

Achievements in forest tree improvement in Australia and New Zealand

9. Genetic improvement of *Eucalyptus nitens* in Australia

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Summary

Eucalyptus nitens is the second most widely planted eucalypt species in Australia. The species is principally grown for the production of pulpwood but substantial areas are also managed for solid-wood production. The first large-scale *E. nitens* progeny trials were established in the 1970s and up to two cycles of breeding have since been completed. Estimates of genetic gains achieved through breeding are not routinely published, but numerous genetic gain trials have been established. Advances in the understanding of *E. nitens* genetic architecture and reproductive biology have been integrated into operational breeding and deployment programs. Despite extensive research into alternative deployment strategies, improved *E. nitens* genotypes are almost universally deployed as seedlings derived from open-pollinated seed-orchards.

Keywords: plantations; tree breeding; genetic improvement; progeny testing; seed orchards; pulpwood; wood products; sawnwood; *Eucalyptus nitens*; Australia

Introduction

The Australian *Eucalyptus nitens* (Deane & Maiden) Maiden plantation estate is about 143 000 ha (Parsons *et al.* 2006), comparable to that of Chile (around 140 000 ha; INFOR 2004) but substantially greater than that of other countries in which the species is grown commercially (e.g. China, New Zealand and South Africa; Tibbits *et al.* 1997). In Australia, *E. nitens* is principally grown in Tasmania (132 000 ha; Parsons *et al.* 2006) in regions where low temperatures (Tibbits and Hodge 2003) or *Mycosphaerella* leaf disease (Mohammed *et al.* 2003) impede the growth or survival of *E. globulus* Labill., the eucalypt most widely planted on mainland Australia.

Eucalyptus nitens has a scattered natural distribution that extends over a wide latitudinal range (30½–38°S) from the Central Highlands of Victoria to the Dorrigo area of New South Wales (Chippendale 1988; Boland *et al.* 1992). It occupies sites with moderate to high rainfall (750–1750 mm y⁻¹) between 600 and 1600 m above sea level which can experience 50–150 severe frosts per year (Boland *et al.* 1992). However, as exemplified by

the distribution of plantations in Australia, suitable bioclimatic conditions for *E. nitens* extend well beyond its natural distribution (Lindenmayer *et al.* 1996).

This paper reviews current *E. nitens* breeding objectives, assessment methodologies, genetic resources, base populations, and breeding and deployment strategies. It also briefly summarises the activities undertaken to date in Australian breeding and deployment programs.

Breeding objectives and selection traits

Pulpwood

Maximising the profitability of plantations for pulpwood production has historically been the sole objective of most *E. nitens* breeders in Australia. Rotation-age volume, basic density and pulp yield have been identified as the most economically important eucalypt kraft pulpwood objective traits (Borralho *et al.* 1993; Greaves *et al.* 1997) and typical selection traits utilised in breeding programs include diameter at breast height (dbh, 1.3 m), wood core basic density and or pilodyn penetration (an indirect measure of wood density). Historically, selection for pulp yield has been undertaken via destructive sampling and laboratory-based pulping (Tibbits and Hodge 1998). However, near infrared reflectance spectroscopy (NIR; Schimleck *et al.* 2004) is increasingly being adopted as a cheap and non-destructive means of selecting trees for high pulp yield.

Solid wood

Over the past decade, improving the profitability of solid-wood (i.e. sawlog and veneer) plantations has become an increasingly important objective of *E. nitens* growers (Neilsen and Pinkard 2000; Anon. 2006, 2007) and the refinement of solid-wood breeding objectives is an ongoing research priority. Harvest volume, log diameter, log straightness, log splitting, by-product value, knot size, timber hardness, timber stability in use, drying degrade (e.g. checking) and strength properties (e.g. stiffness) have been identified as potential solid-wood objective traits (Raymond 2000; Greaves *et al.* 2004; Nolan *et al.* 2005; Hamilton

2007). Current selection traits include dbh, stem straightness, branch diameter, core basic density, pilodyn penetration and core shrinkage traits (Hamilton *et al.* 2004; Kube and Raymond 2005). There is evidence that breeding *E. nitens* for pulpwood does not have a significant negative impact on wood quality for sawlog production (Kube and Raymond 2001).

Site-specific traits

Although *E. nitens* is recognised as being frost tolerant, maximising the profitability of plantations grown on cold sites is a secondary objective of some *E. nitens* growers (de Little *et al.* 1992; Dutkowski *et al.* 2006). Assessment of frost damage and growth in trials established on cold sites is regarded as the most effective means of selecting for cold tolerance (Tibbits and Hodge 2003). Reducing the palatability of seedlings to mammalian herbivores is also a secondary objective of at least one *E. nitens* breeding and deployment program, and a field of ongoing research (Glancy *et al.* 2007).

Tree improvement strategies

Breeding

Genetic resources

Pederick (1979) separated the natural range of *E. nitens* into six geographically distinct provenances: (1) Northern NSW, (2) Southern NSW, (3) Errinundra (East Gippsland, Victoria), and (4) Toorongo, (5) Macalister and (6) Rubicon in the Central Highlands of Victoria (Fig. 1). Pederick (1979) also identified two varieties of *E. nitens*, var. *nitens* and var. *errinundra*. The 'Errinundra type' populations, however, have since been ascribed specific status and renamed *E. denticulata* I.O.Cook & P.Y.Ladiges (Cook and Ladiges 1991). *E. denticulata* includes the Errinundra population (excluding an outlying population at Mt Kaye) and some genotypes interspersed within predominantly *E. nitens* populations in central Victoria (Cook and Ladiges 1991). It is distinguished from *E. nitens* by its denticulate adult leaf margins along with other morphological features (Pederick 1979; Cook and Ladiges 1991). *E. denticulata* has been shown to exhibit an earlier change to adult foliage (about 1 y after planting cf. 2–4 y; Pederick 1979), an absence of stilbene in foliage (Pederick and Lennox 1979), different isozyme (Cook and Ladiges 1998) and oil compositions in foliage (Li *et al.* 1994) and, more importantly from a commercial perspective, slower growth (Pederick 1979), poorer cold hardiness (Tibbits and Reid 1987; Raymond *et al.* 1992; Tibbits and Hodge 2003) and lower kraft pulp yields (Williams *et al.* 1995) than *E. nitens*.

Further to characterising *E. denticulata*, Cook and Ladiges (1991) defined three genetically distinct races of *E. nitens*: (1) Central and Northern NSW, (2) Southern NSW and Mt Kaye, and (3) Central Victoria. Dutkowski *et al.* (2001) further separated *E. nitens* populations in central Victoria into three additional races, Northern, Southern and Connor's Plain, none of which neatly corresponded with the Macalister, Rubicon or Toorongo provenance boundaries of Pederick (1979; Fig. 1). These racial classifications are increasingly utilised in genetic analyses, instead of Pederick's (1979) provenances, as they represent both geographically and genetically distinct populations.

Byrne and Moran (1994) examined diversity in the chloroplast (cp) genome within and between *E. nitens* and *E. denticulata* populations. They identified two cpDNA groups, one consisting of the central Victorian and southern NSW populations and a second of the Errinundra (i.e. *E. denticulata*) and northern NSW provenances. These findings were only partially consistent with geographic patterns of genetic variation observed in morphological, isozyme and leaf oil traits (Cook and Ladiges 1991; Li *et al.* 1994; Cook and Ladiges 1998). In a separate study, Thumma *et al.* (2005) genotyped trees from central Victoria with nuclear DNA microsatellite markers but observed no significant population structure.

Base populations

Australian *E. nitens* base populations include collections from native forests made by private collectors, the Australian Tree Seed Centre (CSIRO) and the State Government of Victoria, as well as infusions from overseas breeding programs (Orme 1986; Tibbits 1988a; Eldridge *et al.* 1993; Johnson 1996; Dutkowski *et al.* 2001) (see Figs 1, 2 and 3 for details). Where possible, *E. denticulata* and its hybrids have generally been excluded from Australian *E. nitens* breeding populations (Tibbits 1988a; Dutkowski *et al.* 2001). Although base populations of most *E. nitens* breeding programs are sizable, it is conceivable that further infusions of under-represented native-forest populations, or populations with favourable characteristics, may be undertaken. Further international infusions are also likely but may be restricted in some cases due to bio-security concerns (e.g. the risk of introducing *Puccinia psidii* from the Americas; Grgurinovic *et al.* 2006). Given the small size of some natural populations (e.g. Barrington Tops; Byrne and Moran 1994) and the possibility of seed transfer between localities in production forests (Pederick 1985), targeted *ex situ* conservation of genetic resources may be necessary.

Breeding strategies

Establishment, selection and mating cycles of around 10–12 y are achievable in *E. nitens* (de Little *et al.* 1992; Griffin 2001). However, biological constraints associated with seed production, combined with limited financial resources and or a desire to maintain breeding populations in discrete generations, has seen breeding cycles extend beyond optimal time frames in most breeding programs. Rolling-front strategies, which make the notion of discrete generation intervals irrelevant (Borralho and Dutkowski 1998), are increasingly being adopted in breeding programs.

Both forward and backward selections are made in *E. nitens* breeding programs. Selections are generally made on the basis of individual-tree breeding values for an economic index (Hazel 1943; Schneeberger *et al.* 1992). However, constraints on relatedness among selected individuals are applied and the specific index or indices utilised depend on the breeding objective(s) of the breeding program in question. Individual-tree breeding values are generally calculated from progeny trial data, from multiple-sites and generations, using best linear unbiased prediction (BLUP: Henderson 1986; Raymond and Apiolaza 2004). Estimates of genetic parameters, such as heritabilities, coefficients of additive genetic variation, and inter-site, inter-age and inter-trait genetic

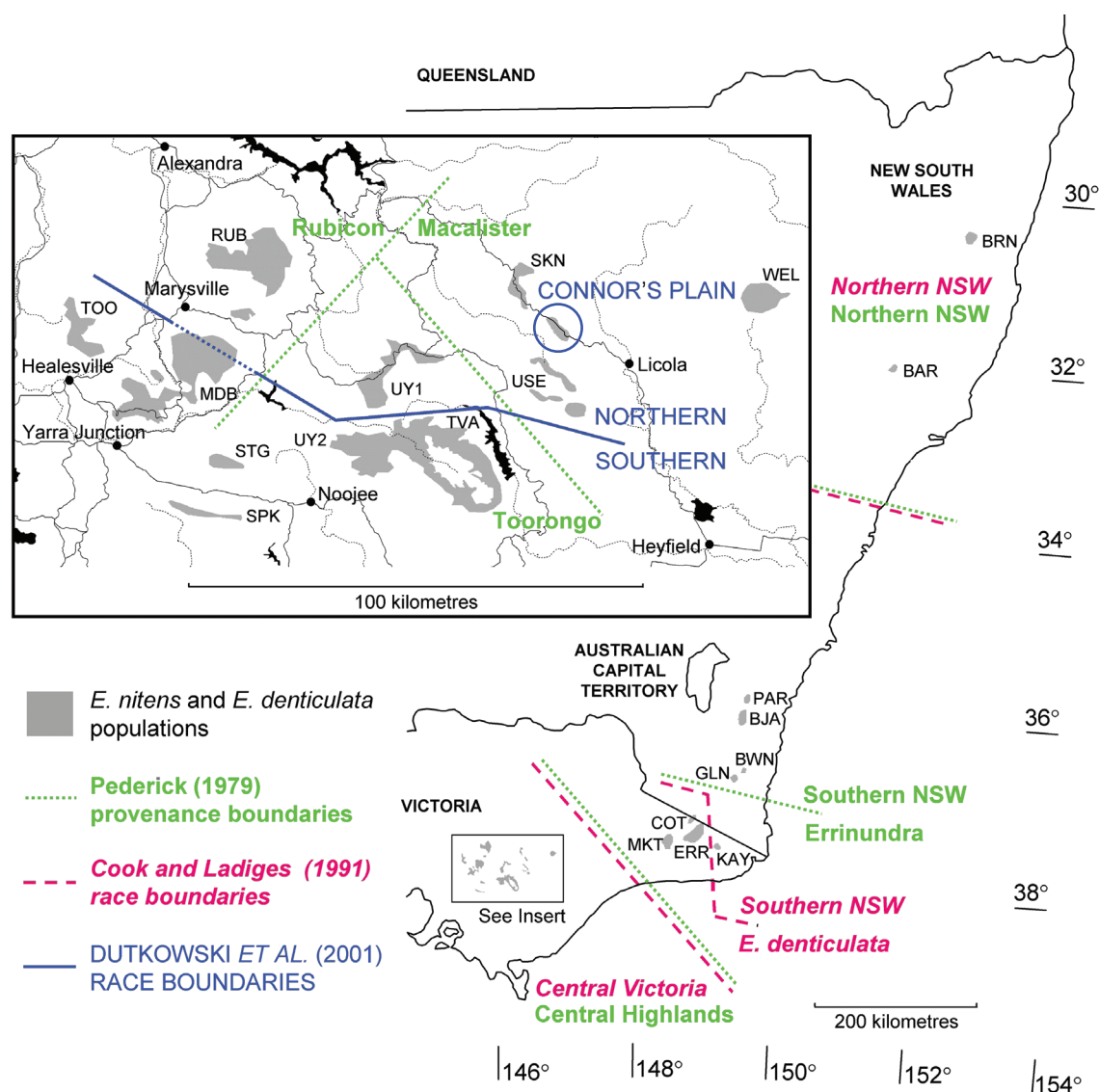


Figure 1. Natural populations of *E. nitens* and *E. denticulata* with provenance and race boundaries. Populations include (Dutkowski *et al.* (2001) sub-provenances are listed in *italics*): BRN (Barren Mt, Point Lookout, Majors Point), BAR (Barrington Tops), PAR (Parker's Gap), BJA (Badja Mt, Pikes Saddle, Anembo Trig), BWN (Brown Mt), GLN (Glen Bog), COT (Cottonwood Tk), MKT (Monkey Top), ERR (Errinundra Camp, Cobb Hill, Gunmark Rd, Hammond's Rd, Coast Range Rd), KAY (Mt Kaye), RUB (*Rubicon*, Barnewall Plains, Royston River, Quartz Creek, Little River), TOO (*Toolangi*, Mt Tanglefoot, Monda Road), MDB (*Mt Donna Buang*, Ben Cairn), STG (*Starling Gap*), SPK (*Spion Kopje*), UY1 and UY2 (*Upper Yarra*, Newlands Road, North of Toorongo, Mount Horsefall, Mount Gregory), TVA (*Thomson Valley*, Mt Erica, Mt St Gwinear Rd, Marshall Spur), USE (*Mt. Useful*), SKN (*Mount Skene/Barkly River*, Lazarini Creek) and WEL (Mt Wellington) (Cook and Ladiges 1991; Dutkowski *et al.* 2001). Although not included in the trials examined by Pederick (1979), Mt Wellington was allocated to the Macalister provenance by Pederick (1985), and the Mt Kaye population was allocated to the Errinundra provenance by Kube (1993) and Li *et al.* (1994). Localities close to Starling Gap were allocated to the Toorongo provenance by Pederick (1985) but Dutkowski *et al.* (2001) allocated both the Starling Gap and Spion Kopje populations to a separate provenance named Powelltown. The Mt Wellington population was not represented in the trials analysed by Dutkowski *et al.* (2001) but is currently considered part of the Northern race based on family branching means from Pederick (1985). Localities in the north of the Mt Donna Buang population contain a high proportion of *E. denticulata* genotypes (Martyn Lavery, Arianda Pty Ltd, 2007 *pers. comm.*) and were not represented in the trials analysed by Dutkowski *et al.* (2001).

correlations, have been reported for a large number of traits in *E. nitens* (Hamilton and Potts in press).

Most *E. nitens* progeny trials test only open-pollinated (OP) families because *E. nitens* control-pollinated (CP) seed is difficult and expensive to produce. Open pollination, however, does not allow complete control and documentation of co-ancestry, resulting in uncertainty relating to the extent and effect of inbreeding in trials; does not allow controlled mating across trials, breeding lines or generations; and enables backward selection of maternal

parents only. Breeders can control the paternal parentage of OP progeny to some extent by establishing genetically superior selections in clonal (i.e. grafted) seed orchards and testing progeny from these seed-orchards in the next generation of trials (Figs 2 and 3; Griffin 2001) but this approach clearly has its own limitations and problems. In the future molecular markers may be used to reconstruct pedigrees from OP seedlots, thus avoiding the cost of controlled pollination and alleviating problems associated with open pollination (Gea *et al.* 2007).

Genotype $\times$ environment interaction

Eucalyptus nitens of central Victorian origin generally outperforms genotypes from NSW populations in trials established in winter-rainfall zones (e.g. south-eastern Australia). However, the opposite is generally true in summer-rainfall zones (e.g. South Africa). This genotype $\times$ environment interaction ($G \times E$) is believed to be partly caused by differences in fungal disease (e.g. *Mycosphaerella*) resistance among populations (Purnell and Lundquist 1986; Eldridge *et al.* 1993). Variation in cold tolerance among genotypes and the frequency of damaging frosts among sites also explains some $G \times E$ observed in *E. nitens* growth (Dutkowski *et al.* 2006). Cold-tolerant germplasm is deployed at high altitudes in Tasmania (Tibbits and Hodge 2003).

Hybrid breeding

Eucalyptus nitens is able to hybridise with a wide range of *Symphyomyrtus* species (Tibbits 2000; Barbour *et al.* 2005a). There are, however, partial barriers to seed set and germination in hybrids (Espejo *et al.* 1995; Barbour *et al.* 2005a) and unilateral cross-incompatibility has been observed between *E. nitens* and *E. globulus* (Gore *et al.* 1990).

Despite overseas interest in *E. nitens* hybrids with *E. globulus* (Griffin 2001) and *E. grandis* (Zwolinski and Bayley 2001), *E. nitens* hybrids are not planted on a commercial scale in Australia and enthusiasm for hybrid breeding is limited, partly due to difficulties with clonal propagation (Tibbits 2000). Furthermore, F_1 populations of *E. nitens* $\times$ *globulus*, the most intensively studied *E. nitens* hybrid in Australia, generally exhibit only intermediate growth, cold hardiness and wood properties compared with parental species populations (i.e. little or no heterosis has been observed in these traits; Tibbits *et al.* 1991, 1995; Volker 2002). *E. nitens* $\times$ *globulus* hybrids were also found to be more susceptible to *Mycosphaerella* leaf disease than parental species in one study (Dungey *et al.* 1997). Furthermore, Volker (2002) found that it was not possible to accurately predict the growth of F_1 hybrid progeny from pure species progeny, suggesting that a reciprocal recurrent selection strategy would be required for hybrid breeding.

Molecular breeding

Quantitative trait loci (QTL; i.e. regions of the genome affecting quantitative traits) for seedling height, seedling leaf area (Byrne *et al.* 1997a) and frost tolerance (Byrne *et al.* 1997b) were identified using RFLP markers in the 1990s. More recently, association mapping has been used to identify single-nucleotide polymorphisms (SNPs) in cell-wall genes (i.e. allelic variants) that are associated with phenotypic variation in microfibril angle and pulp yield (Thumma *et al.* 2005, 2007). The screening of breeding populations for SNPs affecting these important wood-quality traits has commenced on a pilot scale (Simon Southerton, CSIRO Canberra, 2007 *pers. comm.*).

Deployment

Current deployment strategies

Despite extensive research into alternative strategies (de Little 2004), deployment of improved *E. nitens* genotypes into

plantations is almost universally undertaken by means of OP seed-orchard seedlings. *Eucalyptus nitens* has small flowers (buds 6–7 $\times$ 3 mm) in seven-bud umbels (Boland *et al.* 1992), making emasculation and controlled pollination using traditional methodologies (Tibbits 1989) tedious and prohibitively expensive for operational deployment of full-sib families. The species also suffers from low seed yield per control-pollinated flower (Tibbits 1989; Espejo *et al.* 1995; Griffin 2001). Furthermore, new CP techniques such as single-visit-one-stop pollination (Harbard *et al.* 1999; Williams *et al.* 1999a), individual flower isolation and artificially induced protogyny (AIP; Assis *et al.* 2005), appropriate for mass supplementary pollination (MSP) in other species (Patterson *et al.* 2004), are not efficient means of producing *E. nitens* CP seed (Venter and Sivlal 2007).

The vegetative propagation of *E. nitens*, using both micro- and macro-propagation techniques, was the focus of much industry-supported research during the 1980s and 1990s (de Little 1986; Orme 1988; Tibbits 1993; Luckman 1996; Whiteman and Pongracic 1996; de Little 2004). However, low rooting-success and relatively high propagation costs continue to make operational deployment of clones into plantations uncompetitive against OP seed-orchard deployment strategies (Borralho 1997; Griffin 2001). Furthermore, *E. nitens* does not coppice reliably (Little and Gardner 2003). The species, however, can be readily grafted, permitting the capture and concentration of superior genotypes in OP seed orchards.

Open pollinated seed orchard management

Eucalyptus nitens seed orchard managers adopt a number of strategies to reduce production costs, and enhance seed quantity and quality. Trees or ramets are planted at wide spacing (e.g. 6 m $\times$ 6 m) to reduce competition for resources, allow the development of a deep crown and increase ease of access. Tree height is controlled in some orchards by pollarding (i.e. topping) to further increase the ease and safety of seed harvest. Espalier and potted seed orchard systems have also been tested (Moncur and Boland 2000) but are unsuitable for commercial OP seed production for such a fast-growing forest tree species.

Manipulation of flowering

Eucalyptus nitens floral buds are initiated about 2 y before ripe fruit are produced. Floral initiation in *E. nitens* is believed to occur in late winter to spring following a cold winter (Tibbits 1989; Moncur and Hasan 1994; Moncur and Boland 2000; Gardner and Bertling 2005). The species appears to be insensitive to day length, and flower induction seems to result from a cumulative chill process rather than from a single chill event (Gardner and Bertling 2005). Barbour *et al.* (2006) identified significant but limited genetic variation in flowering time at the family and provenance level (e.g. the difference in average median flowering time between the earliest (Toorongu) and the latest provenance (Northern NSW) was about one week). In the same study, flowering time of individual trees was found to be highly correlated across seasons. However, considerable site-to-site variation in flowering time has been observed in *E. nitens*. Trees growing at low altitudes tend to flower earlier (Williams 2000; Barbour *et al.* 2006) and for longer (Moncur and Boland 2000; Williams 2000). In a study that examined the effects of irrigation

on seed production, Williams (2000) found that some irrigated treatments produced fewer flowers than a rain-fed treatment.

Paclobutrazol is routinely applied in some seed orchards as a means of enhancing seed production and managing vegetative growth. Paclobutrazol inhibits the production of gibberellins (GAs), resulting in a range of changes in physiological activity, including, in *E. nitens*, enhanced flower-bud production and reduced vegetative growth (Griffin *et al.* 1993). Other plant growth regulators have been examined but none have been found to be as effective in reducing levels of gibberellins in *E. nitens* seedlings (Williams *et al.* 1999b). Although numerous methods of application have been examined (Hetherington *et al.* 1991; Griffin *et al.* 1993), paclobutrazol is generally applied as a soil drench at a rate of about 0.3 g of active ingredient per centimetre of stem circumference (Anon. 2003). The time of year in which paclobutrazol is applied varies widely among seed orchards. The effects of treatment can be detected a number of years after application (Moncur 1998). The effectiveness of paclobutrazol as a means of increasing seed production varies with tree or scion maturity (Griffin *et al.* 1993; Williams *et al.* 1999b; Gardner and Bertling 2005), temperature (Moncur and Hasan 1994), soil nutrient status (Williams *et al.* 2003) and soil moisture (Lever 1986).

Inbreeding and gene flow

Eucalyptus nitens is predominantly insect pollinated (Hingston *et al.* 2004) and has a mixed mating system. Outcrossing is favoured by protandry (i.e. the stigma is not fully receptive until some days after pollen is shed; Tibbits 1989; Eldridge *et al.* 1993) and partial self-incompatibility, which is believed to be controlled by a post-zygotic mechanism (Pound *et al.* 2003).

Outcrossing rates are known to vary among *E. nitens* genotypes. For example, self-incompatibility levels ranged from 25.8% to 93.6% in a study of five trees (Pound *et al.* 2003), and Grosser (2001) found that the proportion of out-crossed progeny from ten seed-orchard clones ranged from 60% to 100%. Furthermore, outcrossing rates have been observed to vary among years. Moncur *et al.* (1995) reported mean seed orchard outcrossing rates in sequential years of 75% and 100% and suggested that this difference was caused by changes in honeybee (*Apis mellifera* L.) populations. However, Hingston *et al.* (2004) found that honeybees were consistently not attracted to *E. nitens* flowers, suggesting that this difference in outcrossing was more likely caused by temporal variation in the density of flowering and/or other pollinating insects.

Although the deployment of some inbred individuals is currently unavoidable using an OP deployment strategy, the effects of such inbreeding on plantation performance are uncertain. Hardner and Tibbits (1998) revealed substantial and significant inbreeding depression for growth traits (e.g. the dbh of selfed progeny was 28% less than that of outcrossed progeny at 9 y of age) but inbreeding depression was negligible and non-significant for relative bark thickness (5% at 9 y of age), pilodyn penetration (8% at 9 y of age) and frost damage (4% at 2 y of age). However, Volker (2002) found little direct evidence of inbreeding depression in OP progeny — derived from seed orchards and plantations — for either dbh or pilodyn penetration.

Eucalyptus nitens pollen can be dispersed widely (regularly over 100 m but it has been observed up to 1.6 km from its source; Barbour *et al.* 2005b). However, using microsatellite markers, Grosser (2001) found the highest paternal contribution to the progeny of individual trees in a well-isolated clonal seed orchard tended to come from near neighbours. Furthermore, only 2.5% (ranging from 0 to 20% for individual clones) of seed sampled from within the orchard had a pollen parent from outside the orchard. Hybridisation with closely related species growing in close proximity to seed orchards is also possible (Barbour *et al.* 2002) but the extent of such genetic contamination in seed orchard seedlots is not well documented.

Seed yield and physical quality

Eucalyptus nitens seedlings have been induced to flower when as young as 3 y of age (Moncur 1998). However, the first usable volumes of seed from seedling seed orchards are generally not available until age 6–7 y and full production does not occur until age 8–10 y (de Little *et al.* 1992; Tibbits *et al.* 1997; Moncur and Boland 2000; Griffin 2001). Clonal *E. nitens* seed orchards generally produce usable quantities of seed sooner than seedling seed orchards (Moncur and Boland 2000; Griffin 2001). Although seed yields are affected by management practices (e.g. culling, replanting and pollarding), mature, well-managed seed orchards established on appropriate sites can yield in the order of ten million seeds per hectare per year (Peter Gore, Derford Nitens and seedEnergy Pty Ltd Hobart, 2007 *pers. comm.*).

Hingston *et al.* (2004) observed higher capsule set in seed orchards in high rainfall (i.e. >1200 mm y⁻¹) areas than in orchards in drier locations, suggesting that irrigation in dry locations might enhance capsule retention. However, the reverse was observed in *E. globulus* after experimental manipulation of a seed orchard (Suitor *et al.* 2007) and a comparable study is required in *E. nitens* to test this hypothesis. The numbers of viable seeds per capsule, and the weight, viability and germination rate of seeds were not significantly affected by irrigation in a Tasmanian *E. nitens* trial (Williams 2000; Williams *et al.* 2007).

In a study conducted in south-eastern Tasmania, the numbers of seeds per capsule were not significantly different among sites of different altitude (60, 240, 440 and 650 m above sea level) but a trend towards decreasing seeds per capsule with increasing elevation was observed. Furthermore, seeds from low-elevation sites were heavier and exhibited higher viability and germination rates than seeds from higher-elevation sites (Williams *et al.* 2007).

Genetic gains

Most recently-established seed orchards are clonal, consisting of backward-selected individuals from breeding populations. However, first-generation seedling seed orchards continue to supply a large proportion of *E. nitens* seed used to establish plantations. The genetic quality of seed from individual seedling seed orchards is thought to have improved over time through thinning (i.e. roguing) and/or selective harvest of genotypes. Thinning and selective harvests, along with the establishment of specialised seed orchards, have also been utilised to produce seed for secondary or changed deployment objectives (e.g. improved cold tolerance).

Estimates of genetic gains from OP *E. nitens* seed-orchard seed are generally derived from the predicted breeding values of orchard genotypes assuming equal contributions to the pollen pool from each tree (i.e. panmictic pollination) and no non-additive genetic effects such as inbreeding depression. In some instances, however, small-plot genetic gain trials have been established to directly test the performance of individual-tree seed-orchard seedlots against baseline native-forest seedlots. Although few are of rotation age, a number of plantation growers have also established large-plot realised gain trials to verify genetic gains achieved through breeding (Fig. 2 and 3).

Tibbits and Hodge (1998) estimated genetic gains relative to native forest material of central Victorian and NSW origin, based on the predicted breeding values of genotypes in a second generation clonal orchard, to be 23.2% for basal area, 1.2% for basic density and 2.6% for kraft pulp yield. The potential to make rapid genetic gains in wood property traits such as basic density and pulp yield is limited in *E. nitens* by high assessment costs and relatively low levels of additive genetic variation (Hamilton and Potts in press). However, small gains in these traits can be economically important (Borralho *et al.* 1993; Greaves *et al.* 1997; Tibbits and Hodge 1998).

Tree improvement programs

Collaborative breeding

The Southern Tree Breeding Association (STBA)

A collaborative Southern Tree Breeding Association (STBA) breeding program, whose membership included Forestry Tasmania, Australian Paper Plantations Ltd (now HVP Plantations Pty Ltd), Australian Newsprint Mills Ltd (ANM, now Norske Skog Paper Mills Australia Ltd) and Fletcher Challenge Forests Ltd (New Zealand) was established in 1994 but ceased operations in 1999 due to a reduction in establishment of commercial plantations and lack of industry support. The Cooperative Research Centre (CRC) for Temperate Hardwood Forestry, CRC for Sustainable Production Forestry, Centre for Forest Tree Technology (CFTT, Victorian State Government) and CSIRO Forestry and Forestry Products provided technical support to the STBA program. Although brief, this collaboration saw extensive across-organisation genetic analysis and selection, and the establishment of two breeding arboreta and three CP progeny trials.

Ongoing collaboration

Collaboration between *E. nitens* growers, seed suppliers, breeders and researchers is ongoing through CRC for Forestry projects, CRC breeding strategy meetings (Whitlock 2005), CSIRO molecular projects (Simon Southerton, CSIRO Canberra, 2007 *pers. comm.*), the development of a base population database that identifies co-ancestry across breeding populations¹ and numerous bilateral agreements. The STBA and its subsidiary company PlantPlan Genetics Pty Ltd continues to undertake genetic

analyses of *E. nitens* breeding populations, using TREEPLAN®, on behalf of individual companies.

Breeding programs

Victorian State Government

The first *E. nitens* progeny trials were established by Leon Pederick (Forests Commission, Victoria) between 1968 and 1978. Studies based on these trials (Pederick 1977, 1979, 1985; Nicholls and Pederick 1979; Pederick and Lennox 1979) identified the distinctive nature of populations now known as *E. denticulata*, noted the unique nature of the Connor's Plain population and drew attention to the potential of *E. nitens* as a plantation species. Furthermore, seedling and clonal seed orchards were established at Kinglake (currently owned by Timbercorp Ltd; Anon. 1996), Broadford, Sumner Spur and Olinda with genetic material from these trials. The Victorian State Government, through the Centre for Forest Tree Technology (CFTT), was an active member of the STBA breeding program, contributing both trial data and genetic material, but is no longer involved in *E. nitens* breeding.

Gunns

The Gunns Ltd breeding program (previously managed by APPM Ltd, North Ltd and Rio Tinto Ltd; Fig. 2) is the longest-running *E. nitens* breeding program in Australia. Between 1975 and 1986 twelve first-generation progeny trials were established on what is now the Gunns Ltd estate. This base population of more than 300 families was dominated by Central Victorian seedlots but also included material from NSW and a South African breeding program (Tibbits 1988a). Further infusions (126 families) from Central Victoria and overseas breeding programs were introduced in the mid-1990s (Tibbits and Powell 1996). Although the company is about to complete its second cycle of breeding, distinctions between generations are no longer made as a rolling front breeding strategy has now been adopted. In the 1990s, the company endeavoured to progeny-test 248 first-generation selections (Tibbits and Powell 1996) as CP families. However, some selections did not yield sufficient CP seed within the required time; a mix of full-sib CP, pollen-mix CP and OP trials was ultimately established. Between 1984 and 1995 the company undertook extensive research into clonal deployment but the economic gains from such a deployment strategy were deemed not great enough to justify its additional expense over an OP seed deployment strategy (Tibbits and Powell 1996). The company also undertook much research into the deployment of *E. nitens* hybrids (Rasmussen 1991; Rasmussen *et al.* 1995; Tibbits 2000) and established a number of hybrid trials in collaboration with CSIRO (Volker 2002). Gunns Ltd has a kraft pulpwood breeding objective and obtains its seed for deployment from in-house clonal and seedling seed orchards. Specialised clonal seed orchards have been established to meet specific deployment objectives (e.g. cold tolerance) and demonstration and large-plot gain trials have been established to verify genetic gains.

In 2000 Gunns Ltd acquired the *E. nitens* genetic resources of Boral Ltd (previously managed by Forest Resources Pty Ltd) including its first-generation seedling seed orchards at Camden (known as 'Shaws') and Birralelee, a number of second-generation progeny trials, hybrid trials including crosses with *E. gunnii*

¹ Kube, P. and Bail, I. (2002) Database of first generation seedlot pedigrees for *Eucalyptus nitens* in Australia and New Zealand. Confidential report to data providers. Forestry Tasmania, Hobart, Tasmania.

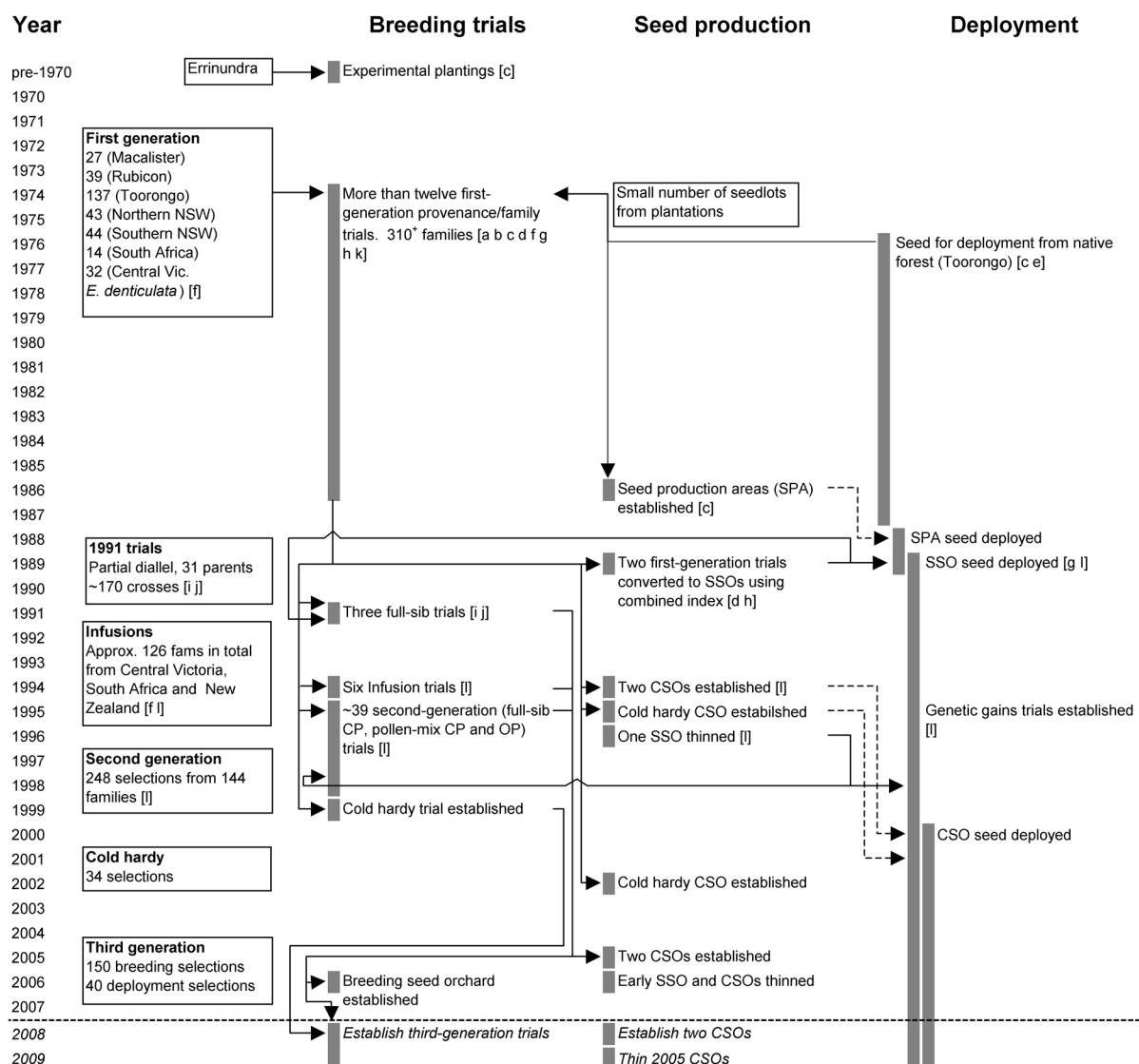


Figure 2. Summary of the Gunns Ltd *E. nitens* breeding program. Letters in square brackets refer to: (a) de Little (1986), (b) de Little (1988), (c) de Little and Dean (1986), (d) de Little *et al.* (1992), (e) Eldridge *et al.* (1993), (f) Tibbits (1988a), (g) Tibbits (1988b), (h) Tibbits (1991a), (i) Tibbits (1991b), (j) Tibbits (1993), (k) Tibbits and Hodge (1995), (l) Tibbits and Powell (1996). The terms ‘clonal seed orchard’ (CSO), ‘seedling seed orchard’ (SSO), ‘open pollinated’ (OP) and ‘control pollinated’ (CP) are expressed as acronyms.

and *E. grandis*, and records of research into clonal propagation (Orme 1988) and wood quality. Boral Ltd had a chemi-mechanical pulpwood breeding objective and its genetic resources are not wholly integrated into the ongoing Gunns Ltd breeding program.

HVP Plantations

HVP Plantations Pty Ltd’s *E. nitens* estate (previously managed by APM Forests Pty Ltd (APMF), Amcor Plantations Pty Ltd, Australian Paper Plantations Ltd, Victorian Plantations Corporation, Grand Ridge Plantations Pty Ltd and Hancock Victorian Plantations Pty Ltd) is located in Gippsland, Victoria. The company’s first *E. nitens* progeny trial was established in 1978 and was subsequently converted into a seed orchard. A further 13 trials were established between 1986 and 1990 providing a base population of 459 families (Whiteman and Cameron 1991). A CP progeny trial was planted in collaboration with the CSIRO in

1990 (Volker 2002), an STBA CP progeny trial was established in 1998 and three second-generation OP progeny trials were planted in 2006–2007. Clonal and hybrid research was undertaken in the 1980s and 1990s (Whiteman and Pongracic 1996) and a hybrid comparison trial was planted in 1999. HVP Plantations’ breeding objective is to maximise the profitability of its pulpwood plantations. The company currently deploys genetic material from an in-house open-pollinated seedling seed orchard that has shown good performance in Gippsland. A clonal seed orchard was established in 2005 and genetic gain trials were established in 2000 and 2004.

Forestry Tasmania

Between 1980 and 1988 the Forestry Commission of Tasmania (now Forestry Tasmania) established a number of relatively small (20–40 seedlots) first-generation provenance–progeny trials (Fig. 3). These contained OP seedlots from the Toorongo

provenance along with some NSW and East Gippsland material (Orme 1986; Kube *et al.* 2001). In 1993, a series of five large base-population trials containing 422 Central Victorian OP families (Dutkowski *et al.* 2001) was established in collaboration with ANM. Second-generation trials have recently been established, including progeny of first-generation selections, and infusions from a New Zealand breeding population and Derford Nitens. The organisation has adopted a primary breeding objective of maximising the production of pulpwood per hectare whilst maintaining or enhancing recovery of logs for solid-wood products (Kube and Raymond 2001). Seed is deployed from both clonal and seedling seed orchards. Small- and large-plot genetic-gain trials, including in-house and external seedlots, have been established on the Forestry Tasmania estate.

Forests NSW

The principal aim of the Forests NSW (previously State Forests of NSW) *E. nitens* breeding program is to maximise the profitability of plantations grown in the tablelands of NSW. Between 1989 and 1993 four progeny trials were established, one near Batlow (Southern Tablelands; Johnson 1996) and three in the Northern Tablelands. A further two progeny trials were established near Nundle in the Northern Tablelands in 2004, principally to test

genotypes from northern NSW populations. A grafted seed orchard of selections from in-house progeny trials was established in 2007. The orchard was separated into two sections of northern NSW and southern (i.e. Victorian and southern NSW) provenances.

Derford Nitens

Derford Nitens is a commercial seed producer that supplies substantial quantities of genetically improved seed to Australian *E. nitens* growers from its Bream Creek seed orchard. The original orchard was established in 1990 with OP families from a first-generation seedling seed orchard planted with families of central Victorian origin. The orchard was selectively thinned in 1997 on the basis of predicted breeding values for a kraft pulp index. Derford Nitens established small-plot genetic gain trials in collaboration with Forestry Tasmania and Forest Enterprises Australia Pty Ltd in 1999. These trials were established to verify genetic gains and enable intense backward selection of seed orchard parents to maximise deployment gains in pulpwood and solid-wood traits. In 2000 a clonal seed orchard was established adjacent to the original orchard. Derford Nitens has contributed genetic material to the breeding and deployment populations of other organisations (e.g. Forestry Tasmania; Fig. 3).

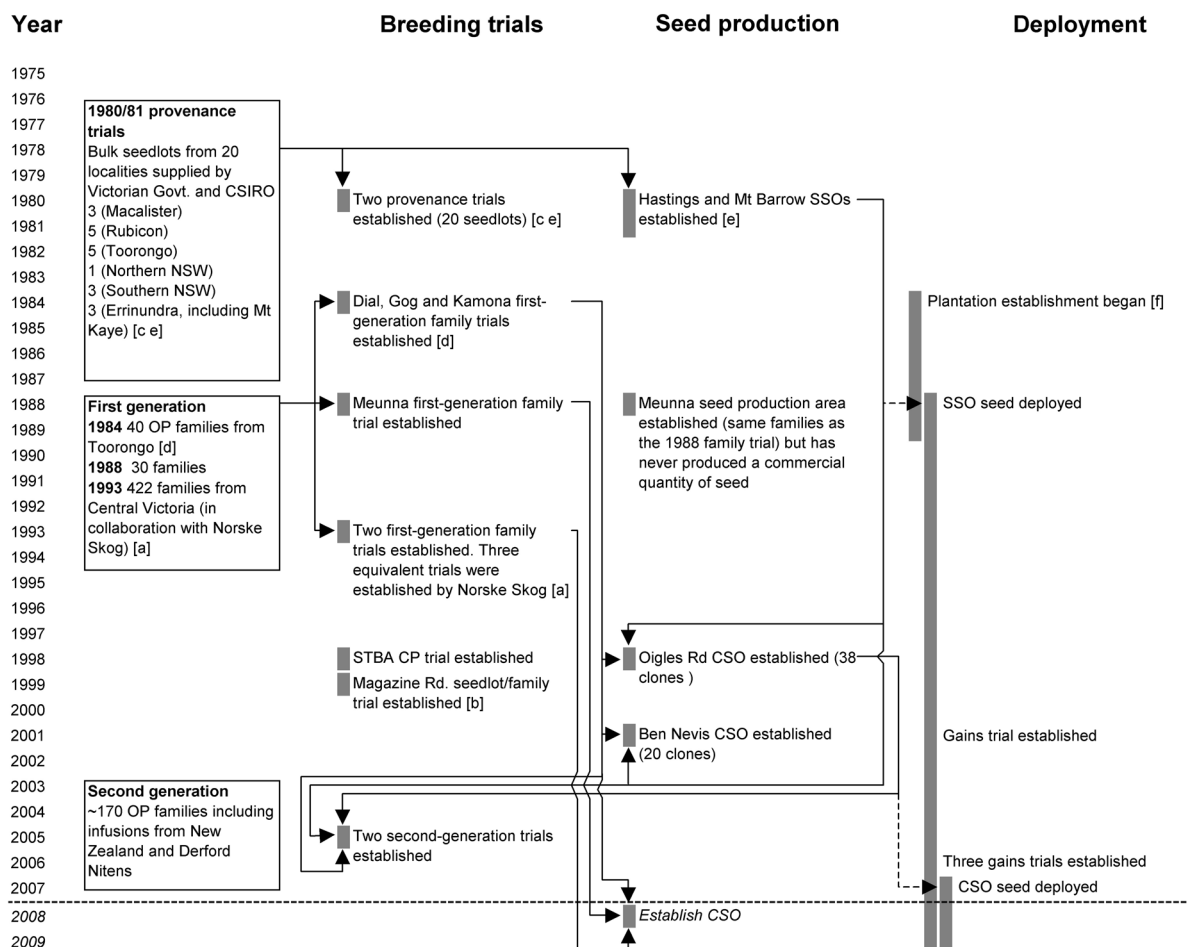


Figure 3. Summary of the Forestry Tasmania *E. nitens* breeding program. Letters in square brackets refer to: (a) Dutkowski *et al.* (2001), (b) Hamilton *et al.* (2004), (c) Kube (1993), (d) Kube *et al.* (2001), (e) Orme (1986) and (f) Volker (1986). The terms ‘clonal seed orchard’ (CSO), ‘seedling seed orchard’ (SSO), ‘open pollinated’ (OP) and ‘control pollinated’ (CP) are expressed as acronyms.

Norske Skog

ANM (now Norske Skog Paper Mills Australia Ltd) established a series of large base-population trials in collaboration with Forestry Tasmania in 1993 (Dutkowski *et al.* 2001). However, Norske Skog no longer has an active *E. nitens* breeding program.

Forest Enterprises Australia

Forest Enterprises Australia Ltd (FEA) has three reproductively mature clonal seed orchards on its Tasmanian estate. These were established using clones obtained from external tree improvement programs. Clones were selected on the basis of best available breeding values for growth and wood property traits of economic relevance. Furthermore, the company has 11 active progeny trials in Tasmania and NSW, testing up to 150 individual-tree OP seedlots from in-house and or external seed orchards. With the expansion of FEA's operations in NSW, the company's immediate priority is to refine the prediction of deployment values for existing clones and to establish further progeny trials and seedling seed orchards in that state, specifically including native and selected seedlots of NSW pedigree.

The future

In coming years, *E. nitens* genetic analyses are likely to become increasingly integrated across organisations in an effort to maximise the precision of estimates of breeding value and to reduce costs. Future research priorities are likely to include the refinement of breeding objectives, the refinement of trial assessment methods (e.g. selection traits for solid wood), overcoming uncertainty caused by open pollination in breeding and deployment, and the adoption of near-infrared reflectance spectroscopy and molecular marker-assisted selection for pulp yield.

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