PLANTING DENSITY EFFECTS ON WATER USE EFFICIENCY OF TREES AND PASTURE IN AN AGROFORESTRY EXPERIMENT

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ABSTRACT

Water use of trees and pasture were studied at three tree densities in an agroforestry experiment where trees were planted at densities of approximately 2150, 304, and 82 stems/ha in a Nelder design. Tree transpiration and pasture evaporation were related to their respective biomass production to estimate water use efficiencies at each tree density over a 2-year study period throughout 1985 and 1986.

Tree planting density was found to modify productivity and water use of both trees and pasture. During dry conditions biomass production per tree was lowest at high tree densities being 19 g/day compared with 69 and 45 g/day at medium and low tree densities respectively. Transpiration rates per tree were also lowest at high tree densities being 12.9×10^{-3} m^3/day compared with 54.5 and 72.9×10^{-3} m^3/day from medium and low densities respectively. However, water use efficiency was found to be highest in the densely planted trees where mean values for 1985 and 1986 were 4.6 and 3.9 kg/m^3 respectively in 1986.

Pasture evaporation was generally lowest under the densely planted trees where soil water contents in the pasture root zone were lowest. Pasture production was greatest at the intermediate tree density and this was associated with a higher water use efficiency than was found from pasture under high and low tree densities.

Keywords: agroforestry; planting density; transpiration; water use efficiency; *Eucalyptus grandis.*

INTRODUCTION

Water stress has been shown to reduce plant growth (Boyer 1968; Acevedo *et al.* 1971), so quantitative studies of water loss from vegetation are important in Australia, where water is frequently limiting. Water use efficiency, defined as the ratio of biomass produced per unit volume of water evaporated, is also important under water-limiting conditions. Potential dry matter production is thought to be approximately linearly related to the amount of radiation intercepted (Jarvis & Leverenz 1983; Linder 1985). The efficiency with which intercepted radiation is used for growth will be modified by

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the effects of plant water stress on photosynthesis, as discussed by Kozlowski (1982). Dry matter production is also thought to be directly proportional to the volume of water transpired (Monteith 1981).

Transpiration (T_c) from continuous canopies is determined by a number of factors described by the Penman-Monteith equation (Monteith 1965). Radiation, vapour pressure deficit, windspeed, and temperature determine the atmospheric demand causing evaporation. As tree density in an agroforestry system decreases, mutual interference between trees both above and below the soil surface will decrease and the magnitude of the parameters controlling transpiration will be modified. More specifically, as tree density decreases, there is likely to be less competition for water by root overlap between trees, mutual shading will be reduced, and canopy boundary layer conductance will be increased. In an agroforestry system, tree density will also affect transpiration of the associated crop or pasture species by modifying microclimate, and trees may also compete with the associated species for water, both by canopy interception of rainfall, and by root uptake of soil water. Modification of the environment by varying tree density is therefore likely to have a complex effect on biomass production and water use efficiency of components of agroforestry systems, through effects on both photosynthesis and water use.

Biomass production of trees and crops in agroforestry can generally be estimated with relative ease. However, overlapping root systems and spatial variation in microclimate make application of standard methods to estimate water use from the separate components less straightforward. There is, therefore, a dearth of published information concerning the water use and water use efficiency of components of agroforestry systems, making it difficult to assess any beneficial or detrimental effects on water use of growing trees and crops in intimate mixtures.

The study reported here formed part of a broader experiment which aimed to identify problems in the development of stable agroforestry systems in a subtropical environment. The experiment focused on interactions between trees and pasture at a continuous range of tree densities. Experimental design and methodology used to estimate tree and pasture production have been reported by Cameron *et al.* (1989). Evaporation measured from pasture growing within lysimeters in the same experiment has been reported by Eastham & Rose (1988). Combined evaporation from pasture and trees, expressed per unit land area, at three of the tree densities has been reported by Eastham *et al.* (1988). Simultaneous studies on rooting and water uptake patterns were undertaken and reported by Eastham & Rose (1990) and Eastham *et al.* (1990). Objectives of this study were to estimate separately tree transpiration and evaporation from pasture not contained within lysimeters at three tree densities. A further objective was to bring together water use and biomass production estimates to elucidate the effect of tree density on the water use efficiency of both tree and pasture components of the system.

METHODS

Experimental Site

The experiment was conducted at the CSIRO Samford Pasture Research Station, approximately 20 km north-west of Brisbane in Queensland, Australia (27° 32′S, 152°

53′ E, altitude 50 m). Experimental design and methodology have been described fully by Cameron *et al.* (1989). Briefly, *Eucalyptus grandis* Maiden was planted at a range of tree densities in a "Nelder design" (Nelder 1962) into pasture dominated by *Setaria sphacelata* cv. Kazungula (Fig. 1). Eight concentric rings of trees were planted at radii ranging from 4.4 to 44.3 m as indicated in Table 1. An additional outer ring was planted as a guard ring and the centre of the circle was planted with a series of smaller rings to form a guard. Each of the experimental rings contained 18 trees planted at equal distances around the circumference, giving a range from 42 to 3580 trees in equivalent planting density (Table 1). Trees in rings 2, 5, and 7 were selected for this study, providing approximate densities of 2150, 304, and 82 stems/ha referred to as the high (HD), medium (MD), and low (LD) tree densities, respectively.

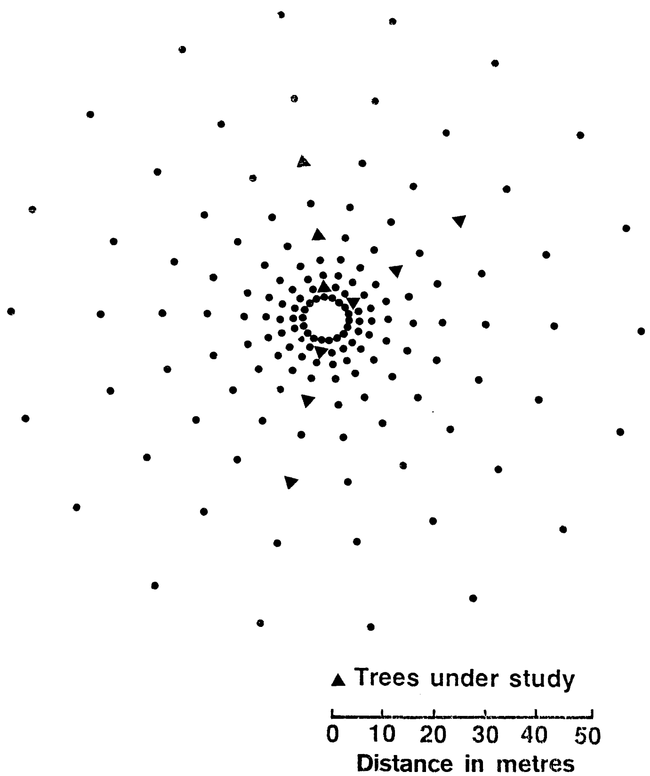

FIG. 1 — Distribution of trees in the Nelder design.

Biomass Production of Trees and Pasture

The methods and results of tree and pasture biomass production measurement have been reported fully by Cameron *et al.* (1989). Briefly, tree biomass was estimated from stem volumes using a linear relationship between stem volume and tree biomass determined by destructive sampling of trees. Tree stems were assumed to be of conical shape, and tree height and stem diameter at breast height (dbh, 1.3 m) were measured

TABLE 1–Planting distances and approximate tree densities in the Nelder design

	Ring No.							
	1	2*	3	4	5*	6	7*	8
Radius (m)	4.4	6.2	8.6	11.9	16.5	23.0	31.9	44.3
Distance to the next ring (m)	1.8	2.4	3.3	4.6	6.5	8.9	12.4	–
Density (stems/ha)	3580	2150	1140	594	304	158	82	42

* Indicates rings studied

at approximately 6-weekly intervals allowing calculation of stem volumes. Standing biomass of pasture was estimated at each tree spacing in spring (September-October) and autumn (April-May) of 1985 and 1986 using BOTANAL sampling procedures (Tothill *et al.* 1978) described more fully by Cameron *et al.* (1989).

Tree and Pasture Water Use

Tree transpiration and pasture evaporation were studied at the three selected tree densities in the Nelder design. As described by Eastham *et al.* (1988), estimates of combined evaporation from trees and pasture were made using the soil water balance equation with changes in soil water content measured by neutron moisture meter (NMM) at approximately fortnightly intervals for a period of 2 years, commencing on 12 December 1984 for HD and MD, but not until 20 March 1985 at LD. The combined evaporation from trees and pasture (E) may be separated into its individual components:

$$E = G + T + I \qquad (1)$$

where G is pasture evaporation, T is tree transpiration, and I is tree canopy interception, with each component expressed in millimetres per day. With pasture evaporation and tree canopy interception estimated as described below, tree transpiration was calculated from Equation (1). Transpiration was expressed as volume transpired per day (T_v m³/day) by multiplying by the area $\pi\ r_m{}^2$, where r_m is the midpoint between trees at each studied density (1.2, 3.25, and 6.2 m at HD, MD, and LD, respectively).

Pasture evaporation was estimated from mean soil water contents measured by NMM in the upper 0.3 m of the pasture root zone, using previously established relationships between soil water content and pasture evaporation rate. The relationships used were determined from small lysimeters (0.15 m square, 0.30 m deep) containing pasture installed at the three tree densities over the study period. These relationships and methods used in determining them have been described fully by Eastham & Rose (1988).

Tree canopy interception was estimated using a series of rain gauges (12 cm diameter) installed to measure precipitation (P) and throughfall (F) beneath the tree canopy. The mean reading from four rain gauges installed in the open and monitored daily was used to measure P. A further three rain gauges were installed beneath the eucalypt canopy at each tree density to measure daily throughfall resulting from one or more rainfall events occurring in any 24 hours. Throughfall, taken as the mean of the nine rain gauges beneath the canopy was subtracted from precipitation to estimate interception loss. I was calculated from P using a single linear relationship between I and P found to apply for the three studied tree densities:

$$I = 0.13\,P + 0.70 \qquad (2)$$

The correlation coefficient for this relationship obtained from 151 measurement periods of 24 hours with rainfall was 0.94. Rainfall was excluded from this regression when rainfall was insufficient to saturate the canopy (i.e., F was zero). Interception loss was expressed as millimetres per day by dividing the total interception loss occuring between NMM measurements, by the number of days between measurements. Since (P–F) is the sum of interception loss and stemflow, interception loss will be overestimated by assuming it is equal to (P–F). Stemflow in eucalypts has been shown to vary between species (Westman 1978), with Feller (1981) reporting published eucalypt stemflow values ranging from 0.5 to 7.0% of annual precipitation. However, regression coefficients for the relationship between rainfall and interception found in these experiments were similar to those found by Dunin *et al.* (1985) for young eucalypt forest, determined by lysimetry.

Calculation of Tree and Pasture Water Use Efficiencies

In this study, tree water use efficiency was expressed as the volume of water transpired per unit dry matter produced, and may therefore be considered a "transpiration efficiency". Evaporation of intercepted water was omitted from the calculation, as it is likely to vary considerably with time, depending on the frequency of rainfall and environmental conditions. Evaporation of intercepted water from pasture was not measured in these experiments, although pasture interception losses may be expected to be small compared with losses from trees (Rutter 1975). Pasture evaporation as estimated by lysimeters in this study will also include a soil evaporation component, so pasture water use for calculating water use efficiency will be the sum of transpiration, soil evaporation, and evaporation of intercepted water.

RESULTS AND DISCUSSION

Pasture Evaporation

Pasture evaporation during 1985 and 1986 under each of the three tree densities is shown in Fig. 2. At LD there are no data prior to 20 March 1985 when NMM measurements were commenced at this density. Mean soil water content in the upper 0.3 m of the soil profile midway between trees is a good indicator of water content in the pasture root zone since >90% of pasture roots occurred in the upper 0.3 m (Eastham & Rose 1990). These data are given for both 1985 and 1986 in Fig. 3. Maximum monthly mean pan evaporation rates occurred in January in both years of the study, being 6.7 and 6.8 mm/day in 1985 and 1986 respectively. Minimum values were 2.4 mm/day in June 1985 and 3.0 mm/day in July 1986.

Pasture evaporation was generally highest under LD and evaporation and soil water contents were lowest under HD (Fig. 2 and 3), indicating increased competition for

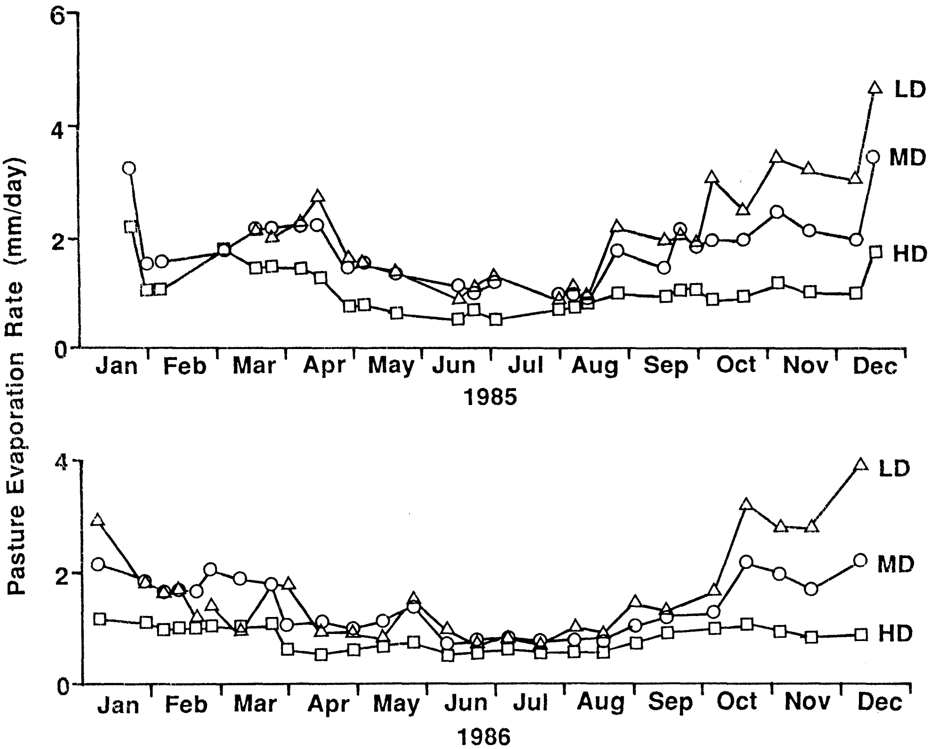

FIG. 2 — Pasture evaporation throughout 1985 and 1986 at the high (□), medium (○), and low (△) tree densities. Average evaporation rates were calculated for 2-weekly periods as described in the text. Symbols are located at the midpoint in time of each measurement period.

water from trees as tree density increased. A drought period occurred between November 1985 and September 1986 during which the total rainfall was 555 mm below normal (Table 2). As a result of the dry conditions, surface soil water contents and pasture evaporation under all three tree densities in 1986 were generally lower than in 1985 (Fig. 2 and 3).

TABLE 2–Monthly rainfall (mm) at the Samford Pasture Research Station

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean*	162.8	159.9	139.0	81.4	65.9	59.9	54.6	32.1	46.0	85.1	91.0	121.6	1099.3
1985	95.2	91.0	150.0	78.7	52.2	43.6	102.7	52.0	53.0	136.9	26.2	81.6	963.1
1986	45.3	41.0	38.3	16.3	74.3	5.7	49.2	46.1	35.5	120.7	145.6	120.5	738.6

* 65-year mean (Cook & Russell 1983)

Pasture Growth and Water Use Efficiency

Pasture biomass production and water use efficiency under each tree density are shown in Table 3. Pasture yields and water use efficiency were consistently highest

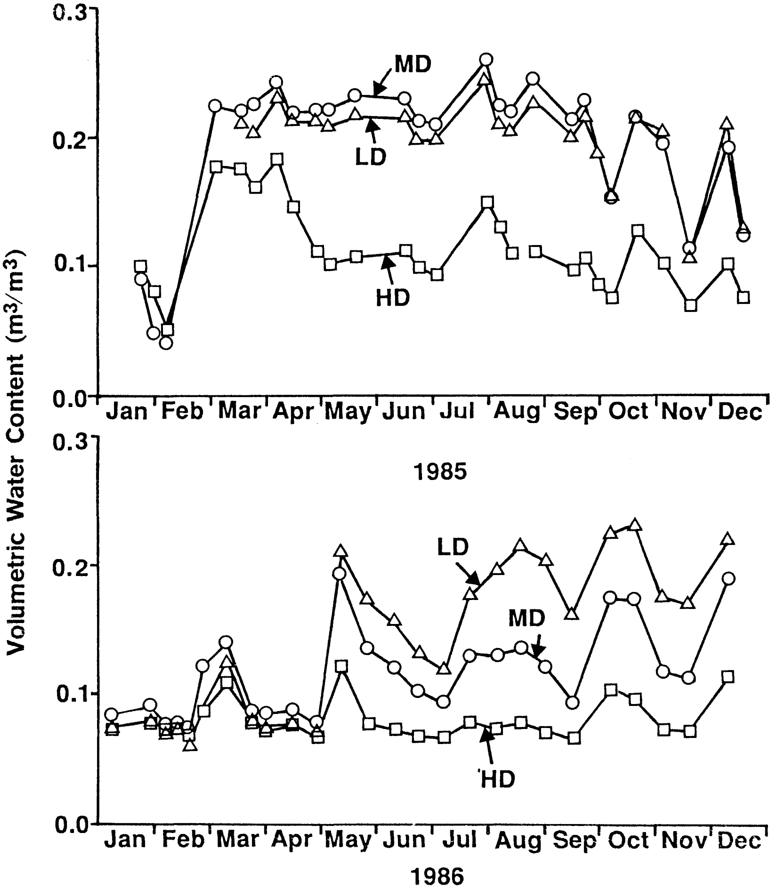

FIG. 3 — Mean soil water contents throughout 1985 and 1986 in the upper 0.3 m of the soil profile, at the midpoint between trees planted at the high (□), medium (○), and low (△) tree densities.

TABLE 3–Pasture production and water use efficiencies of pasture under the high (HD), medium (MD), and low (LD) tree densities for the three sampling periods in 1985 and 1986

Sampling dates	Production (kg/ha)			Water use efficiency (kg/m^3)		
	HD	MD	LD	HD	MD	LD
15.4.85–24.9.85	–545*	432	171	*	0.21	0.08
24.9.85–8.5.86	2153	5578	1500	0.67	1.15	0.30
8.5.86–20.10.86	1088	3906	2478	0.87	1.92	1.29

* Decline in standing biomass occurred at this tree density as a result of mortality

under MD, due in part to a smaller proportion of assimilate allocated to root production, as root:shoot ratios of pasture in May 1986 were 8.5, 2.0, and 3.3 at the HD, MD, and LD respectively (Eastham & Rose 1990). Biomass production and water use efficiency were generally low from pasture under HD where root production was proportionately higher than at other tree densities. This agrees with findings of a number of studies which indicate a decrease in pasture production with increase in tree density (Beale 1973; Anderson & Batini 1979; Percival *et al.* 1984). However, between 24 September 1985 and 8 May 1986, which included a period of drought, pasture production was lowest at LD, probably because of more severe water stress under higher evaporative demand associated with higher radiation at this spacing (Eastham & Rose 1988). Variations in pasture water use efficiency at LD may be caused by reduced leaf area index due to frosting or drought, when soil evaporation may contribute a larger proportion to evaporation (Ritchie 1982). The efficiency of water use of pasture under each of the tree densities studied tended to increase with time, probably because of lower soil evaporation and interception during the dry conditions in 1986.

Tree Transpiration

Transpiration rates per tree (m^3/day) during 1985 and 1986 at each of the three densities are given in Fig. 4. As an indicator of water contents in the tree root zone during 1985 and 1986, the mean soil water contents to the maximum depth of rooting (Eastham & Rose 1990) measured at 1.2 m from the tree at the three studied tree spacings are shown in Fig. 5.

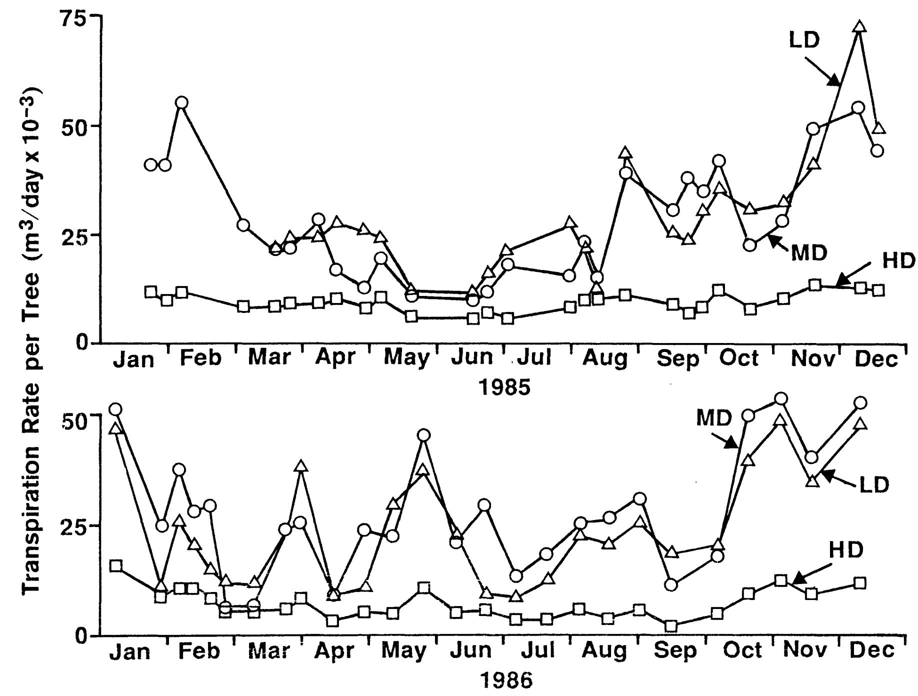

FIG. 4 — Transpiration per tree throughout 1985 and 1986 at the high (□), medium (○), and low (△) tree densities. Average transpiration rates were calculated for 2-weekly periods as described in the text. Symbols are located at the midpoint in time of each measurement period.

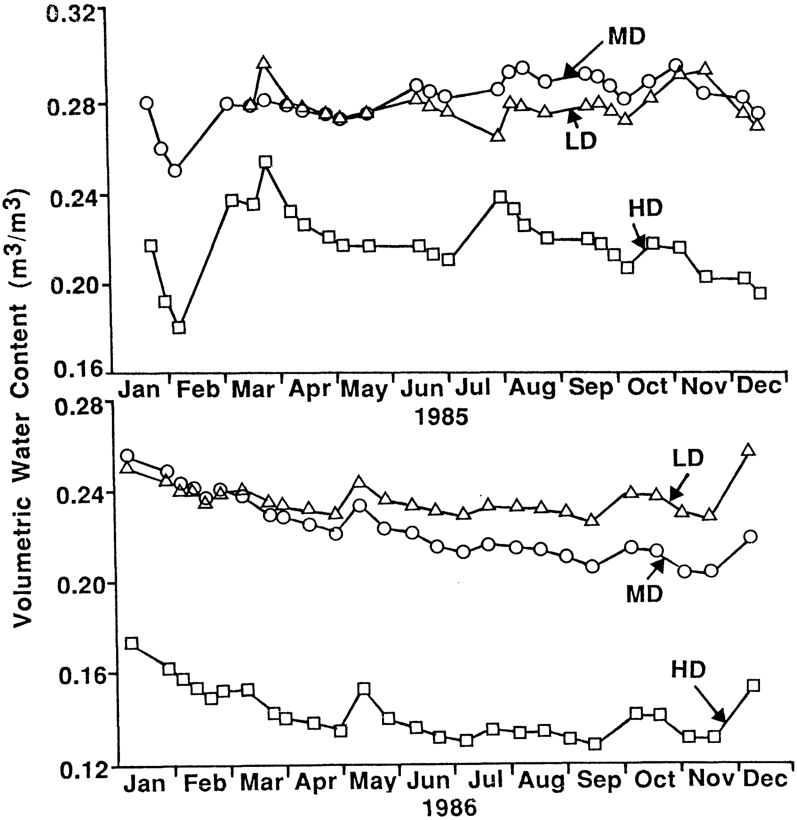

FIG. 5 — Mean soil water contents throughout 1985 and 1986 at 1.2 m from the tree stem, at the high (□), medium (○), and low (△) tree densities.

Transpiration per tree in both years was lowest from HD. In 1985, transpiration rates were lower during winter (5.6, 9.9, and 11.8 $\times$ 10^{-3} m^3/day in mid-June from HD, MD, and LD respectively) than in summer (12.9, 54.5, and 72.9 $\times$ 10^{-3} m^3/day in December from HD, MD, and LD respectively). Soil water contents under HD tended to decline from March 1985 until September 1986 (Fig. 5), and transpiration from HD during 1986 was generally lower than during 1985 (Fig. 4). Soil water contents in the root zones at MD and LD were similar throughout 1985, showing no net decrease with time (Fig. 5). During the drought period in 1986, mean water content at MD and LD declined, with larger decreases occurring at MD (Fig. 5), and transpiration from MD was higher than from LD in all but seven of the 26 measurement periods in 1986.

During 1986 when rainfall was below normal (Table 2), transpiration from MD and LD increased after significant rainfall (Fig. 4), suggesting low soil water contents (Fig. 5) may have been limiting transpiration. However, during 1985 when soil water contents were generally higher than in 1986 (Fig. 5), transpiration rates from trees planted at MD and LD (Fig. 4) showed a less marked response to rainfall, particularly during the winter period.

Trees planted at MD and LD were able to maintain higher transpiration rates per tree than HD trees (Fig. 4) despite higher evaporation from pasture under the lower tree densities (Fig. 2). This indicates that trees may successfully compete with pasture for soil water, possibly because rooting patterns (Eastham & Rose 1990) lead to withdrawal of water predominantly from different soil horizons.

Whilst evaporation rates will vary according to environment, Greenwood *et al.* (1982) found similar evaporation rates to those reported here from regenerating *Eucalyptus wandoo* Blakely using the ventilated chamber technique under a mediterranean climate in south-western Australia. Evaporation from a tree with a leaf area of 20 m^2 varied seasonally from 14 to 104 $\times$ 10^{-3} m^3/day, whilst evaporation from a tree with a leaf area of 10 m^2 varied from 11 to 67 $\times$ 10^{-3} m^3/day.

The Nelder design has the advantage of allowing a wide range of tree densities to be studied in a relatively small area, but estimates of transpiration may be limited by disadvantages associated with the use of very small plots, which have been discussed by Jarvis & McNaughton (1985).

Tree Growth and Water Use Efficiency

Early in the experiment (approximately 16 months after planting) trees planted at HD were largest with mean tree heights of 5.3, 4.3, and 3.7 m, and dbh of 4.5, 4.2, and 3.8 cm at the HD, MD, and LD respectively (measured on 4 March 1985). By the end of the study period in December 1986, mean tree heights had increased to 10.1, 9.8, and 8.3 m, and their diameters to 9.2, 12.0, and 11.9 cm at the HD, MD, and LD respectively.

Rates of tree above-ground biomass production at the three studied densities during 1985 and 1986 are given in Fig. 6(a) and 7(a) respectively. Biomass production per tree between planting and the first sampling period in 1985 was greatest at HD and decreased with decrease in tree density, probably because of decreased competition from pasture for water at HD where pasture evaporation was lower than at MD and LD (Fig. 2). During July 1985 biomass production tended to increase at all three densities as leaf areas per tree increased (data not shown), with biomass production being greatest at MD and lowest at HD between 25 October and 13 December 1985.

Rates of biomass production at each tree density during 1986 showed little change with time until 25 September 1986, with productivity consistently lower in HD trees than trees planted at MD and LD, and biomass production rates highest at MD. Biomass production increased in all treatments after relief of drought in October 1986. Low biomass production per tree at HD during 1986 was due to low soil water contents limiting root water uptake (Fig. 5). Although biomass production per tree in 1986 was generally highest at MD and LD, biomass production per unit ground area was greatest at HD and decreased with tree density (data not shown).

These results are in keeping with those reported previously which generally indicate greater tree diameter growth in lower density stands (Barrett 1970; Butcher & Havel 1976; Butcher 1977). As was found in these experiments, some studies attributed decreased growth at high tree densities to limited soil water availability (Della Bianca & Dils 1960; Zahner & Whitmore 1960).

Water use efficiencies throughout 1985 (Fig. 6b) showed little change with time, being greatest at HD with a mean value of 4.6 kg of dry matter produced per cubic

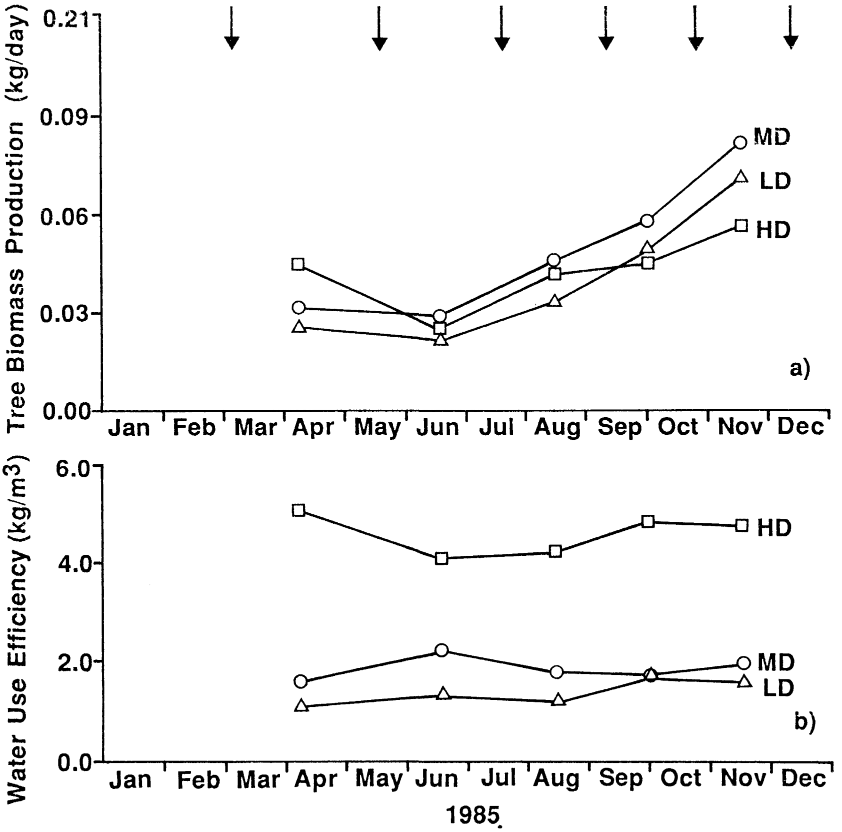

FIG. 6 — (a) Tree biomass production and (b) water use efficiencies throughout 1985 at the high (□), medium (○), and low (△) tree densities. Arrows in (a) represent biomass measurement dates.

metre of water transpired in 1985. Water use efficiency decreased with decreasing tree density with mean water use efficiencies during 1985 of 1.9 and 1.3 kg/m³ at the MD and LD respectively (Fig. 6b). The decrease in the rate of biomass production at HD in early 1986 coincided with a decrease in water use efficiency (Fig. 7b), which became similar to the water use efficiency of trees planted at MD and LD from 13 December 1985 to 19 March 1986. This period was characterised by both low rainfall (Table 2) and high evaporative demand, as indicated by pan evaporation figures (data not shown). During 1986, water use efficiencies at each tree density were more variable with time than in the previous year, although water use efficiency was consistently highest at HD after 19 March 1986. Mean water use efficiency at HD (3.9 kg/m³) was lower during 1986 than during 1985. However, mean water use efficiencies at MD and LD were 2.7 and 2.9 kg/m³ respectively, which represented an increase in water use efficiency from 1985.

Higher water use efficiency of trees planted at HD can be partially explained by lower root production, as root:shoot ratios measured in May 1986 were 0.19, 0.32, and 0.77 at the HD, MD, and LD respectively (Eastham & Rose 1990). Since use of stem

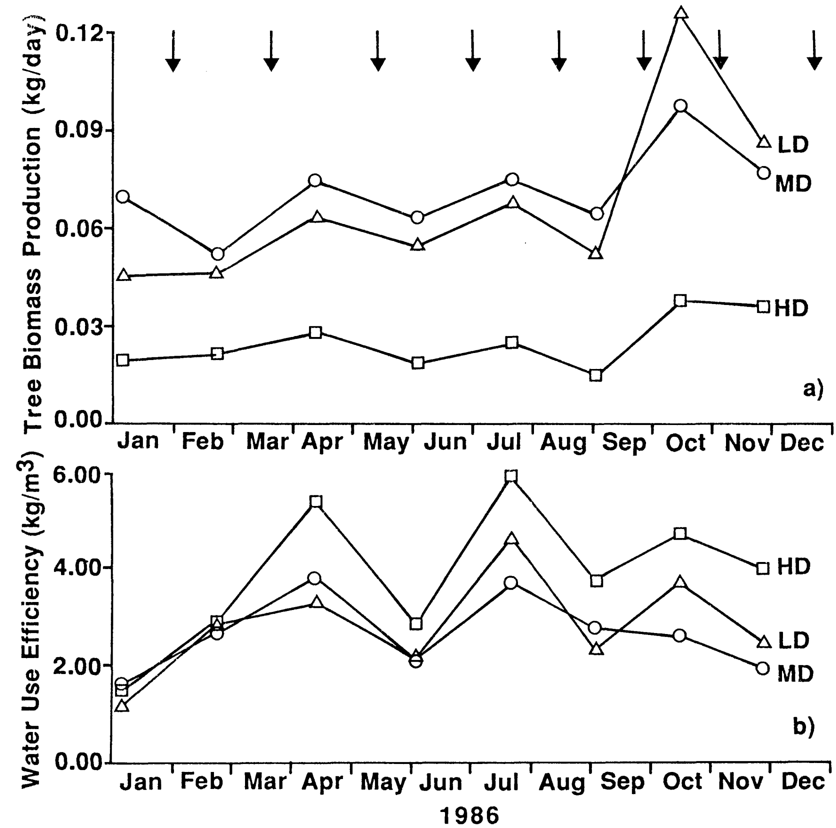

FIG.7 — (a) Tree biomass production and (b) water use efficiencies throughout 1986 at the high (□), medium (○), and low (△) tree densities. Arrows in (a) represent biomass measurement dates.

volumes to estimate biomass production does not take into account leaf or root production and turnover, fluctuations in water use efficiency occurring at each tree density throughout 1986 (Fig. 7b) may be caused by flushes of root and leaf production associated with periodic partial relief of drought after rainfall. Fluctuations may also be due to errors associated with use of measured stem diameter to estimate biomass production. Variation in the height of measurement, shrinkage and swelling of stems and bark due to varying degrees of hydration, and bark shedding may obscure changes due to growth (Buell *et al.* 1961; Kozlowski 1967).

The generally lower water use efficiency of trees planted at low densities may be caused by higher vapour pressure deficits associated with closer coupling with the regional vapour pressure deficit. Dunin & Mackay (1982) reported water use efficiencies of 1.0 kg/m^3 from eucalypt forest compared with 2.5 kg/m^3 from conifers. They attributed the difference in efficiency to differences in temporal variations in transpiration, with reduced transpiration efficiency in eucalypts associated with high vapour pressure deficits. The influence of vapour pressure deficit on transpiration efficiencies has previously been reported for agricultural crops (Fischer & Turner 1978; Tanner & Sinclair 1982).

CONCLUSIONS

The productivity and water use of trees and pasture in this agroforestry experiment were modified by tree density. Transpiration rates were lowest from trees planted at high densities where soil conditions were consistently drier than under low tree densities. Between the time trees were planted in November 1983 and measurements made in March 1985, biomass production per tree was highest in densely planted trees, probably because there was less competition from surrounding pasture for water than occurred at lower tree densities. During dry conditions in 1986, biomass production per tree was lowest, whilst production per unit area was highest from densely planted trees. This was associated with a higher water use efficiency attributed partly to proportionately lower root production at high planting densities. However, densely planted trees depleted soil water reserves throughout the study period, suggesting that biomass production would become rainfall dependent unless trees could withdraw sufficient water from beyond the maximum depth of water content measurement.

Low pasture production associated with reduced radiation beneath the tree canopy and low soil water contents because of competition from trees for water suggested that the high tree density (2150 stems/ha) was unsuitable for grazing. Pasture evaporation was lower, and water use efficiencies were higher under the intermediate tree density (304 stems/ha) than from pasture under low density trees (82 stems/ha). The apparently higher water use efficiencies found in pasture under the intermediate tree density may be partially a result of less assimilate being partitioned to roots. In terms of pasture production, the intermediate tree density appeared most suitable for grazing, although other factors affecting grazing (for example, pasture digestibility) were not studied. However, further tree growth and subsequent canopy closure may decrease pasture productivity at this and lower densities in future years. Hence any optimal planting density will change with tree development through time.

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