identified (Appendix A: Table 5). Height to phase change was lower (implying transition to adult foliage occurred at a younger age) in the *E. denticulata* populations than the central Victorian races. This is

in keeping with the observations of Pederick (1979) who noted that early heteroblastic phase change and narrow juvenile leaves were distinguishing features of *E. denticulata*. Juvenile and adult leaves of *E. nitens*/*E. denticulata* differ markedly in morphology, orientation, anatomy and physiology. Many pest organisms exhibit a preference for either juvenile or adult foliage (Hamilton et al., 2011). Accordingly, racial variation in the timing of heteroblastic phase change in *E. denticulata*/*E. nitens* is likely to have broad ecological consequences in both native and planted stands, with potential implications for the control of pests and diseases in the latter.

Significant differences in juvenile leaf dimensions (i.e. leaf area, leaf length, leaf shape and leaf width) between some *Eucalyptus nitens* and *E. denticulata* races were evident following Tukey-Kramer adjustment for multiple comparisons (Appendix A: Table 5). Although the SNSW race was not significantly different from other *E. nitens* races, juvenile leaf area, leaf shape, and leaf width means for the SNSW race were more similar to those of the two *E. denticulata* races than other *E. nitens* races, in keeping with the observations of Pederick (1979) and Cook and Ladiges (1991).

Conclusions

Significant race × rainfall zone interaction in growth traits was indicative of broad-scale adaptation within *Eucalyptus nitens* to differences in the season of rainfall. In winter-rainfall zones, central Victorian *E. nitens* races exhibited superior growth to NSW races but the opposite was true in zones of summer-rainfall zones. On average, the best-performing *E. nitens* races exhibited more rapid growth than *Eucalyptus denticulata* races, particularly in winter-rainfall zones. Although a scarcity of published information relating to some commercially important traits (e.g. pulp yield) was evident, significant racial differences in basic density, branch size and form (straightness) were identified, based on data from a broad range of trial environments. As no one race was superior for all commercially important traits, careful consideration of the proportional representation of *E. nitens*/*E. denticulata* races in breeding populations is necessary, particularly in breeding programmes with multiple-trait breeding objectives.

Acknowledgements

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APPENDIX A: Back transformed means of various traits (expressed as a percentage of the overall mean) for *Eucalyptus denticulata* (D) (Central Victoria, CV; Errinundra, ERR) and *E. nitens* (N) (Connor's Plain, CON; Northern Central Victoria, NCV; Southern Central Victoria, SCV; Northern New South Wales, NNSW; and Southern New South Wales, SNSW) races, number of trials analysed, and significance (*P*-value) of race x rainfall zone interactions and racial differences. Races with common superscript letters for the same trait are not significantly different at *P* < 0.05 following a Tukey-Kramer adjustment for multiple comparisons. References from which data for each trait were derived are indicated.

TABLE 1: Growth traits.

Trait	Rainfall zone	Number of trials	Race x rainfall zone	Race	(D) CV	(D) ERR	(N) CON	(N) NCV	(N) SCV	(N) NNSW	(N) SNSW	References
Basal area	Summer	2	0.004	0.028	-	71 ^b	-	-	71 ^b	141 ^a	117 ^{ab}	39
Basal area	Winter	9	-	0.002	-	62 ^c	142 ^a	121 ^{ab}	104 ^{ab}	83 ^{bc}	88 ^{abc}	22, 43, 46, 47
Diameter	Summer	16	<.001	0.001	-	101 ^{ab}	-	98 ^{ab}	87 ^a	109 ^b	106 ^b	37, 38, 41, 44, 45, 49
Diameter	Winter	57	-	<.001	86 ^c	82 ^c	114 ^a	111 ^a	108 ^a	99 ^b	99 ^b	1, 3, 9, 10, 13, 19, 21, 23, 24, 27, 33, 34, 43, 51-53, 55
Height	Summer	14	<.001	0.013	-	93 ^b	-	100 ^{ab}	94 ^b	108 ^a	104 ^{ab}	36-39, 41, 44, 49
Height	Winter	37	-	<.001	95 ^{bc}	92 ^c	103 ^{ab}	106 ^a	107 ^a	98 ^b	98 ^{bc}	1, 9, 10, 13, 21, 22, 27, 33, 34, 53
Mean annual increment	Summer	2	-	0.057	-	69	-	87	46	156	142	38
Volume	Summer	4	0.046	0.026	-	85 ^{ab}	-	97 ^{ab}	63 ^b	133 ^a	122 ^a	36, 38, 49
Volume	Winter	22	-	<.001	77 ^{bc}	76 ^c	117 ^{ab}	116 ^a	112 ^a	98 ^b	105 ^{ab}	1, 9, 13, 21, 24, 27, 33, 34, 43
Volume (green boards)	Winter	1	-	-	-	-	89	102	110	-	-	3
Volume (log)	Winter	1	-	-	-	-	95	99	106	-	-	3

TABLE 2: Wood property traits.

Trait	Rainfall zone	Number of trials	Race x rainfall zone	Race	(D) CV	(D) ERR	(N) CON	(N) NCV	(N) SCV	(N) NNSW	(N) SNSW	References
Density/moisture content												
Basic density	Combined	11	0.17	<.001	100 ^{abc}	102 ^{ab}	98 ^{bc}	99 ^{bc}	100 ^{abc}	103 ^a	98 ^c	5, 10, 19, 30, 37, 39
Moisture content	Summer	1	-	-	-	-	-	-	-	97	103	37
Pilodyn penetration	Winter	1	-	-	-	-	99	101	99	-	-	25
Pulping properties												
Alkali consumption	Summer	2	-	0.39	-	-	-	-	-	99	101	5
Burst strength of pulp	Summer	2	-	0.10	-	-	-	-	-	97	103	5
Cellulose content	Summer	2	-	0.26	-	-	-	-	-	100	100	5
Cellulose content	Winter	2	-	0.035	-	-	99 ^b	100 ^b	101 ^a	-	-	19
Extractives content	Summer	2	-	0.77	-	-	-	-	-	102	98	5
Lignin content	Summer	2	-	0.53	-	-	-	-	-	99	101	5
Pulp brightness	Summer	2	-	0.88	-	-	-	-	-	100	100	5
Pulp yield	Summer	2	-	0.16	-	-	-	-	-	101	99	5
Pulp yield	Winter	1	-	-	-	-	-	-	-	99	101	46
Tear strength	Summer	2	-	0.29	-	-	-	-	-	102	98	5
Tensile energy absorption	Summer	2	-	0.25	-	-	-	-	-	94	106	5
Solid-wood properties												
Collapse	Winter	2	-	0.020	-	-	114 ^a	99 ^{ab}	88 ^b	-	-	19
Shrinkage (net volumetric)	Winter	2	-	0.30	-	-	100	98	102	-	-	19
Shrinkage (total volumetric)	Winter	3	-	0.004	-	75 ^b	93 ^{ab}	88 ^{ab}	88 ^{ab}	130 ^a	126 ^a	19, 29

TABLE 3: Tree architecture traits

Trait	Rainfall zone	Number of trials	Race x rainfall zone	Race	(D) CV	(D) ERR	(N) CON	(N) NCV	(N) SCV	(N) NNSW	(N) SNSW	References
Bark thickness	Winter	1	-	-	-	106	-	-	-	106	88	31
Branch angle (flat = high score)	Winter	1	-	-	-	-	-	-	117	92	91	22
Branch frequency	Winter	1	-	-	-	79	-	-	-	118	104	28
Branch quality (high quality = high score)	Winter	1	-	-	-	-	101	105	94	-	-	53
Branch retention (lower 1.5 m of stem)	Winter	1	-	-	-	-	-	-	82	111	107	22
Branch size (small = high score)	Winter	9	-	<.001	110 ^{ab}	114 ^a	97 ^{bcd}	95 ^{bcd}	106 ^{abc}	86 ^d	92 ^{cd}	22, 24, 25, 34, 52
Branching	Winter	1	-	-	-	112	-	89	114	91	93	53
Forks	Winter	6	-	0.91	109	101	69	106	76	103	137	22, 33, 43, 53
Form (malformation) (malformed = low score)	Winter	4	-	0.30	-	93	100	104	101	100	102	27, 43
Form (straightness) (straight = high score)	Combined	22	0.20	0.005	95 ^{ab}	101 ^{ab}	105 ^{ab}	104 ^{ab}	106 ^a	97 ^{ab}	92 ^b	3, 22-24, 27, 34, 36, 38, 39, 43, 52, 53
Ramiforms	Winter	1	-	-	-	-	-	-	77	103	120	22
Taper (log)	Winter	1	-	-	-	-	108	104	88	-	-	3
Taper (stem)	Winter	1	-	-	-	87	-	-	-	125	87	28

TABLE 4: Fitness traits.

Trait	Rainfall zone	Number of trials	Race x rainfall zone	Race	(D) CV	(D) ERR	(N) CON	(N) NCV	(N) SCV	(N) NNSW	(N) SNSW	References
Frost (field trial) (most damaged = high)	Winter	3	-	0.21	107	127	69	84	89	115	108	10, 47
Frost (leaf disk RC, -5.0 °C) (most damaged = low RC)	Nursery	1	-	-	-	-	-	-	-	101	99	40
Frost (leaf disk RC, -6.5 °C) (most damaged = low RC)	Nursery	1	-	-	-	-	-	-	-	101	99	40
Frost (leaf disk RC, -8.0 °C) (most damaged = low RC)	Nursery	1	-	-	-	-	-	-	-	105	95	40
Frost (leaf disk T50) (most damaged = low T50)	Nursery	1	-	-	-	-	109	100	92	104	94	47
Frost (leaf, -3.2 °C) (most damaged = high)	Nursery	1	-	-	-	95	-	-	-	62	143	48
Frost (leaf, -3.5 °C) (most damaged = high)	Nursery	1	-	-	-	107	-	-	-	83	110	48
Frost (leaf, -3.8 °C) (most damaged = high)	Nursery	1	-	-	-	110	-	-	-	82	108	48
Frost (leaf, -4.1 °C) (most damaged = high)	Nursery	1	-	-	-	97	-	-	-	99	103	48
Frost (stem, -3.2 °C) (most damaged = high)	Nursery	1	-	-	-	103	-	-	-	52	145	48
Frost (stem, -3.5 °C) (most damaged = high)	Nursery	1	-	-	-	115	-	-	-	67	118	48
Frost (stem, -3.8 °C) (most damaged = high)	Nursery	1	-	-	-	129	-	-	-	64	106	48
Frost (stem, -4.1 °C) (most damaged = high)	Nursery	1	-	-	-	106	-	-	-	87	107	48
Health (healthy = high score)	Winter	4	-	0.039	-	111 ^a	63 ^a	73 ^a	79 ^a	144 ^a	129 ^a	27, 43
Insect damage	Winter	1	-	-	-	-	99	99	104	-	97	10
Mortality (later)	Winter	3	-	0.51	-	-	-	-	115	111	73	43
Mortality and thinning (early)	Winter	3	-	0.13	-	-	-	-	108	89	104	43
Mycosphaerella (defoliated = high score)	Summer	1	-	-	-	-	-	105	112	93	91	38
Mycosphaerella (defoliated = high score)	Winter	1	-	-	-	-	-	68	109	-	124	4
Survival	Combined	23	0.76	0.12	-	75	138	107	97	90	93	3, 13, 21, 23, 24, 27, 38, 39, 41, 47, 49, 53
Runts	Winter	3	-	0.62	-	-	-	-	61	114	126	43
Windfirmness	Winter	1	-	-	-	13	-	-	178	91	117	23

TABLE 5: Morphological and developmental traits.

Trait	Rainfall zone	Number of trials	Race x rainfall zone	Race	(D) CV	(D) ERR	(N) CON	(N) NCV	(N) SCV	(N) NNSW	(N) SNSW	References
Amplexical leaves	Nursery	1	-	-	-	1	-	-	-	149	149	6
Distance to leaf (max. width:length)	Nursery	1	-	-	-	88	-	-	-	116	96	6
Dry weight of seeds	Winter	1	-	-	-	90	-	-	110	-	-	15
Foliage (height to phase change)	Winter	2	-	0.007	52 ^{ab}	47 ^b	174 ^{ab}	142 ^a	114 ^{ab}	85 ^{ab}	85 ^{ab}	33, 34
Foliage (juvenile %)	Winter	1	-	-	-	-	102	102	96	-	-	53
Foliage (trees with adult foliage)	Winter	1	-	-	161	201	-	7	31	-	-	33
Glaucousness	Nursery	1	-	-	-	89	-	-	-	166	45	6
Internode distance	Nursery	1	-	-	-	116	-	-	-	93	91	6
Leaf area (juvenile)	Winter	2	-	0.027	79 ^b	77 ^b	125 ^{ab}	129 ^a	105 ^{ab}	107 ^{ab}	77 ^{ab}	33, 34
Leaf length	Nursery	1	-	-	-	96	-	-	-	96	108	6
Leaf length (juvenile)	Winter	2	-	0.048	94 ^b	100 ^{ab}	102 ^{ab}	106 ^a	98 ^{ab}	99 ^{ab}	101 ^{ab}	33, 34
Leaf length:width (juvenile)	Winter	1	-	-	103	115	-	90	92	-	-	34
Leaf max. width:length	Nursery	1	-	-	-	94	-	-	-	122	84	6
Leaf shape (juvenile) (length:width)	Winter	2	-	0.028	108 ^{ab}	123 ^a	80 ^b	88 ^{ab}	90 ^{ab}	89 ^{ab}	121 ^{ab}	33
Leaf tip angle	Nursery	1	-	-	-	94	-	-	-	125	81	6
Leaf width (juvenile)	Winter	2	-	0.022	86 ^{bc}	82 ^c	121 ^{ab}	116 ^a	105 ^{abc}	107 ^{abc}	82 ^{abc}	33, 34
Reddening of node-4 leaf	Nursery	1	-	-	-	87	-	-	-	87	126	6
Secondary vein angle	Nursery	1	-	-	-	103	-	-	-	115	82	6