

# Growth indices and stomatal control of transpiration in *Acacia koa* stands planted at different densities

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**Summary** We examined the influences of selected environmental variables on stomatal behavior and regulation of transpiration in 26-month-old *Acacia koa* Gray (koa) stands planted at spacings of 1 × 1 m or 2.5 × 2.5 m and grown without irrigation. Field measurements were made during recovery from an extended 60-day dry period with only 38 mm of precipitation. Biomass and leaf area were also measured at 3-month intervals over the first 24 months after planting and again following completion of the transpiration (*T*) and stomatal conductance (*g<sub>s</sub>*) measurements at about 26 months after planting. Transpiration was measured as sap flow through intact branches by a heat balance method.

After a 22-day period during which 130 mm of rain were recorded, average *T* was substantially higher in the 2.5 × 2.5 m stand on both a leaf area and ground area basis even though leaf area index was about 3.5 times higher in the 1 × 1 m stand. After an additional 25 mm of rain during an 8-day period, *T* was still slightly higher on a leaf area basis in the 2.5 × 2.5 m stand but was about 3 times higher on a ground area basis in the 1 × 1 m stand. A strong stomatal response to humidity limited the increase in *T* with increasing evaporative demand. Values of *g<sub>s</sub>* in koa phyllodes were comparable to those reported for leaves of other mesic tropical forest trees, but were several times higher than those reported for *Acacia* species native to arid and semi-arid regions. The 1 × 1 m planting yielded three times more biomass per unit ground area than the 2.5 × 2.5 m planting. However, greater stand density, which resulted in more rapid depletion of soil water between rainfall inputs, was associated with lower growth efficiency and lower radiation conversion efficiency.

**Keywords:** biomass productivity, crown conductance, growth efficiency, leaf area index, radiation conversion efficiency, stomatal conductance, vapor pressure deficit, wind speed.

## Introduction

Koa (*Acacia koa* Gray) is an endemic Hawaiian tree, which is valued for its high quality wood and is important in native forest ecosystems. Although it has been suggested that sclero-

morphic phyllodes of *Acacia* species are an adaptation to arid environments, koa is a dominant species over a large range of dry to wet forest in Hawaii (Judd 1920). Previously, we found that development and growth of natural koa stands were reduced along a gradient of decreasing rainfall, as reflected by lower leaf area index (LAI), lower growth per unit leaf area (*E*) and higher intrinsic water-use efficiency (Harrington et al. 1995). However, because stand characteristics covaried with rainfall and vapor pressure deficit (VPD) along the gradient, we could not separate effects of environment from effects of stand development on water use of koa. Therefore, we established an experiment at two stand densities to create differences in canopy characteristics at a single site. The objectives of this study were (1) to examine the influence of selected environmental variables on stomatal behavior, crown conductance, and regulation of transpiration in koa, and (2) to assess the effect of stand leaf area index on the regulation of transpiration, biomass productivity, and growth efficiency under a natural rainfall regime.

In arid environments, stomatal conductance (*g<sub>s</sub>*) in phyllodes and leaves of Australian and African *Acacia* species is reported to decrease with increasing VPD (Lange et al. 1987) and decreasing predawn xylem pressure (Ullman 1989). However, the environments in these studies were more xeric than the montane sites occupied by koa. Furthermore, transpiration was calculated from the stomatal conductance and VPD measurements made within the porometer chamber, which would not be representative of actual transpiration unless the prevailing ratio of stomatal to boundary layer conductance for unenclosed leaves was duplicated in the porometer chamber (Jarvis and McNaughton 1986, Meinzer 1993).

Although gas exchange characteristics of koa phyllodes differ little from those of true (bipinnate) leaves, it has been suggested that the vertical orientation of phyllodes reduces radiant energy loading and thus transpiration in the field (Walters and Bartholomew 1984, 1990). In a study of field-grown koa saplings, multiple regression analysis showed that phyllode water vapor conductance was negatively related to increasing ambient air temperature, photosynthetic photon flux density (PPFD), and saturation deficit (Hansen 1986). How-

ever, light and VPD typically covary in the field and are known to have opposing effects on  $g_s$ . Thus, it is often necessary to normalize  $g_s$  or VPD by PPFD to reveal stomatal responses to humidity (e.g., Grantz and Meinzer 1990, Gutierrez et al. 1994b, Meinzer et al. 1995). There may also be a strong interaction between wind and humidity in determining stomatal regulation of transpiration. Gutierrez et al. (1994b) concluded that apparent partial stomatal closure in response to increasing wind speed in coffee hedgerows was mediated by increases in boundary layer conductance causing drier air to be imposed at the leaf surface with increasing wind speed. To obtain a better understanding of how stomatal conductance and transpiration of koa are controlled in the field, we made concurrent measurements of environmental variables, stomatal conductance, and transpiration rates of intact branches by means of a stem heat balance technique (Gutierrez et al. 1994a).

Physiological controls on transpiration at the leaf level may also be linked to total plant and canopy leaf area, independently of differences in external environmental stress factors (Meinzer and Grantz 1990, Donovan and Ehleringer 1992, Ovaska et al. 1992). Adjustments in total leaf area in response to limited availability of water and other resources have also been observed to confer some degree of homeostasis on leaf-level properties such as photosynthesis and nutrient content (Pereira 1990, Meinzer et al. 1992). We have observed adjustments in both leaf- ( $\delta^{13}\text{C}$ ) and stand-level (LAI and  $E$ ) characteristics of koa growing in natural stands along a rainfall gradient (Harrington et al. 1995); however, we could not isolate the influence of variation in water availability from that of other factors along the gradient. In the present study, in which we established plantings of young trees at two stand densities at a single site where soil and atmospheric conditions were uniform, we have tested the hypothesis that although transpiration rates on a leaf area basis may not differ between stands of different densities, a stand with a higher LAI will have higher transpiration rates per ground area than a stand with a lower LAI when soil water is not limiting. Further, we postulated that following rainfall, a stand with higher LAI will deplete soil water faster, and therefore its transpiration rates per leaf area and ground area will decrease sooner than in a stand with lower LAI.

We also tested the hypothesis that lower  $E$  is causally related to reduced stomatal conductance during periods of low water availability (Harrington et al. 1995). However, because  $E$  decreases with increasing stand LAI throughout stand development (Waring 1983, Fownes and Harrington 1990, Harrington and Fownes 1995a), low  $E$  in stands with a high LAI at a single site could also be a result of mutual shading as well as water stress. To account for mutual shading effects, we analyzed the growth data as biomass accumulation per unit of intercepted radiation ( $\epsilon$ , radiation conversion efficiency) (Monteith 1977). Harrington and Fownes (1995b) found that, in another phyllocladous species, *Acacia auriculiformis* A. Cunn. ex Benth.,  $\epsilon$  was relatively constant over a wide range of stand development and stem densities, but decreased under water shortage. In the present study, we predicted that if the decrease in  $E$  at higher LAI is caused by mutual shading, then  $\epsilon$  will be similar in

stands planted at the two densities. Conversely, if lower  $E$  in the higher density stand is caused by water stress, then  $\epsilon$  will also be lower in the higher density planting.

## Materials and methods

### Site

Measurements were made in *Acacia koa* stands located at Waiawa, Oahu at an elevation of 260 m. The soil is classified as a Waiawa silty clay (Oxisol) with a Ustic soil water regime. Mean annual rainfall is 1400 mm over the life of the koa stands, and is often less than 50 mm per month between April and July. In March 1991, *A. koa* seedlings were planted in the field at  $1 \times 1$  m spacing in  $10 \times 10$  m plots (HD) or  $2.5 \times 2.5$  m spacing in  $20 \times 15$  m plots (LD).

### Growth measurements and sampling techniques

Growth measurements were made on the central 25 trees in the HD plots and on the central 12 trees in the LD plots. Stem diameter was measured at 15 cm above ground and total stems per plot were counted at 3-month intervals over the first 24 months after planting, and also at the time of harvest at approximately 26 months after planting. Following harvest, we generated allometric equations relating tree biomass and leaf area to diameter (Fownes and Harrington 1992, Harrington and Fownes 1993). Tree biomass and leaf area were calculated at 3-month intervals from the diameter measurements and the allometric equations. Growth per unit leaf area,  $E$ , was calculated as:

$$E = 2\Delta B / (LA_1 + LA_2), \quad (1)$$

where  $\Delta B$  is the mean biomass increment per tree over the 3-month interval and  $LA_1$  and  $LA_2$  are the mean leaf area per tree at the beginning and end of the interval, respectively. Total aboveground stand biomass ( $W$ ,  $\text{kg m}^{-2}$ ) and leaf area index (LAI) were calculated and used to estimate intercepted radiation ( $Q_i$ ) at 3-month intervals:

$$Q_i = Q_0(1 - e^{-kLAI}), \quad (2)$$

where  $Q_0$  is the total incident radiation over the interval and  $k$  is the extinction coefficient. Light interception by koa canopies was significantly correlated with solar angle over the range of solar elevation from  $45$  to  $90^\circ$  during clear sky conditions ( $r^2 = 0.66$ ), but not during cloudy conditions, so an average  $k$  of  $-0.45$  (SE =  $\pm 0.03$ ) was used. Average intercepted radiation,  $Q_i$ , was calculated as:

$$Q_i = Q_0(2 - e^{-kLAI_1} - e^{-kLAI_2})/2, \quad (3)$$

where  $LAI_1$  and  $LAI_2$  are the leaf area indices at the beginning and end of the interval (Harrington and Fownes 1995b). The radiation conversion efficiency ( $\epsilon$ ) over a given interval was calculated as the increment in aboveground biomass produced

over the interval ( $\Delta W$ ) divided by the corresponding  $Q_i$  over that interval.

### Transpiration

Transpiration ( $T$ ) was estimated from mass flow of sap through individual intact branches by a heat balance method as described by Baker and van Bavel (1987). Sap flow gauges (Models SGB-13, SGB-16, SGB-19 and SGB-25, Dynamax Inc., Houston, TX) consisting of a heating element, a thermopile and individual thermocouples, were attached to branches having an average phyllode area of 1.1 m<sup>2</sup> distal to the gauge. The gauges and adjacent portions of the stem were wrapped with foam insulation in addition to that supplied by the manufacturer and the entire assembly was enclosed in a layer of aluminum foil. An outer shield constructed of reflective automobile windshield liner was added to minimize spurious temperature gradients caused by radiant heating of the stem (Gutierrez et al. 1994a). Eight branches on three trees in each stand were fitted with gauges. Two of the trees had three gauges and the remaining tree had two gauges. One gauge in each stand was operated without power applied to the heater to verify that stem temperature differentials from below to above the gauge heater were near zero under these conditions (Gutierrez et al. 1994a). The remaining gauge heating elements were operated at constant power and the radial and longitudinal heat fluxes were evaluated with the thermopile and thermocouples, respectively. In each stand, a data logger (Model CR21X or CR10, Campbell Scientific Corp., Logan, UT) equipped with a 32-channel multiplexer (Model AM-416, Campbell Scientific) recorded data continuously and 30-min averages were stored in a solid state storage module (Model SM 192, Campbell Scientific). The sheath conductance for each gauge, a proportionality constant relating the thermopile output to the radial heat loss at zero flow, was determined from the average values of sheath conductance calculated in the data logger program between 0300 and 0500 h local time when  $T$  was assumed to be zero. Sap flow measurements were carried out over a 13-day period commencing on May 7, 1993 and ending on May 19, 1993. On completion of the measurements, all phyllodes distal to the gauges were removed from the branches for determination of their area with an area meter (Model 3100, Li-Cor, Inc., Lincoln NE). Half-hourly averages of  $T$  on a unit leaf area basis for each stand were obtained by first computing an average value for each of the three trees fitted with gauges, then taking an overall average for the three trees. These values were multiplied by the appropriate LAI to scale  $T$  to a ground area basis.

### Micrometeorological measurements

A weather station was located on site. Global radiation was measured with a pyranometer (Li-Cor Model LI-200S), rainfall was measured with a tipping bucket raingauge (Model TE525, Texas Electronics, Inc., Dallas, TX), and wind speed was measured with a cup anemometer (Model 03101, RM Young Co., Traverse City, MI). Measurements were made at 15-s intervals, and 15-min averages as well as daily global

radiation and rainfall totals were stored in a data logger (Model CR10, Campbell Scientific).

The temperature of four phyllodes on each of the plants fitted with sap flow gauges was determined with fine wire (0.08 mm) copper-constantan thermocouples. Thermojunctions were constructed to allow approximately 3 cm of constantan wire to extend beyond the junction. The phyllode was pierced with a small needle to permit the constantan wire to be inserted through the blade from one side and pulled until the thermocouple junction and about 2 cm of the copper-constantan duplex wire appeared on the opposing face. The phyllode was pierced again at a point about 3 cm from the original perforation and the constantan wire was pushed through until about 2 cm appeared above the surface. The thermojunction was brought into contact with the opposing face by pulling on the constantan and duplex wires until they were relatively taut. Each wire was then secured to the surface with a small piece of water-resistant adhesive tape. This attachment procedure did not encumber the thermojunction itself, thereby avoiding undue interference with the phyllode energy balance near the thermojunction. Phyllode-to-bulk air VPD ( $VPD_a$ ) was calculated as the difference between saturation vapor pressure at phyllode temperature and ambient vapor pressure determined from frequent measurements of humidity and temperature made with a ventilated porometer chamber (Li-Cor Model LI-1600) held open at a distance of about 1 m from the foliage. Crown conductance ( $g_c$ , mol m<sup>-2</sup> s<sup>-1</sup>) was calculated as:

$$g_c = \frac{TP}{VPD_a}, \quad (4)$$

where  $P$  is atmospheric pressure. All values of  $g_c$  are expressed on a unit phyllode area basis. Crown conductance as defined here includes a stomatal component and boundary layer components whose magnitude is determined both by phyllode dimensions and by attenuation of wind by the surrounding vegetation. It can therefore be regarded as partially analogous to a canopy conductance, even though the latter is traditionally expressed on a unit ground area basis (Meinzer et al. 1993, 1995).

### Stomatal conductance

Stomatal conductance ( $g_s$ ) was measured with a steady-state porometer (Li-Cor Model LI-1600) in four premarked phyllodes on each of the three trees fitted with sap flow gauges in each stand. The positions of the four phyllodes corresponded approximately to the four cardinal directions. Precautions were taken to maintain the phyllodes' natural orientation during measurement. Incident PPFD reported for  $g_s$  measurements was recorded with a quantum sensor mounted on the porometer chamber parallel to the phyllode surface. Three to seven complete sets of measurements were obtained during each of 6 days of measurements between May 10 and 19, 1993. Both the bulk air and the phyllode surface were used as external reference points for characterizing stomatal responses to humidity. Phyllode-to-bulk air VPD ( $VPD_a$ ) was calculated as described above. The phyllode-to-air vapor pressure difference

at the phyllode surface ( $VPD_s$ ; Meinzer and Grantz 1989, Grantz and Meinzer 1990, Meinzer et al. 1993) was estimated as:

$$VPD_s = TP/g_s \quad (5)$$

## Results

### Stomatal regulation of transpiration

Planting density influenced transpiration ( $T$ ) both on a leaf area and ground area basis (Figure 1). On May 11, average  $T$  per unit leaf area was about five times higher in the LD stand than in the HD stand (Figure 1A). The difference in  $T$  diminished when  $T$  was expressed on a unit ground area basis because of the higher LAI in the HD stand (Figure 1C). On this day,  $T$  was highest during midmorning (about 0900 h) in both stands and declined throughout the rest of the day. This pattern was particularly apparent in the HD stand (Figure 1C). Preceding these physiological measurements was an unusually severe dry period, with only 38 mm of rain falling from mid-February to mid-April (Figure 2). From mid-April until our measurements on May 11, 130 mm of rain fell, but this amount was insufficient to relieve the water deficit that reduced  $T$  in the HD treatment. These results indicate that stand density influenced the rate of soil water depletion between precipitation events with the HD stand depleting soil water faster than the LD stand. When  $T$  was measured 8 days later (May 19) after an additional 25 mm of rain fell, it was only slightly higher on a unit leaf area basis in the LD stand than in the HD stand (Figure 1B). On a ground area basis, however, average  $T$  was about three times higher in the HD stand than in the LD stand (Figure 1D). The ratio of  $T$  in the HD stand to that in the LD stand during this period when water became less limiting, was

less than the ratio of LAI between the two stands (3.45). Patterns of regulation of  $T$  related to stand density thus depended on the time elapsed from the previous precipitation inputs and their cumulative amount.

There was no clear stomatal response to variation in phyllode-to-bulk air VPD (Figure 3A). However, when the phyllode-to-air VPD at the phyllode surface ( $VPD_s$ ) was estimated according to Equation 5,  $g_s$  was observed to decline sharply

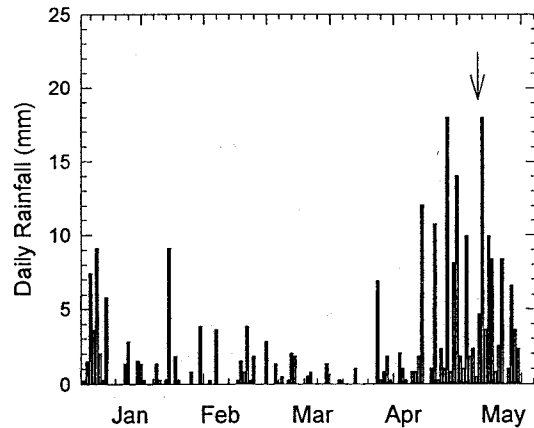


Figure 2. Daily rainfall for January through May 1993 at Waiawa, Hawaii. The arrow indicates the start date for sap flow measurements.

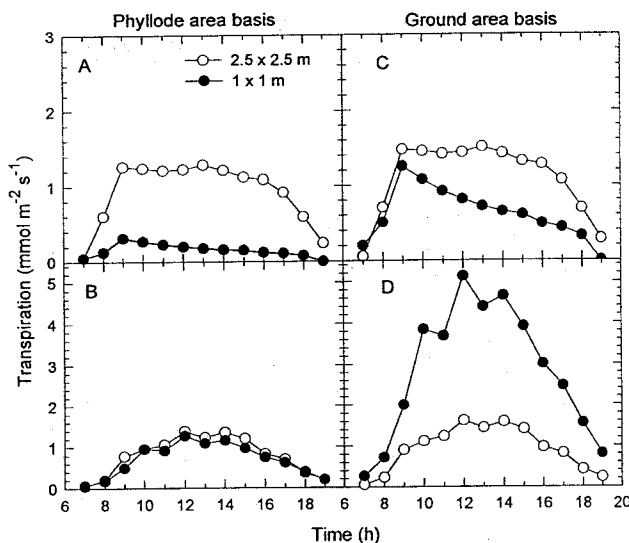


Figure 1. Daily courses of transpiration on a phyllode area and ground area basis in *A. koa* stands on May 11, 1993 (A and C) and May 19, 1993 (B and D).

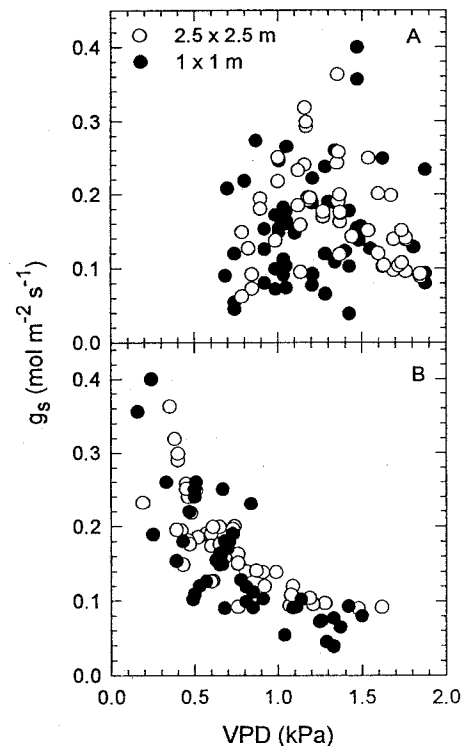


Figure 3. Stomatal conductance ( $g_s$ ) in relation to phyllode-to-bulk air VPD (A) and VPD at the phyllode surface (B) on May 10–14 and 19, 1993.

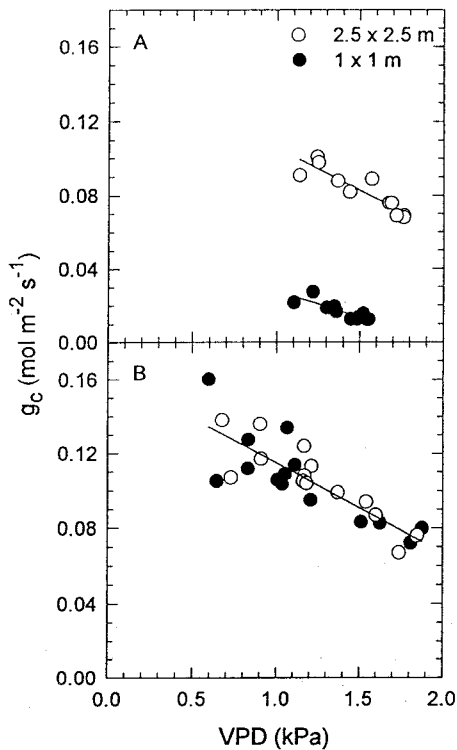


Figure 4. Crown conductance ( $g_c$ ) in relation to phyllode-to-bulk air VPD on May 11, 1993 (A) and May 19, 1993 (B).

with increasing  $VPD_s$  (Figure 3B). The relationship between  $g_s$  and  $VPD_s$  was similar in the HD and LD stands.

In contrast with  $g_s$ ,  $g_c$  declined with increasing  $VPD_a$  (Figures 4A and B). On May 10–14,  $g_c$  was substantially higher in the LD stand than in the HD stand (Figure 4A), consistent with the higher transpiration rate in the LD stand during this period (cf. Figures 1A and C). On May 18 and 19, the relationship between  $g_c$  and  $VPD_a$  was similar for both stands (Figure 4B) again indicating that recovery from previous water deficit in the HD stand was complete by May 18.

Increasing wind speed appeared to cause  $g_c$  to decrease (Figures 5A and B). On May 11, at a given wind speed,  $g_c$  was higher in the LD stand than in the HD stand (Figure 5A). As recovery from soil water deficits progressed, the relationship between  $g_c$  and wind speed became similar for both stands on a given day but differed among days (Figure 5B). When  $T$  was plotted as a function of wind speed, it remained relatively constant or decreased slightly with increasing wind speed when recovery from soil water deficit was incomplete (Figure 6A); however, after further recharge of soil water by rainfall,  $T$  generally increased with wind speed in the same manner for both stands (Figure 6B), but the slope of the relationship varied from day to day (data not shown).

Transpiration increased curvilinearly with  $VPD_a$ , becoming asymptotic with increasing evaporative demand, or appearing to reach a maximum at a critical value of  $VPD_a$  beyond which it began to decline with further increases in  $VPD_a$  (Figures 7A

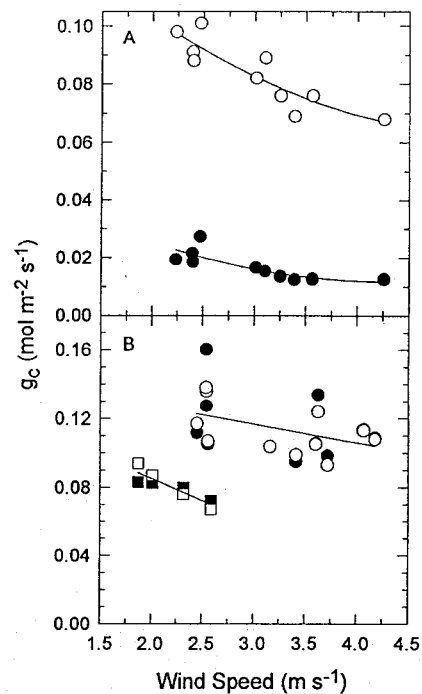


Figure 5. Crown conductance ( $g_c$ ) in relation to wind speed on (A) May 11, 1993, (B) May 14, 1993 (■ □) and May 19, 1993 (● ○) in A. *koa* stands planted at a  $1 \times 1$  m spacing (closed symbols) or  $2.5 \times 2.5$  m spacing (open symbols).

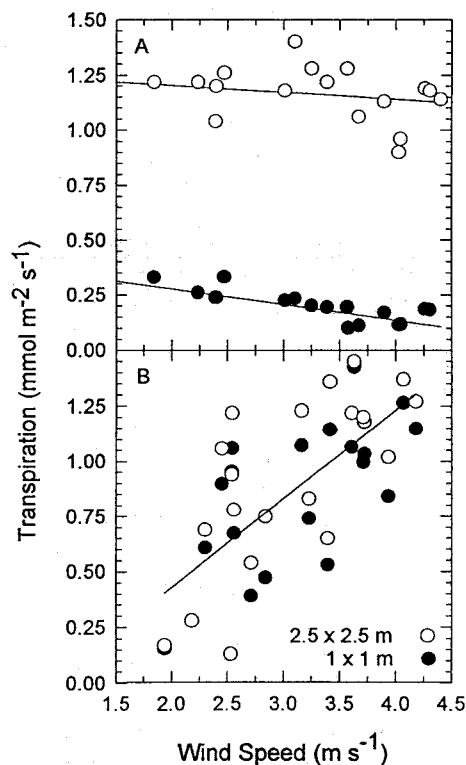


Figure 6. Transpiration in relation to wind speed on (A) May 11, 1993 and (B) May 19, 1993.

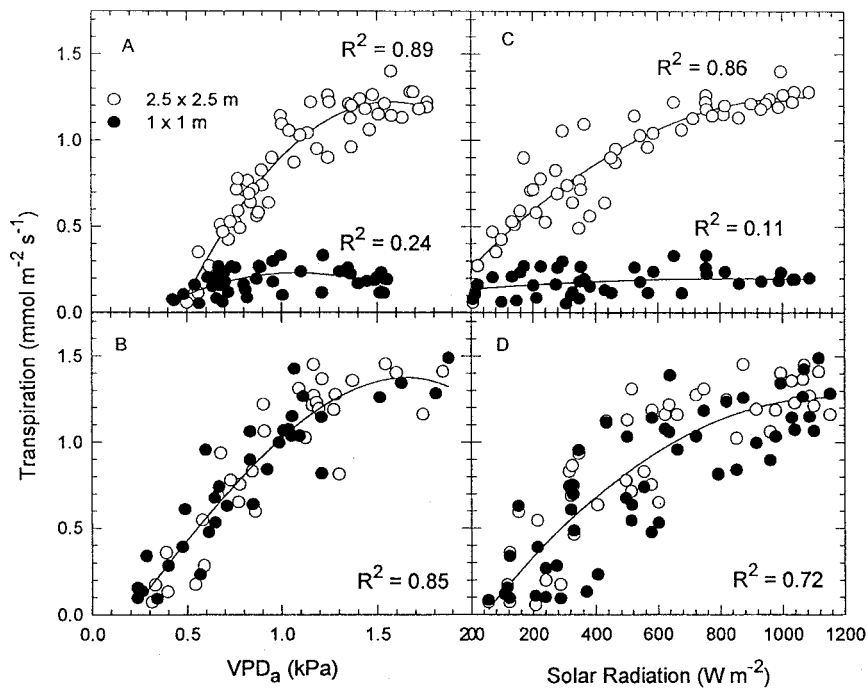


Figure 7. Transpiration in relation to phyllode-to-bulk air VPD and solar radiation in *A. koa* stands on (A and C) May 10–12, 1993 and (B and D) May 14, 18 and 19, 1993.

Table 1. Stand characteristics at 26 months and selected growth analysis variables for *Acacia koa* stands. Intercepted radiation, growth efficiency ( $E$ ), and radiation conversion efficiency ( $\epsilon$ ) are calculated from 21 to 26 months. The maximum radiation conversion efficiency ( $\epsilon_{\max}$ ) is that measured before canopy closure in the  $1 \times 1$  m spacing (3 to 15 months).

Plant spacing (m)	Tree density ( $\text{ha}^{-1}$ )	Aboveground biomass ( $\text{Mg ha}^{-1}$ )	Leaf/Wood ratio	Specific leaf mass ( $\text{g m}^{-2}$ )	LAI	Intercepted radiation ( $\text{GJ m}^{-2}$ )	$E$ ( $\text{kg m}^{-2} \text{y}^{-1}$ )	$\epsilon$ ( $\text{g MJ}^{-1}$ )	$\epsilon_{\max}$ ( $\text{g MJ}^{-1}$ )
$1 \times 1$	8800	20.77	0.505	202	4.04	1.936	0.330	0.255	0.761
$2.5 \times 2.5$	1600	5.70	0.694	194	1.17	0.810	0.619	0.292	0.681

and B). The significant  $R^2$  values shown in Figure 7 were higher when data for individual days were plotted separately. When recovery from soil water deficit was incomplete, the critical value of  $\text{VPD}_a$  at which transpiration began to decrease was greater in the LD stand than in the HD stand (Figure 7A). When soil water was not limiting, the relationship between  $T$  and  $\text{VPD}_a$  was similar for the two stands with  $\text{VPD}_a$  accounting for 85% of the variation in  $T$  (Figure 7B). On May 10–12,  $T$  increased curvilinearly with solar radiation in the LD stand (Figure 7C), whereas  $T$  was independent of solar radiation in the HD stand. After additional soil water recharge, the dependence of  $T$  on solar radiation was similar for both stands (Figure 7D), but the coefficient of determination was lower than that obtained when  $T$  was plotted as a function of  $\text{VPD}_a$  (cf. Figures 7B and D).

#### Stand characteristics and growth analysis

At 26 months after planting, tree density in the LD stand remained at the original density of 1600 trees per hectare, whereas tree density in the HD stand was reduced from 10,000 to 8800 trees per hectare as a result of mortality. The HD stand

had approximately three times the aboveground biomass and 3.5 times the LAI of the LD stand, although the HD stand had a lower phyllode/wood biomass ratio (Table 1). Despite differences in LAI between stands, they had similar average canopy specific leaf mass.

From 21 to 26 months, the biomass increment per unit leaf area was higher in the LD stand than in the HD stand. Intercepted radiation over 21 to 26 months was approximately 2.5 times greater in the HD stand than in the LD stand, but  $\epsilon$  was lower in the HD stand than in the LD stand at this stage of development. Before canopy closure,  $\epsilon_{\max}$  was about 10% greater in the HD stand than in the LD stand (Table 1), suggesting that greater stand-level water use and ensuing water deficit in the HD stand were partly responsible for its lower  $\epsilon$ .

#### Discussion

At the single leaf scale, stomatal regulation of transpiration was similar in the HD and LD stands when soil water was nonlimiting; however, on a land area basis, transpiration was three times greater in the HD stand than in the LD stand when soil water was adequate (Figure 1D). During periods of low

precipitation input, this behavior led to more rapid depletion of soil water and lower transpiration per ground area in the HD stand than in the LD stand (Figure 1C). These stand-level water use characteristics did not prevent the HD stand from yielding three times more biomass per ground area at the end of 24 months than the LD stand (Table 1). However, greater stand density, and thus more rapid depletion of soil water between precipitation inputs, were associated with lower  $E$  and lower  $\epsilon$ , particularly during the time interval immediately preceding harvest (Table 1). The greater LAI in the HD stand was thus rendered less efficient in terms of biomass production because partial stomatal closure restricted photosynthesis more frequently in the HD stand than in the LD stand.

Our results indicate a strong stomatal response to humidity that limited the increase in  $T$  with increasing evaporative demand (Figures 7A and B). The tendency for  $T$  to decline above a critical value of VPD has been observed previously under field conditions (Gutierrez et al. 1994b, Monteith 1995) and is characteristic of the "feedforward" stomatal response to humidity (Farquhar 1978). Despite the evidence for a strong stomatal response to humidity implied in the relationship between  $T$  and  $VPD_a$ , no clear relationship between  $g_s$  and  $VPD_a$  was detected (Figure 3A). A stomatal response to humidity at the leaf level was evident only when  $g_s$  was plotted in relation to a measure of VPD using the leaf surface rather than the bulk air as the external reference point (Figure 3B). In contrast,  $g_c$ , a total vapor phase conductance consisting of stomatal and boundary layer components in series, declined with increasing  $VPD_a$  (Figures 4A and B). These observations indicate the importance of selecting appropriate reference points for measurement of external vapor pressure in characterizing stomatal responses to humidity (Meinzer 1993, Meinzer et al. 1993). The bulk air is an appropriate reference point for characterizing responses of  $g_c$  to humidity because it coincides with the external reference point for determining the leaf-to-air VPD used to calculate  $g_c$ . On the other hand,  $g_s$  is calculated from transpiration and the VPD imposed at the leaf surface inside a ventilated porometer chamber. The degree to which this VPD corresponds to that experienced by the unenclosed leaf depends on its boundary layer conductance, which in turn depends on leaf size and wind speed.

The decline in  $g_c$  with increasing wind speed (Figures 5A and B) is consistent with a strong interaction between wind and humidity in determining stomatal regulation of transpiration in koa stands. Gutierrez et al. (1994b) concluded that apparent stomatal responses to wind in coffee hedgerows were mediated by increases in boundary layer conductance causing drier air to be imposed at the leaf surface with increasing wind speed. In koa, variations in wind speed and therefore in boundary layer conductance and vapor pressure at the leaf surface is a likely explanation for the absence of a clear relationship between  $g_s$  and  $VPD_a$  (Figure 3A). Variation in the dependence of  $T$  on wind speed (Figures 6A and B) was associated with variation in factors such as soil water availability and ambient saturation deficit. When soil water availability was adequate, the slope of the transpiration–wind speed relationship differed from day to day and appeared to be smaller on days with higher prevailing  $VPD_a$  (data not shown). In well-irrigated coffee

hedgerows, transpiration normalized by net radiation invariably decreased with increasing wind speed, presumably reflecting an underlying stomatal response to humidity (Gutierrez et al. 1994b).

Monteith (1995) has pointed out that the mechanistic basis of the dependence of  $g_s$  on VPD or relative humidity is weak and has proposed a reinterpretation of stomatal responses to humidity based on the dependence of  $g_s$  on transpiration rate. Inspection of our data revealed no clear relationship between  $g_s$  and  $T$ . In contrast the data reanalyzed in Monteith's study showed a strong dependence of  $g_s$  on  $T$ . However, most of the studies cited by Monteith were carried out under controlled conditions in which  $T$  was varied by varying VPD while holding other variables constant. Indeed, Monteith's analysis showed that the relationship between  $g_s$  and  $T$  can be influenced by variables such as temperature and ambient  $CO_2$  concentration. Also, if part or all of the stomatal response to humidity is governed by epidermal rather than stomatal transpiration (e.g., Bunce 1985), then variation in boundary layer conductance ( $g_b$ ) caused by factors such as wind could result in different values of  $g_s$  at the same transpiration rate, depending on the partitioning of total vapor phase conductance ( $g_c$ ) between its stomatal and boundary layer components. Variation in  $g_b$  would influence epidermal transpiration through its effect on vapor pressure imposed at the leaf surface. Thus, at a given value of ambient VPD and  $g_c$ , different combinations of  $g_s$  and  $g_b$  could result in the same total transpiration rate, thereby confounding interpretation of relationships between  $g_s$  and  $T$  in field data. The relative contributions of stomatal and epidermal transpiration to apparent stomatal responses to humidity are difficult to evaluate in field data where relevant environmental variables covary. Nevertheless, our data are consistent with a role for epidermal transpiration in the response of *A. koa* stomata to humidity (Figure 3B).

It was not necessary to normalize  $g_s$  or VPD by PPFD to detect stomatal responses to humidity in koa, suggesting that the threshold of PPFD above which  $g_s$  became relatively unresponsive to variation in PPFD was low. Most of our  $g_s$  measurements were made when PPFD was  $> 200 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Although no data describing stomatal responses to PPFD in koa are available,  $g_s$  in several tree species has been shown to be relatively unresponsive to increasing PPFD above a threshold of about 200–400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (e.g., Whitehead et al. 1981, Ceulemans et al. 1989, Roberts et al. 1990, Kostner et al. 1992). Furthermore, Lange et al. (1987) reported a high degree of synchrony in diurnal courses of  $g_s$  on opposing faces of *Acacia* phyllodes exposed to large differences in PPFD and suggested that a combination of internal and external signals other than light served to coordinate  $g_s$  of the two faces of the phyllodes.

Maximum values of  $g_s$  measured in *A. koa* phyllodes were several times higher than those reported for phyllodes of *Acacia* spp. native to arid and semiarid regions (Lange et al. 1987, Ullmann 1989). However, the latter measurements were carried out under generally hot, dry conditions. The relative importance of environmental and genetic factors in determining these differences in  $g_s$  is therefore not known. It is possible that the magnitude of  $g_s$  in phyllodes of arid-zone *Acacia* species

grown under the conditions of our study would be similar to that of *A. koa*. The range of  $g_s$  observed in *A. koa* corresponds to that reported for other mesic tropical forest trees (Roberts et al. 1990, Dolman et al. 1991, Meinzer et al. 1993, Koch et al. 1994). The presence of phyllodes is thus not inherently incompatible with the ability to attain relatively high rates of transpiration.

Our previous work suggested that a trade-off between intrinsic water- and canopy-level nutrient-use efficiencies exists across the wide range of rainfall, humidity and stand development (LAI) spanned by *A. koa* forests (Harrington et al. 1995). However, the physiological mechanisms underlying the trade-off and the role of potential genetic differences among populations remain unknown. In the present experiment, comparison of two stands planted at different densities at the same site, but derived from the same population, showed strong stomatal responses to ambient VPD and soil water depletion. These findings support the hypothesis that differences in intrinsic water-use efficiency and stand-level indices of growth efficiency observed along natural gradients of rainfall and VPD are determined largely by physiological responses of stomata.

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