

**Quantitative genetics of
Eucalyptus globulus, *E. nitens* and
their F₁ hybrid**

by

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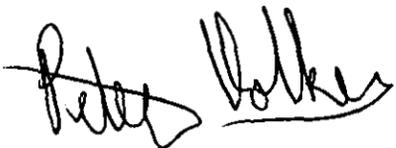
Declarations

This Thesis contains no material which has been accepted for a degree or diploma by the University of Tasmania or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by any other person except where due acknowledgment is made in the text of the Thesis.

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Abstract

This thesis examines the quantitative genetics of intra- and inter-specific hybrids of *E. globulus* ssp. *globulus* and *E. nitens*. The trials established to make this study are unique in forestry, due to the fact that the same parents have been used in open-pollination, intra- and inter-provenance (or intra-species) crosses and inter-species F₁ hybrids. This has allowed direct comparison of genetic parameters derived from different cross types. The traits examined include frost resistance using an electrical conductivity method, growth (diameter at breast height over bark DBHOB, at ages 2, 3, 4, 6 and 10 years) and Pilodyn penetration at age 6 years as an indirect measure of wood density.

The results demonstrate that the measured performance of frost, growth and Pilodyn traits in the inter-specific F₁ hybrid *E. nitens* x *globulus* is always intermediate or comparable with one or other of the parent species. In the frost trait, the inter-specific hybrid was no better than the frost sensitive *E. globulus*, so there is no overall advantage in producing the hybrid for this trait. Negative mid-parent heterosis was observed for early age growth traits in inter-specific *E. nitens* x *globulus* F₁ hybrids involving Taranna *E. globulus* male parents. The inter-specific F₁ hybrids demonstrated generally poor survival and a high proportion of abnormal and slow growing phenotypes, which eventually died. This latter phenomenon was not evident in pure species crosses, either within or between provenances.

It is shown that in *E. globulus* open-pollinated progeny estimates of additive genetic parameters are inflated and that breeding values for growth in *E. globulus* are poorly estimated, possibly due to the confounding effects of variation in inbreeding. This was not the case for traits of high heritability such as Pilodyn. Within the *E. nitens* population studied, open-pollinated estimates compared well with control-pollinated estimates for all traits.

Genetic parameter estimates from control-pollinated progeny indicate low heritability for growth in *E. globulus* which diminish over time. Dominance effects were low and comparable with additive genetic effects but were site specific. In *E. nitens* heritability for growth is moderate to high, tending to increase over time with significantly low levels of dominance, which diminish over time. Pilodyn has low to moderate heritabilities with low levels of dominance in both species. Moderate levels of heritability were demonstrated for frost resistance in both species, but dominance effects could not be accurately estimated.

The correlation of performance of parents in intra-specific crosses through their General Combining Ability (GCA) is compared with performance in inter-specific hybrids through General Hybridising Ability (GHA). It is shown that there is little or no correlation between GCA and GHA in inter-specific F₁ hybrids for growth or frost resistance, but there was a good correlation for Pilodyn. This indicates that, for growth and frost resistance, there may be different genes, which contribute to expression between species and these may not combine according to classical quantitative genetic theory. In contrast, within *E. globulus* there was very high correlation of within-provenance GCA with between-provenance GHA for growth and Pilodyn, indicating the same genes are acting within the species, regardless of provenance.

It is demonstrated that standard quantitative genetic models do not cope adequately with inter-specific F₁ hybrid populations for growth traits in this case. In addition, the implication for breeding and deployment of inter-specific F₁ hybrids is compromised by the lack of ability to predict performance of potential hybrid combinations from pure species performance of parents.

Publications arising from this project

- Gore, P.L., Potts, B.M., **Volker, P.W.** and Megalos, J. (1990) Unilateral cross-incompatibility in *Eucalyptus*: the case of hybridisation between *E. globulus* and *E. nitens*. *Australian Journal of Botany* 38, 383-94.
- Potts B.M., **Volker P.W.** and Dungey H.S. (1992). Barriers to the production of interspecific hybrids in *Eucalyptus*. In 'Mass Production Technology for Genetically Improved Fast Growing Forest Tree Species.' Proc. IUFRO/AFOCEL Symposium, Bordeaux, France, Sep. 1992 pp. 193-204. (AFOCEL, Paris).
- Dungey, H., **Volker, P.W.**, Potts, B.M. and Owen, J. (1993) Inter-specific hybridisation between *Eucalyptus nitens* and *E. globulus*: preliminary analysis of early growth and frost resistance. In Proceedings of Meeting of Research Working Group One (Forest Genetics) of the Australian Forestry Council held in Canberra, ACT 15-18 Feb. 1995 (ed. M.U. Slee). (Australian National University, Canberra).
- Volker P.W.**, Borralho N.M.G. and Owen J.V. (1994). Genetic variances and covariances for frost tolerance in *Eucalyptus globulus* and *E. nitens*. *Silvae Genetica* 43, 366-372.
- Volker, P.W.** (1995). Evaluation of *Eucalyptus nitens* x *globulus* for commercial forestry. In 'Eucalypt Plantations: Improving Fibre Yield and Quality'. Proc. of CRCTHF-IUFRO Conf. Conference, Hobart, Tasmania, Australia, 19-24 Feb. 1995. (Eds. B.M. Potts, N.M.G. Borralho, J.B. Reid, R.N. Cromer, W.N. Tibbits and C.A. Raymond) pp. 222-225. (CRC for Temperate Hardwood Forestry, Hobart).
- Potts, B.M., **Volker, P.W.**, Hodge, G.R., Borralho, N.M.G., Hardner, C.H. and Owen, J.V. (1995). Genetic limitations to the exploitation of base populations of *Eucalyptus globulus* ssp. *globulus*. In 'Eucalypt Plantations: Improving Fibre Yield and Quality'. Proc. of CRCTHF-IUFRO Conf. Conference, Hobart, Tasmania, Australia, 19-24 Feb. 1995. (Eds. B.M. Potts, N.M.G. Borralho, J.B. Reid, R.N. Cromer, W.N. Tibbits and C.A. Raymond) pp. 217-221. (CRC for Temperate Hardwood Forestry, Hobart).
- Vaillancourt, R.E., Potts, B.M., Watson, M., **Volker, P.W.**, Hodge, G.R., Reid, J.B. and West, A.K. (1995). Detection and prediction of heterosis in *Eucalyptus globulus*. *Forest Genetics* 2, 11-19.
- Hodge G.R., **Volker P.W.**, Owen J.V. and Potts B.M. (1996). A comparison of genetic information from open-pollinated and control-pollinated progeny tests in two eucalypt species. *Theoretical and Applied Genetics* 92, 53-63.
- Potts, B.M., **Volker, P.W.**, Tilyard, P.A. and Joyce, K. (2000). The genetics of hybridisation in the temperate *Eucalyptus*. In 'Hybrid Breeding and Genetics of Forest Trees'. Proc. of QFRI/CRC-SPF Symposium, 9-14 April 2000, Noosa, Queensland, Australia. (Eds. Dungey, H.S., Dieters, M.J. and Nikles, D.G.) pp. 200-211. (Queensland Department of Primary Industries, Brisbane)

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