

Mixed-species plantations of nitrogen-fixing and non-nitrogen-fixing trees



David Ian Forrester June 2004

A thesis submitted for the degree of Doctor of Philosophy of The Australian National University.

STATEMENT OF ORIGINALITY

This thesis is an original piece of work and does not contain the work of another individual except where acknowledged.

The results of Chapter 6 (Growth dynamics of a mixed-species plantation of *Eucalyptus globulus* ssp. *pseudoglobulus* and *Acacia mearnsii*) were published in Forrester et al., 2004 and the co-authors of the paper helped to write this chapter.

The statistical analyses of Chapter 8 (Effects of changing the supply of nitrogen, phosphorus and water on growth and interactions between *Eucalyptus globulus* and *Acacia mearnsii* in a pot trial) were carried out by Dr Jeff Wood (Statistical Consulting Unit, The Australian National University) after discussing the analyses with me.

Contributions including professional advice and help with data collection from others is detailed in the acknowledgments.

David Forrester
The Australian National University
June 28, 2004

Acknowledgments

I would like to thank my supervisors, Professor Jürgen Bauhus and Dr's Annette Cowie, Ryde James and John Evans. Jürgen has been a mentor to me, not only for this PhD but also prior to this when I was an undergraduate forestry student. I enjoyed and learnt a great deal from the time that we have worked together. Annette's supervision and guidance is also much appreciated. Annette's attention to detail and our discussions about experimental designs and methodologies for various sections of this thesis were particularly useful. Ryde and John also provided valuable advice and encouragement throughout the project.

Dr's Marcus Schortemeyer, John Brockwell, Partap Khanna and Chris O'Hara, Professor William Stock and Suzette Searle provided valuable professional advice that is greatly appreciated.

Thankyou also to Matt Forrester, Aaron van Winden, Robert Forrester, Heather Forrester, Kris Jacobsen, John Smith, Hery Suhartoyo, Wenhua Xiang, Julia Dordel, John Kane, Andrew Britton, John Marsh, Wanda Pienkowski, Julie Davis, Mauro Davanzo, Ljube Cvetkoski, Luke Wensing, for technical support with field and lab work.

I would like to thank the staff and students of the School of Resources, Environment and Society at The Australian National University who have helped me with this project. I would also like to thank the staff and students of the Institute for Silviculture at the University of Freiburg in Germany, who made me feel very welcome during the final stages of this work.

Thankyou also to FWPRDC (PG01.3102), CSIRO Forestry and Forest Products, the CRC for Greenhouse Accounting, CSIRO Plant Industry, South East NSW Private Forestry, ACT Forests and Harris Daishowa for financial assistance and the use of study sites.

Help with the statistical design and data analyses of parts of this study from Robert Forrester and Jeff Wood is most gratefully acknowledged.

Finally, thank you to my family, Jennifer, Matt, my parents Heather and Robert, relatives and friends for your support.

Abstract

Mixed-species plantations of eucalypts and acacias have the potential to improve stand productivity over that of respective monocultures through the facilitative effect of nitrogen-fixation by acacias, and increased resource capture through above- and belowground stratification. However, growth in mixed-species plantations may not be improved compared to that of monocultures when competitive interactions outweigh the effects of improved nutrient availability and resource capture. Careful selection of sites and species is therefore critical to successfully improving stand productivity using mixed-species plantations. This study set out to examine some of the processes and interactions that occur in mixed-species plantations, and the effect nutrient and water availability can have on the growth of mixtures.

In three out of four mixed-species field trials examined in this study, growth was not increased in mixtures compared to monocultures. However, in the fourth field trial, heights, diameters, stand volume and aboveground biomass were higher in mixtures of *E. globulus* and *A. mearnsii* from 3-4 years after planting.

The range in outcomes from mixing species in these four trials shows that a fundamental understanding of the underlying processes is required to enable a greater predictive capacity for the circumstances under which mixtures will be successful. Therefore the growth dynamics, processes and interactions were examined in the mixtures of *E. globulus* and *A. mearnsii*. The difference in productivity between mixtures and monocultures in this trial increased with time up to age 11 years, when 1:1 mixtures contained twice the aboveground biomass of *E. globulus* monocultures. The positive growth response of trees in mixture compared to monocultures was the result of accelerated rates of nutrient cycling, a shift in C allocation and reductions in light competition through canopy stratification.

Nitrogen contents of foliage and soil clearly showed that *A. mearnsii* influenced the N dynamics in this trial. If these changes in N contents were due to N fixation by *A. mearnsii*, then about 51 and 86 kg N ha⁻¹ yr⁻¹ was fixed in the 1:1 mixtures and *A. mearnsii* monocultures, respectively. Nitrogen fixation was also examined using the natural abundance method. The $\delta^{15}\text{N}$ values of foliage collected at 10 years were

grouped according to the mycorrhizal status of the host plant. Therefore the discrimination of ^{15}N during transfer from mycorrhizae to the host plant appeared to vary with mycorrhizal status, and the natural abundance of ^{15}N was not used to quantify N fixation.

Rates of N and P cycling in litterfall were significantly higher in stands containing at least 25% *A. mearnsii* ($>31 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and $>0.68 \text{ kg P ha}^{-1} \text{ yr}^{-1}$) compared to *E. globulus* monocultures ($24 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and $0.45 \text{ kg P ha}^{-1} \text{ yr}^{-1}$). Rates of litter decomposition and N and P release were about twice as high in 1:1 mixtures compared to *E. globulus* monocultures and were even higher in *A. mearnsii* monocultures. It is therefore important to select N-fixing species that are capable of cycling nutrients quickly between the plant and soil, and that have readily decomposable litter.

The total belowground C allocation was not significantly different between mixtures and monocultures (14 to $16 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). However, since aboveground net primary production was greater in 1:1 mixtures, the changes in nutrient availability appears to have increased total productivity (both above- and belowground), and reduced the proportion of C allocated belowground in mixtures compared to *E. globulus* monocultures.

In a pot trial containing mixtures of *E. globulus* and *A. mearnsii* both species grew larger in mixture than in monoculture at low N levels, and mixtures were more productive than monocultures. However, at high N levels, *E. globulus* suppressed *A. mearnsii* and mixtures were less productive than *E. globulus* monocultures. Similar effects were found for high and low levels of P.

Therefore resource availability can have a strong influence on the interactions and growth of mixtures. The productivity of mixtures may only be increased on sites where the resource for which competition is reduced in mixture is a major limiting growth resource. For example, if N is not a limiting growth factor then an increase in N availability from N-fixation may not increase growth, and the N-fixing species may compete for other resources such as soil P, moisture or light.

This study has shown that mixtures containing a N-fixing trees and a non-N-fixing trees can be more productive than monocultures, but that this increase in productivity will only occur on certain sites. Examination of the growth, interactions and processes that occurred in mixtures in this study provide useful information that can aid the selection of species combinations and sites.

Table of contents

Acknowledgments.....	i
Abstract.....	iii
List of figures.....	ix
List of tables.....	xii
1. Introduction.....	1
2. Literature review.....	4
2.1 Ecological theory.....	4
2.1.1 Niche separation.....	4
2.1.2 Symmetry of competition in mixed stands.....	4
2.1.3 Interspecific and intraspecific competition.....	5
2.2 Interactions in mixed stands.....	8
2.2.1 Competitive reduction.....	8
2.2.1.1 Canopy stratification.....	8
2.2.1.2 Root stratification.....	15
2.2.2 Facilitation.....	17
2.2.2.1 Litter fall and nutrient cycling.....	18
2.2.2.2 Nitrogen fixation.....	20
2.2.2.3 Physiological and morphological changes in response to improved nitrogen nutrition.....	27
2.3 Effects of site quality on species interactions.....	29
3. Productivity of mixed-species plantations containing N-fixing and non-N-fixing trees.....	31
3.1 Methodology.....	31
3.1.1 Study sites and experimental designs.....	31
3.1.2 Growth measurements.....	34
3.1.3 Foliar nutrition.....	38
3.1.4 Statistical techniques.....	38
3.2 Results.....	39
3.2.1 Eleven-year-old trial of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> (Trial 1).....	39
3.2.2 Five-year-old trial of <i>Eucalyptus nitens</i> and <i>Acacia mearnsii</i> (Trial 2).....	45
3.2.3 Two-year-old trial of <i>Eucalyptus saligna</i> and <i>Acacia mearnsii</i> (Trial 3).....	50
3.2.4 Five year old trial of <i>Pinus radiata</i> with <i>Acacia mearnsii</i> , <i>Acacia decurrens</i> , <i>Eucalyptus benthamii</i> or <i>Eucalyptus smithii</i> (Trial 4).....	51
3.3 Discussion.....	55
3.3.1 Mixtures of <i>Eucalyptus</i> and <i>Acacia mearnsii</i>	55
3.3.2 Mixtures of <i>Pinus radiata</i> with <i>Acacia mearnsii</i> , <i>Acacia decurrens</i> , <i>Eucalyptus benthamii</i> or <i>Eucalyptus smithii</i> (Trial 4).....	59
3.4 Conclusions.....	62
4. Nitrogen fixation in a mixed-species plantation of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	64
4.1 Methodology.....	64
4.1.1 Study site and experimental design.....	64
4.1.2 Data collection.....	64
4.1.3 Chemical analysis.....	67
4.1.4 Statistical techniques.....	67
4.2 Results.....	67
4.3 Discussion.....	73
4.3.1 Nitrogen fixation.....	73
4.3.2 Discrimination of ¹⁵ N by different mycorrhizal groups.....	73
4.4 Conclusions.....	77
5. Nutrient cycling in a mixed-species plantation of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	78
5.1 Methodology.....	78
5.1.1 Study site and experimental design.....	78
5.1.1.1 Climate.....	78
5.1.2 Litterfall.....	80
5.1.3 Nutrient use efficiency.....	80

5.1.4	Rate of litter decomposition and nitrogen and phosphorus release	81
5.1.5	Chemical analysis	82
5.1.6	Statistical techniques	82
5.2	Results	83
5.2.1	Seasonal influence on litterfall and litter nutrition	83
5.2.2	Influence of species composition and density on litterfall and litter nutrition	85
5.2.3	Litter decomposition and nutrient release	88
5.2.4	Nutrient use efficiency	89
5.3	Discussion	90
5.3.1	Nitrogen and phosphorus cycling through litterfall	90
5.3.2	Forest floor litter mass, rates of litter decay and nutrient release	91
5.3.3	N and P use efficiency	94
5.3.4	Conclusions	95
6.	Growth dynamics of a mixed-species plantation of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	96
6.1	Methodology	96
6.1.1	Study site and experimental design	96
6.1.2	Growth measurements	96
6.1.3	Statistical techniques	99
6.2	Results	99
6.2.1	Mortality	99
6.2.2	Height growth	100
6.2.3	Diameter growth	102
6.2.4	Aboveground biomass and stem volume	104
6.3	Discussion	108
6.3.1	Ecological interactions	108
6.3.2	Competition and competitive reduction	108
6.3.3	Facilitation	110
6.3.4	Silvicultural implications	110
6.4	Conclusions	112
7.	Carbon allocation in a mixed-species plantation of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	113
7.1	Methodology	113
7.1.1	Soil surface respiration	114
7.1.2	Litterfall and forest floor litter	115
7.1.3	Carbon in coarse roots and aboveground net primary production	115
7.1.4	Fine-root and soil carbon	117
7.1.5	Carbon contents of plant material	118
7.1.6	Statistical techniques	119
7.2	Results	119
7.3	Discussion	127
7.3.1	Total belowground carbon allocation	127
7.3.2	Proportion of carbon allocated above- and belowground	128
7.3.3	Soil surface CO ₂ efflux and litterfall carbon	130
7.3.4	Changes in root, litter layer and soil carbon pools	132
7.4	Conclusions	134
8.	Effects of changing the supply of nitrogen, phosphorus and water on growth and interactions between <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> in a pot trial	136
8.1	Methodology	136
8.1.1	Species selection and seed source	136
8.1.2	Experimental design and treatments	137
8.1.3	Seed propagation and seedling establishment	139
8.1.4	Data collection	140
8.1.5	Statistical techniques	143
8.2	Results	143
8.2.1	Biomass and leaf area	143
8.2.2	Nitrogen and phosphorus in soils and plants	150
8.2.3	Resource use efficiency	155
8.3	Discussion	157
8.3.1	Effects of species combination at low N	157
8.3.2	Effects of species combination at high N	159

8.3.3	Effects of species combination at high and low P.....	159
8.3.4	Implications.....	161
8.4	Conclusions.....	162
9.	Discussion and synthesis.....	164
9.1	Processes and interactions in mixed-species plantations.....	164
9.1.1	Facilitation - N fixation, nutrient cycling and changes in C allocation.....	164
9.1.2	Increased light capture	168
9.2	Site selection	169
9.3	Examining and managing processes and interactions in mixtures	170
9.4	Conclusions.....	171
References		172

List of figures

Figure 2.1. The yield of mixtures containing species A and B, where the proportion of each species in mixture changes from no individuals (0) up to x individuals and the total number of individuals remains constant (a-d). Part (e) shows the yield-density function of both species and the combined yield if these species were planted in mixture and experienced no interspecific competition (adapted from Harper (1977)).	6
Figure 3.1. Diameter distributions of (a) <i>Eucalyptus globulus</i> and (b) <i>Acacia mearnsii</i> at 11 years of age in the monocultures and mixtures at the 2 x 3.3 m spacing.	44
Figure 3.2. Diameter distributions of (a) <i>Eucalyptus nitens</i> and (b) <i>Acacia mearnsii</i> at five years of age in the monocultures and mixtures.	49
Figure 3.3. Diameter distributions of (a) <i>Pinus radiata</i> and (b) other species at 4.5 years of age in the monocultures and mixtures.	53
Figure 4.1. Box and whiskers plot of soil $\delta^{15}\text{N}$ values and leaf $\delta^{15}\text{N}$ values of plants from different mycorrhizal groups at age ten years in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> .	68
Figure 5.1. Monthly and annual precipitation at Cann River, Victoria, Australia. Data provided by the Department of Sustainability and Environment, Victoria.	79
Figure 5.2. Mean monthly minimum and maximum temperatures at Cann River, Victoria, Australia. Data provided by the Department of Sustainability and Environment, Victoria.	79
Figure 5.3. Litterfall mass of (a) <i>Eucalyptus globulus</i> , (b) <i>Acacia mearnsii</i> and (c) Total (both species combined) collected for over two years in mixtures and monocultures.	84
Figure 5.4. Relationship between annual litterfall (averaged over two years from 9.25 to 11.25 years) and aboveground biomass, across all species proportion, at 11 years of age.	87
Figure 5.5. Forest floor litter mass at different times during the experimental period.	89
Figure 6.1. Height growth of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> in the monocultures and mixtures at the 2 x 3.3 m spacing to age 11 years.	101

Figure 6.2. Diameter growth of (a) <i>Eucalyptus globulus</i> and (b) <i>Acacia mearnsii</i> to age 11 years in the monocultures and mixtures at the 2 x 3.3 m spacing.	103
Figure 6.3. Development of aboveground stand biomass to age 11 years in the monocultures and mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> at the 2 x 3.3 m spacing.	105
Figure 6.4. Mean annual increment of stand aboveground biomass ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) to age 11 years in the monocultures and mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> at the 2 x 3.3 m spacing.	106
Figure 6.5. Periodic annual increment of stand aboveground biomass ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) to age 11 years for (a) <i>E. globulus</i> , (b) <i>A. mearnsii</i> and (c) both species combined (Total) at the 3 x 3.3 m spacing.	107
Figure 7.1. Relationship between annual litterfall C (F_A) and annual soil surface respiration C (F_S) between year 10.5 and 11.5 years of age.....	120
Figure 7.2 Climatic data and soil surface respiration measured over the experimental period.	121
Figure 7.3. Relationship between annual litterfall C (F_A) (from year 10.5 to 11.5) and aboveground biomass C at year 11.5 ($P = 0.01$).....	124
Figure 7.4. Relationship between annual litterfall C (F_A) and annual aboveground C increment between year 10.5 and 11.5 years of age ($P = 0.978$) and between year 8.5 and 10.5 years of age ($P = 0.223$).....	124
Figure 7.5. Differences in annual coarse root C increment estimated using techniques described in Section 7.1.3 compared to that estimated using the allometric equation developed by Misra et al. (1998) (calculated for year 10.5 to 11.5).....	125
Figure 7.6. The effect of using different estimates of various components of TBCA to calculate TBCA, compared to TBCA calculated as $\text{TBCA} = F_S - F_A + \Delta C_R$ (for the year 10.5 to 11.5).	126
Figure 7.7. The effect of overestimating or underestimating (by 10%) different components of TBCA as compared to TBCA calculated as $\text{TBCA} = F_S - F_A + \Delta C_R$ (calculated for year 10.5 to 11.5), in monocultures and mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	127
Figure 8.1. Relative yield of aboveground biomass for (a) <i>E. globulus</i> at low and high levels of N, (b) <i>A. mearnsii</i> at low and high levels of N, (c) <i>E.</i>	

<i>globulus</i> at low and high levels of P and (d) <i>A. mearnsii</i> at low and high levels of P.	148
--	-----

List of tables

Table 2.1. Productivity of mixed species stands of trees in field and pot trials.....	10
Table 3.1. Details of trial designs and sites.....	32
Table 3.2. Allometric equations for aboveground biomass and stem volume estimated from diameter (D; cm) and height (H; m).	36
Table 3.3. Survival (%) at age 11 years in monocultures and mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	40
Table 3.4. Average height (H) of all trees or only the largest 200 stems ha ⁻¹ at age 11 years in the monocultures and mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	40
Table 3.5. Average diameter (D) of all trees or only the largest 200 stems ha ⁻¹ at age 11 years in the monocultures and mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	41
Table 3.6. Aboveground stand biomass of all trees or only the largest 200 stems ha ⁻¹ at age 11 years in the monocultures and mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	42
Table 3.7. Stand volume of all trees or only the largest 200 stems ha ⁻¹ at age 11 years in the monocultures and mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	43
Table 3.8. Survival (%) up to age five years of <i>Eucalyptus nitens</i> and <i>Acacia mearnsii</i> in the monocultures and mixtures.....	45
Table 3.9. Height (H) and diameter (D) at age five years in the monocultures and mixtures of <i>Eucalyptus nitens</i> and <i>Acacia mearnsii</i>	45
Table 3.10. Aboveground stand biomass (Mg ha ⁻¹) up to age five years in the monocultures and mixtures of <i>Eucalyptus nitens</i> and <i>Acacia mearnsii</i> ..	46
Table 3.11. Stand volume (underbark; m ³ ha ⁻¹) up to age five years in the monocultures and mixtures of <i>Eucalyptus nitens</i> and <i>Acacia mearnsii</i> ..	47
Table 3.12. Relative yield of stand aboveground biomass and volume up to age five years in the monocultures and mixtures of <i>Eucalyptus nitens</i> and <i>Acacia mearnsii</i>	47
Table 3.13. Height (H), diameter (D), stand aboveground biomass and volume (underbark) of largest 200 stems ha ⁻¹ at age five years in the monocultures and mixtures of <i>Eucalyptus nitens</i> and <i>Acacia mearnsii</i> ..	48

Table 3.14. Survival, height (H), diameter (D) and height to diameter ratio at age two years in the monocultures and mixtures of <i>Eucalyptus saligna</i> and <i>Acacia mearnsii</i> .	50
Table 3.15. Stand aboveground biomass and volume (overbark) at age two years in the monocultures and mixtures of <i>Eucalyptus saligna</i> and <i>Acacia mearnsii</i> .	51
Table 3.16. Foliage nitrogen and phosphorus concentrations at age two years in the monocultures and mixtures of <i>Eucalyptus saligna</i> and <i>Acacia mearnsii</i> .	51
Table 3.17. Survival, height (H), diameter (D) and height to diameter ratio at age 4.5 years in the monocultures of <i>P. radiata</i> and mixtures of <i>P. radiata</i> with <i>A. decurrens</i> , <i>A. mearnsii</i> , <i>E. benthamii</i> and <i>E. smithii</i> .	52
Table 3.18. Aboveground stand biomass, volume (overbark) and relative yields at age 4.5 years in the monocultures of <i>P. radiata</i> and mixtures of <i>P. radiata</i> with <i>A. decurrens</i> , <i>A. mearnsii</i> , <i>E. benthamii</i> and <i>E. smithii</i> .	54
Table 3.19. Foliage nitrogen and phosphorus concentrations at age five years in the monocultures of <i>P. radiata</i> and mixtures of <i>P. radiata</i> with <i>A. decurrens</i> , <i>A. mearnsii</i> , <i>E. benthamii</i> and <i>E. smithii</i> .	55
Table 4.1. Mycorrhizal status of different species sampled in the mixed-species trial of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> .	66
Table 4.2. Leaf $\delta^{15}\text{N}$ values of plants from different mycorrhizal groups at age ten years in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> .	68
Table 4.3. Leaf and leaf litter $\delta^{15}\text{N}$ and N concentrations and age two and ten years in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> .	69
Table 4.4. Leaf N concentrations (mg g^{-1}) of different mycorrhizal groups at age ten years in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> .	70
Table 4.5. Foliage N and P contents at the level of the tree (kg tree^{-1}) or at the level of the stand (kg ha^{-1}) at the 3 x 3.3 m spacing.	71
Table 4.6. Soil $\delta^{15}\text{N}$ values at age ten years in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> .	72
Table 4.7. Soil N concentrations (mg g^{-1}) at age ten years in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> .	72

Table 5.1. Litter P concentrations (mg g^{-1}) in the monocultures and 50E:50A mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> during periods of high and low litterfall, at the 2 x 3.3 m spacing.	85
Table 5.2. Nitrogen and phosphorus concentrations of litterfall (mg g^{-1}) in the monocultures and mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> from age 9.25 to 10.25 years.	86
Table 5.3. Leaf and leaf litter C: N ratios at age two and ten years in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	86
Table 5.4. Annual litterfall ($\text{Mg ha}^{-1} \text{ yr}^{-1}$), forest floor litter mass (Mg ha^{-1}), N and P content (kg ha^{-1}) and rates of decomposition ($k; \text{yr}^{-1}$) and N and P release from forest floor litter in the monocultures and mixtures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> from age 9.25 to 11.25 years.....	87
Table 5.5. Nutrient concentrations (mg g^{-1}) of forest floor litter at different sampling times in <i>A. mearnsii</i> monocultures, at the 3 x 3.3 m spacing.	88
Table 5.6. Nitrogen and phosphorus use efficiencies (annual net primary production in Mg ha^{-1} per kg ha^{-1} nutrient in annual litterfall) in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	89
Table 6.1. Allometric height equations for <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	98
Table 6.2. Stocking of large trees, skewness of diameter distribution and height to diameter (H/D) ratio for <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> at the 2 x 3.3 m spacing at age 11 years.	104
Table 7.1. Carbon quantities ($\text{kg C ha}^{-1} \text{ yr}^{-1}$) for the components of total belowground carbon allocation and aboveground net primary production in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	122
Table 7.2. Soil surface respiration ($\text{kg C m}^{-2} \text{ yr}^{-1}$) for different microsites (Flat and Mound) in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	123
Table 7.3. Soil moisture content (gravimetric, %; 0-5 cm) at different sampling times in mixtures and monocultures of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	123
Table 7.4. Total below ground C allocation (TBCA) and annual soil surface respiration C (F_s) estimated from annual litterfall C (F_A) using relationships derived from a global data set by Raich and Nadelhoffer	

(1989) where $TBCA = 1300 + 1.92 F_A$ ($R^2 = 0.52$, $P < 0.001$), and $F_S = 1300 + 2.92 F_A$ ($R^2 = 0.71$, $P < 0.00001$).	132
Table 8.1. Provenance data for <i>Eucalyptus globulus</i> ssp. <i>globulus</i> and <i>A. mearnsii</i> seed.	137
Table 8.2. Fertiliser applied to the pot trial of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	138
Table 8.3. Nutrient concentrations of soil substrate (two parts coarse river sand to one part subsoil) used in the experiment.	139
Table 8.4. P values for all significant treatment effects for all measured variables.	144
Table 8.5. Aboveground biomass (g) and Relative Yield (RY) of aboveground biomass of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> in mixtures and monocultures at high and low levels of N and P fertiliser.....	146
Table 8.6. Root: shoot ratio of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> in mixtures and monocultures at high and low levels of N and P fertiliser.....	149
Table 8.7. Leaf area (m ²) of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> in mixtures and monocultures at high and low levels of N and P fertiliser.....	149
Table 8.8. The total soil N and P (g pot ⁻¹) in mixtures and monocultures at high and low levels of N and P fertiliser.	150
Table 8.9. Nitrogen concentration (mg g ⁻¹) of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> foliage at 20 weeks of age in mixtures and monocultures at high and low levels of N and P fertiliser, from the medium level of water... ..	151
Table 8.10. Phosphorus concentration (mg g ⁻¹) of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> foliage at 20 weeks of age in mixtures and monocultures at high and low levels of N and P fertiliser, from the medium level of water... ..	151
Table 8.11. Nitrogen concentration (mg g ⁻¹) of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> foliage at 50 weeks of age in mixtures and monocultures at high and low levels of N and P fertiliser.	152
Table 8.12. Phosphorus concentration (mg g ⁻¹) of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> foliage at 50 weeks of age in mixtures and monocultures at high and low levels of N and P fertiliser.	152
Table 8.13. Nitrogen in aboveground biomass (g) of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> in mixtures and monocultures at high and low levels of N and P fertiliser.....	153

Table 8.14. Phosphorus in aboveground biomass (g) of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> in mixtures and monocultures at high and low levels of N and P fertiliser.....	154
Table 8.15. Nitrogen and phosphorus (g) in plant biomass (above- and belowground biomass of both plants in a pot) in mixtures and monocultures at high and low levels of N and P fertiliser	154
Table 8.16. The percent of total system N or P (N or P in soil and plant biomass) in plant biomass in mixtures and monocultures at high and low levels of N and P fertiliser.....	155
Table 8.17. Nitrogen use efficiency (aboveground biomass in g / nitrogen in aboveground plant biomass in g) of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> in mixtures and monocultures at high and low levels of N and P fertiliser.....	156
Table 8.18. Phosphorus use efficiency (aboveground biomass in g / phosphorus in aboveground plant biomass in g) of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> in mixtures and monocultures at high and low levels of N and P fertiliser.....	156
Table 8.19. Leaf area ratio (LAR; aboveground biomass in g / leaf area in m ²) of <i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> in mixtures and monocultures at high and low levels of N and P fertiliser.	157