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Water supply regulates structure, productivity, and water use efficiency of *Acacia koa* forest in Hawaii

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Abstract We studied changes in stand structure, productivity, canopy development, growth efficiency, and intrinsic water use efficiency (WUE=photosynthesis/stomatal conductance) of the native tree koa (*Acacia koa*) across a gradient of decreasing rainfall (2600–700 mm) with increasing elevation (700–2000 m) on the island of Hawaii. The stands were located on organic soils on either smooth (pahoehoe) or rough (aa) lava flows. In the greenhouse, we also examined growth and WUE responses to different water regimes of koa seedlings grown from seeds collected in the study area. We tested the hypotheses that (1) stand basal area, aboveground net primary productivity (ANPP), leaf area index (LAI), and growth per unit leaf area decreased with decreasing rainfall, (2) WUE increased with decreasing rainfall or water supply, and (3) WUE responses were caused by stomatal limitation rather than by nutrient limitations to photosynthesis. The carbon isotope composition of phyllode tissues ($\delta^{13}\text{C}$) was examined as an integrated measure of WUE. Basal area and LAI of koa stands on both pahoehoe and aa lava flows, and ANPP on aa lava flows decreased with elevation. Basal area, LAI, and ANPP of koa in mixed stands with the exotic tropical ash (*Fraxinus udhei*) were lower compared to single-species koa stands at similar elevations. Along the gradient, phyllode $\delta^{13}\text{C}$ (and therefore WUE) increased with elevation from -30.2 to -26.8‰ . Koa in mixed stands exhibited higher (less negative) $\delta^{13}\text{C}$ than in single-species stands suggesting that koa and tropical ash competed for water. In the greenhouse, we observed the same trend observed in the field, as phyllode $\delta^{13}\text{C}$ increased from -27.7 to -24‰ as water supply decreased. Instantaneous gas exchange measurements in the greenhouse showed an inverse correlation of both maximum

(morning) photosynthesis (A) and conductance (g) with $\delta^{13}\text{C}$ values and, also, a good agreement between instantaneous (A/g) and integrated measures of WUE. Phyllode $\delta^{13}\text{C}$ was not correlated with foliar concentrations of N or other nutrients in either the field or the greenhouse, indicating that differences in $\delta^{13}\text{C}$ were caused by stomatal limitation rather than by nutrient-related changes in photosynthetic capacity. This study provided evidence that long-term structural and growth adjustments as well as changes in WUE are important mechanisms of koa response to water limitation.

Key words Forest productivity · Koa · Hawaii mountain forests · Water supply · Carbon isotope discrimination

Introduction

Forests adjust both structurally and physiologically to the limitations of insufficient water. Leaf area index (LAI), for example, has been observed to increase with water availability in forests dominated by a single species across landscapes varying systematically in site water balance (Grier and Running 1977; Gholz 1981; Harrington et al. 1995). It is also reasonable to hypothesize that plants use resources more efficiently when these are in scarce supply, and indices of intrinsic water use efficiency (WUE) have been found to increase with site dryness (Meinzer et al. 1992; Harrington et al. 1995; Jaendl et al. 1995). If WUE is increased through stomatal closure, however, other aspects of performance and use of resources should be compromised (Field et al. 1983; Harrington et al. 1995) leading to what is generally described as a tradeoff relationship (Fownes 1995). In this research, we studied a landscape gradient in rainfall to investigate whether net primary productivity of the native Hawaiian tree species koa (*Acacia koa* Gray) was limited by water availability, how forest structure, canopy development and resource use efficiency varied with this limitation, and whether these patterns reflected general trends of plant adaptation to water limitation.

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Gradients of ecosystem state factors such as climate, organisms and parent material can be used to test predictions about how soils and plants interact in regulating productivity and other aspects of ecosystem function. Because gradients in landscapes generally vary in more than one property, it is important to isolate as far as possible the hypothesized causal variable from confounding effects. Many previous studies have utilized the relatively predictable gradients in the landscape of Hawaii to study the development and dynamics of *Metrosideros polymorpha* Gaud. ecosystems (Vitousek et al. 1988, 1992). Although less widespread than *M. polymorpha*, koa is the premier commercial timber of Hawaii as well as an important link in biological conservation and restoration of native ecosystems (Whitesell 1990), yet the controls of koa productivity are relatively poorly known.

Along a gradient of increasing water availability with elevation in the island of Kauai, koa forest had increasing basal area and a close inverse relationship between WUE and LAI, primary productivity, and production per unit leaf area (Harrington et al. 1995). Along this gradient, nutrients were unlikely to limit koa growth because koa is a legume and under some conditions can fix substantial atmospheric nitrogen (Pearson 1996), and because the higher-productivity sites had lower cation and P availability, probably as a result of higher rainfall and thus leaching rates (Austin and Vitousek 1998). The goals of the research reported here were to test the generality of the conclusions presented by Harrington et al. (1995) by (1) recording observations along an elevation transect representing an opposite pattern of precipitation (i.e., rainfall decreasing with elevation), (2) working on soils of different development and nutrient status, and (3) obtaining direct physiological evidence that variation in $\delta^{13}\text{C}$ represented variation in stomatal conductance and WUE.

Characterization of the water status of tall trees and soils beneath them is not an easy task: approaches based on instantaneous measures require frequent sampling and canopy access, while results are difficult to relate to long-term productivity. Furthermore, the methodological approaches to measure water potential and its functional significance have not been free of controversy (Zimmerman et al. 1994). For example, water-stressed plants can have a water potential similar of those of unstressed plants because of closed stomata (Ludlow et al. 1990). Measurement of soil water status is difficult in rocky and stony sites where the real extent of root systems may be unknown. To face some of these difficulties, integrated measures of physiological performance related to soil or atmospheric drought such as carbon isotope discrimination are increasingly used in ecological studies of plant responses to the environment.

Discrimination against the stable isotope $\delta^{13}\text{C}$ occurring during CO_2 fixation in plants represents the difference between the carbon isotope ratio ($^{13}\text{C}/^{12}\text{C}$) of plant tissue and the isotope ratio of source CO_2 and is largely determined by the ratio between intercellular and atmospheric CO_2 partial pressures (pi/pa) (Farquhar et al.

1982). In turn, pi/pa is related to the ratio between assimilation rates (A) and stomatal conductance (g), an index of intrinsic WUE (Hubick and Farquhar 1989). Consequently, the carbon isotope composition of leaf tissues ($\delta^{13}\text{C}$) reflects environmental effects exerted upon pi/pa . Increased $\delta^{13}\text{C}$ in plants has been associated with reduced soil moisture (Meinzer et al. 1992), but when water availability was not a major limitation to plant growth, $\delta^{13}\text{C}$ also related positively to vapor pressure deficit (Sharifi and Rundel 1993), photosynthetic photon flux density (Zimmerman and Ehleringer 1990), and leaf N content (Sparks and Ehleringer 1997), and negatively to temperature (Morecroft and Woodward 1990). Hence, the relationship between $\delta^{13}\text{C}$ and environmental factors is seldom unequivocal, as different factors may affect the ratio between CO_2 assimilation and conductance. Therefore, it is essential to compare $\delta^{13}\text{C}$ values from field studies with independent data in which presumed causative factors are varied one at the time, especially in cases where environmental factors are related.

For this study, we predicted that a decrease in productivity of the N-fixing koa with elevation would likely be caused by decreased water supply rather than by reduced N (or other nutrient) availability. Therefore, we followed an observational approach, studying patterns of soil and foliar nutrients, and carbon discrimination in mature koa stands, and a manipulative approach, in which koa seedlings were subjected to different water regimes resembling those in the field. We tested the hypotheses that (1) stand basal area, aboveground net primary productivity (ANPP), LAI, and growth per unit leaf area (E) decreased with decreasing rainfall, (2) WUE increased with decreasing rainfall or water supply, and (3) WUE responses were caused by stomatal limitation rather than by nutrient limitations to photosynthesis.

Materials and methods

The study area

The study area is the Honaunau Forest ranging from 670 to 1450 m elevation on the southwestern slopes of Mauna Loa, island of Hawaii (Fig. 1). Annual precipitation ranges from about 2600 mm at the lowest elevation to 1200 mm at the upper limit of the forest (Kamehameha Schools Bishop Estate, unpublished data for the period 1958–1971). One koa plot was at a 2000-m-elevation site outside the Honaunau Forest with an estimated average rainfall of 700 mm (State of Hawaii 1986). In the Honaunau Forest, approximately 35% of the total rainfall occurs in the summer and the driest period lasts from October to December. Summer rainfall is caused by the large mass of Mauna Loa which drives a land-sea breeze cycle on its southwestern side (Giambelluca et al. 1986). Mean daily temperature ranges between 19°C and 14°C across the gradient.

The soil landscape consists mainly of well-drained, organic soils developed on both rough (aa) and smooth (pahoehoe) lava flows which are about 1200 and 2400 years old, respectively (J. Lockwood and F. Trusdell, unpublished geologic maps). These soils are extremely gravelly and stony with more than 90% coarse fractions (>2 mm). They were originally classified as Lithic (on pahoehoe) and Typic (on aa) Tropofolists in the soil survey of the island of Hawaii (Sato et al. 1973). The taxonomic classification of some of these soils has been proposed to change to Andic

Fig. 1 Location of the study area in South Kona, Island of Hawaii

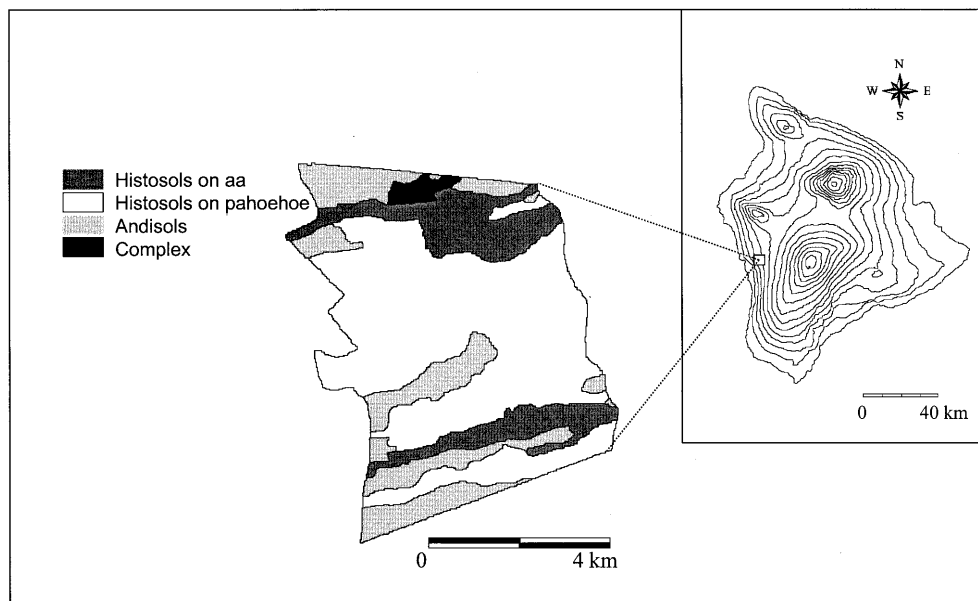


Table 1 Site and stand characteristics of single-species and mixed stands of koa in the Honaunau Forest. Basal area and leaf area index were measured in all plots (*pah* smooth (pahoehoe) lava, *aa* rough (aa) lava; *k* koa, *a* tropical ash)

Elevation (m)	Soil type	Soil pH	Soil organic C (%)	Soil N (%)	Soil P (mg kg ⁻¹)	Foliar N (%)	Foliar P (%)	Stand age (years)	Stem density (trees ha ⁻¹)	Mean diameter at breast height (cm)
Koa stands										
760 ^{a, b}	pah	4.5	23.6	1.69	13	2.55	0.10	28	287	25.6
780 ^{a, b}	pah	4.5	25.5	1.84	12	3.12	0.13	28	575	21.1
1060 ^{a, b}	aa	4.5	37.1	2.24	6	3.19	0.14	37	685	24.8
1065	pah	—	—	—	—	—	—	31	71	58.3
1180 ^{a, b}	aa	5.1	27.0	2.14	11	2.67	0.09	28	859	17.9
1350	aa	—	—	—	—	—	—	36	318	29.3
1420 ^{a, b}	aa	5.0	34.3	1.92	10	2.42	0.11	36	376	30.9
2000 ^b	pah	5.7	32.6	2.49	12	2.30	0.08	—	58	55.5
Mixed stands										
1420 ^{a, b}	aa	5.4	34.6	2.27	6	2.26	0.08 k	36	735 k	16.2 k
						1.60 a	0.08 a		750 a	16.8 a
1420 ^{a, b}	aa	5.6	35.0	2.42	10	2.57	0.09 k	36	424 k	19.1 k
						1.71 a	0.09 a		721a	18.7 a
						2.14 k	0.08 k		212 k	21.0 k
1360 ^{a, b}	aa	5.4	21.9	1.29	6	1.54	0.08a	36	792 a	18.1 a

^a Plots where aboveground net primary productivity was measured

^b Plots where $\delta^{13}\text{C}$ was determined

Udifolists to account for the presence of different amounts of volcanic ash mixed with organic materials (R. Gavenda, personal communication).

The land was historically covered by koa and mixed koa-ohia forests that were logged in various increments since 1923. After the forest was completely fenced in 1956, cattle were removed and some areas were allowed to regenerate in koa while others were planted with a variety of introduced tree species.

The understory of the koa plots was mostly tree fern (*Cibotium* spp.) and some other natives while kikuyu grass (*Pennisetum clandestinum*) dominated in two plots at 1300 m elevation. Mixed stands of koa and tropical ash (*Fraxinus udhei*) arose when koa regenerated spontaneously at about the same time that tropical ash was planted.

Stand measurements

We set up one circular 10- to 20-m-radius plot within each of eight single-species and three mixed stands of koa on organic soils (Table 1). In each plot, every tree was permanently marked at 1.37 m aboveground on opposite sides of the stem (i.e., two marks per tree) and stem diameter (DBH) was measured on the marks with a thin diameter tape over 6-month intervals. Stand basal area was calculated as the sum of the individual tree basal areas in each stand. Litterfall was collected approximately monthly from May 1995 to June 1997 in all but three plots with four 0.18-m² litter traps and sorted into foliage, twig (<1 cm diameter), and reproductive components.

LAI measurements

LAI was calculated using an allometric equation derived from two separate koa harvests carried out in areas geographically close to the Honaunau Forest (Grace 1995). We were not able to harvest koa, a native, highly prized timber species, in the study area in order to develop our own equations. We estimated leaf area per tree (LA, m²) with a two-step procedure calculating (1) tree sapwood area (SW, cm²) from tree basal area (BA_i, cm²) and (2) leaf area per tree from sapwood area as follows:

$$SW = 2.38BA_i^{0.779}$$

$$LA = 0.061SW^{1.17}$$

LAI was then calculated as the summation of all tree leaf area in the plot divided by the area of the plot. LAI was also estimated optically from nine points within each plot using a LI-COR LAI-2000 (Lincoln, Neb.) plant canopy analyzer (Welles and Norman 1991) in September 1996. We used allometric measures of LAI in the subsequent analysis as they compared well to those from the optical method (data not shown). In another study in the island of Hawaii, LAI values from an allometric equation developed "in situ" were almost identical to LI-2000 measurements in koa stands of age 6, 13, and 20, although optical readings were lower in a 9-year-old stand (H. Pearson, unpublished data). This suggests that a clumping index to correct LAI values from the LAI-2000 instrument is not systematically necessary for koa.

Primary productivity and *E* estimates

We calculated ANPP as the sum of litterfall, stem mortality, and biomass growth estimated from diameter increments over 6-month periods by biomass allometrics. We estimate total aboveground biomass per tree (*B*, kg) with an equation originated during the same koa harvests used to derive the equation for LAI (Grace 1995):

$$B = 0.102DBH^{2.33}$$

Growth per unit leaf area, *E* (kg m⁻¹), was calculated as:

$$E = 2ANPP / (LA_2 + LA_1)$$

where LA₂ and LA₁ are the allometric stand leaf area at the end and the beginning of the measurements, respectively (Fownes and Harrington 1990). Results for ANPP and *E* were expressed on a yearly basis.

Foliage and soil analysis

We sampled fully expanded koa phyllodes from the uppermost part of the crowns of at least five trees at each plot during mid-season in 1995. Foliage samples were composited to make up a single sample from each plot. Phyllode area was measured on fresh samples with a leaf area meter (LI-COR LI-3100) for the subsequent determination of specific leaf mass (SLW, g m⁻¹). The foliage samples were dried at 70°C to constant weight and ground to pass a 1-mm sieve. They were then analyzed for total concentration of N by a micro-Kjeldahl procedure (Nelson and Sommers 1972), and for P, Ca, Mg, K, S, Fe, Mn, Mo, Cu, Zn, and Na by inductively coupled plasma emission spectroscopy (Isaac and Johnson 1983), and for B with the azomethine-H method (Wolf 1974).

Phyllode samples were reground with a mortar and pestle and sent to the Duke University Phytotron Facility in Durham, N.C., for determinations of δ¹³C. Ratios of ¹³C/¹²C were measured on a SIRA Series II mass spectrometer (VG Isotech, Middlewich, UK) operated in automatic trapping mode after combustion of samples in an elemental analyzer (NA1500, Carlo Erba, Milan, Italy). The reference CO₂ calibrated against standard Pee Dee belemnite was obtained from Oztech (Dallas, Tex.). Koa phyllode δ¹³C was determined for five single-species and three mixed stands.

We also collected soil samples to 15 cm depth from eight positions along two transects (N-S and E-W) in each plot. The soils were then analyzed for organic C by chromatic acid digestion and

spectrophotometric methods (Heanes 1984), total N by micro-Kjeldahl, K by Technicon continuous-flow flame emission spectrophotometry and P, Ca, and Mg by inductively coupled plasma emission spectrometry.

Weather data

We set up three weather stations in clearings at 700, 1050, and 1400 m elevation. We recorded rainfall with a TE525 tipping bucket rain gage (Texas Electronics, Dallas, Tex.), global solar radiation with a LI-200 SZ pyranometer (LI-COR) and air temperature and relative humidity with an HMP35C probe (Vaisala, Woburn, Mass.). Soil temperature was measured at 50 cm depth with a 107B probe (Campbell Scientific, Logan, Utah). Measurements were taken at 15-s intervals and hourly averages and totals were stored in dataloggers. Potential evapotranspiration by the Priestley-Taylor method (Priestley and Taylor 1972) and a soil water balance were estimated with the DSSAT crop model (Hoogenboom et al. 1994). Input data for calculation of the water balance included soil depth, textural fractions, bulk density, organic carbon, percent coarse fraction >2 mm, slope, permeability, drainage, and soil surface color. This model has not been calibrated for the Hawaii uplands and results should be considered as approximate.

Greenhouse experiment

Koa seeds were collected at 880 m elevation in the Honaunau forest and sown in flats in a greenhouse of the University of Hawaii at Manoa, island of Oahu. The seedlings were transplanted to 3.3-l pots containing an organic soil-perlite mix with slow-release fertilizer (Osmocote 20-20-20). After about 5 months when phyllodes started to develop, the seedlings were randomly subdivided into three equal-sized groups and subjected to three water regimes receiving either 2.6, 5.2 or 7.8 mm H₂O day⁻¹, maintaining soil moisture at about 30, 60, and 90% of field capacity, respectively. A completely randomized design with ten replicates was followed and pots were rerandomized weekly. The experiment lasted from February to June 1996. The seedling tops were tagged with light plastic rings to differentiate new growth. Mean temperature throughout the experiment was 24.5°C and relative humidity was 77.8%.

Assimilation (*A*), stomatal conductance (*g*), and the ratio of intercellular to ambient CO₂ partial pressure (pi/pa) were measured on the greenhouse-grown seedlings over several days before their harvest. Measurements were taken on fully expanded phyllodes as close to their natural orientation as possible with a LI-COR 6200 portable photosynthesis system. The CO₂ analyzer was calibrated daily against standard CO₂ gases. All seedlings were harvested at 130 days. Roots were cleaned of soil and plants were divided into roots, stem, phyllodes, and juvenile leaves. Phyllode and juvenile leaf areas were measured with a LI-3000 leaf area meter. Plant materials were then dried at 70°C to constant weight and SLW, root:shoot ratio (RSR: root mass divided by shoot mass; g g⁻¹) and leaf area ratio (LAR: total leaf area divided by the total seedling mass; m² g⁻¹) were determined. Fifteen phyllode samples (five per water regime treatment) were randomly chosen for determinations of δ¹³C. Gas exchange measurements became available for ten plants for which δ¹³C was determined. Linear regression was used to analyze growth and biomass partitioning variables against water supply rate.

Results

Weather conditions

A mean air temperature decrease of 6.4 C every 1000 m (Table 2) agreed with previous estimates of lapse rates

Table 2 Weather data at three elevations in the Honaunau Forest from May 1995 to June 1997

	700 m	1050 m	1400 m
Mean air temperature (°C)	18.6	16.5	14.1
Total rainfall (mm)	11,947	8916	4968
Mean total solar radiation (MJ m ⁻² day ⁻¹)	9.47	7.48	10.47
Mean maximum vapor pressure deficit (kPa)	0.85	0.63	1.06
Months with potential evapotranspiration exceeding rainfall	Oct. 1995	Oct. 1995	May 1995, Sep. 1995, Oct. 1995, Nov. 1995, May 1996, Aug. 1996, Oct. 1996, Feb. 1997
Months with estimated zero soil water storage	None	Oct. 1995	All the above except Sep. 1995

for the island of Hawaii (Juvik and Nullet 1994). The rainfall pattern for the first year of study was similar to historical records but the second year was extremely rainy although relative differences in rainfall among weather station sites were maintained. According to the calculations of potential evapotranspiration by the Priestley-Taylor method, evapotranspiration exceeded rainfall in several months at 1400 m elevation while at 700 m elevation this situation only occurred in October 1995. An estimated water balance indicated that zero water storage in the soil may have occurred at 1400 m elevation in about 1 out of 3 months during the study period. The lowest value for both solar radiation and vapor pressure deficit occurred at mid-elevation within the Honaunau Forest. Solar radiation increased above the top of the forest according to the general sunshine maps for the island of Hawaii.

Koa stand characteristics

Basal area and LAI of koa stands on both pahoehoe and aa lava flows decreased with elevation (Fig. 2A,B). ANPP of koa on aa lava flows also decreased as elevation increased (Fig. 2C).

In general, koa showed lower basal area, LAI, and ANPP in mixed stands than in single-species stands at similar elevations (Fig. 2A–C) suggesting a detrimental effect of competition by tropical ash on koa growth. Accordingly, koa in the mixed stands showed signs of stagnation and added little biomass during the 2-year measurement period.

Growth per unit leaf area of koa showed no obvious trend along the gradient while *E* of koa in mixed stands appeared to be lower than in single-species stands (Fig. 2D).

Foliar and soil nutrients

Only foliar Ca and Mg increased with elevation in koa stands and were negatively correlated with ANPP (data not shown). There was neither a significant trend of koa

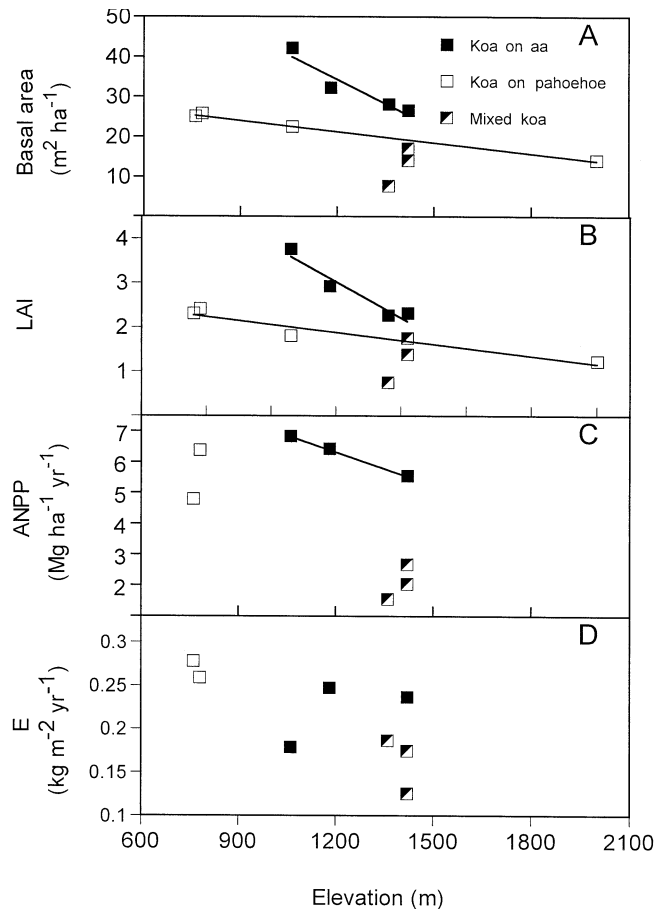


Fig. 2 Elevation in the Honaunau Forest versus: basal area for koa stands on aa lava flows ($r^2=0.90$, $P=0.05$), koa stands on pahoehoe ($r^2=0.99$, $P=0.003$), and mixed koa stands on aa (A); leaf area index (LAI) for koa stands on aa lava flows ($r^2=0.93$, $P=0.04$) koa stands on pahoehoe ($r^2=0.94$, $P=0.04$), and mixed koa stands on aa (B); aboveground net primary productivity (ANPP) of single-species stands of koa on aa ($r^2=0.99$, $P=0.05$) and on pahoehoe, and of mixed koa stands on aa (C); growth per unit leaf area (*E*) for koa stands on aa and pahoehoe, and mixed stands on aa (D)

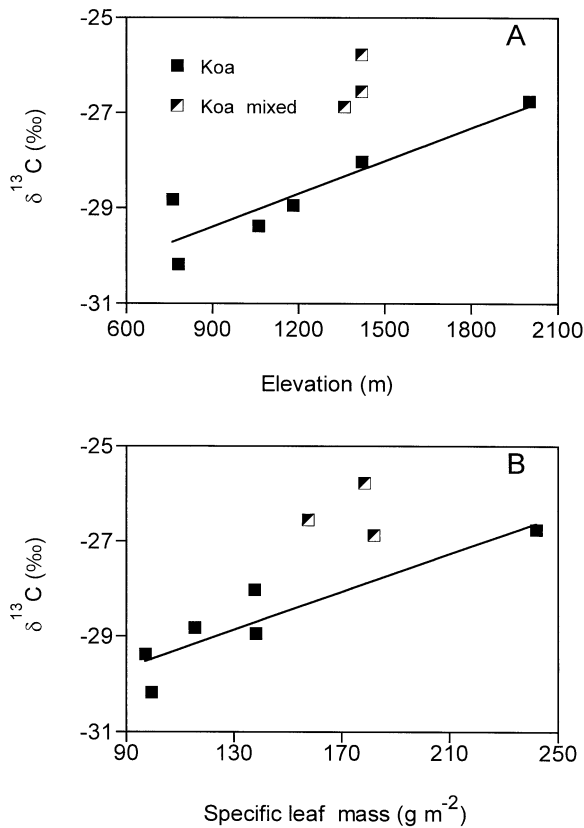


Fig. 3 Carbon isotope discrimination versus elevation ($r^2=0.82$, $P=0.01$) (A), and specific leaf mass ($r^2=0.83$, $P=0.01$) (B) for koa in single-species and mixed stands in the Honaunau Forest

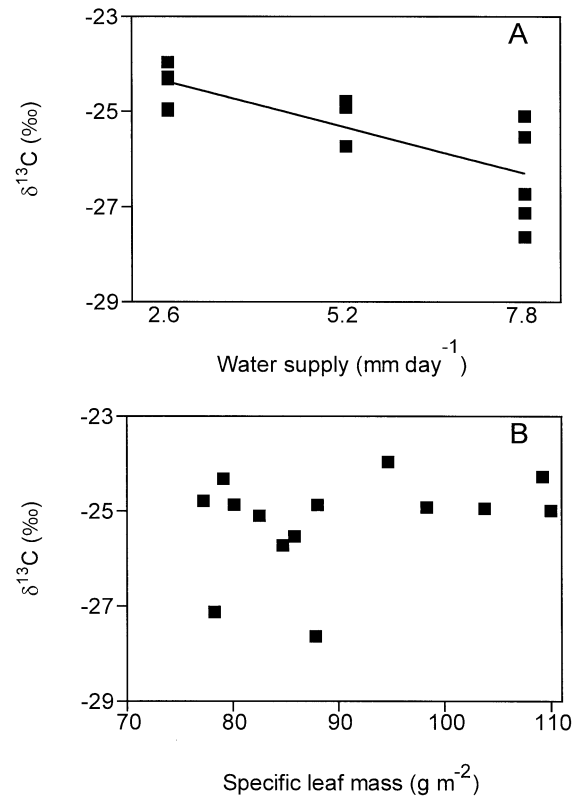


Fig. 4 Carbon isotope discrimination versus water supply ($r^2=0.58$, $P=0.001$) (A) and specific leaf mass (B) for koa seedlings in the greenhouse

foliar N across the gradient nor a correlation of leaf N with ANPP. Soil nutrients did not correlate to koa productivity or other stand variables.

Phyllode $\delta^{13}\text{C}$

Phyllode $\delta^{13}\text{C}$ of koa increased (less negative) with increasing elevation and decreasing rainfall (Fig. 3A). The $\delta^{13}\text{C}$ values spanned 3.4‰ along the 1240-m-elevation gradient. The $\delta^{13}\text{C}$ values of koa were higher in mixed stands than in single-species stands at comparable elevations suggesting that tropical ash competed with koa for water (Fig. 3A). Phyllode $\delta^{13}\text{C}$ was positively correlated to SLW (Fig. 3B) but was unrelated to foliar concentrations of N or other nutrients. The data suggested a negative correlation between $\delta^{13}\text{C}$ and stand basal area but the trend was not statistically significant ($P=0.13$).

In the greenhouse experiment, phyllode $\delta^{13}\text{C}$ of koa seedlings increased as water supply decreased (Fig. 4A), a response similar to that found in the field. Phyllode $\delta^{13}\text{C}$ values spanned 3.8‰ and were not correlated to either SLW (Fig. 4B) or N concentration. Maximum (morning) net CO_2 assimilation and stomatal conductance were negatively correlated to $\delta^{13}\text{C}$ (Fig. 5A,B). Instantaneous measures of intrinsic WUE (A/g) correlated positively with $\delta^{13}\text{C}$ (Fig. 5C). Variations in $\delta^{13}\text{C}$ were correlated

with pi/pa values in the koa seedlings in which gas exchange was measured ($\delta^{13}\text{C}=-20.2-10.3\text{pi}/\text{pa}$, $r^2=0.57$, $P<0.05$). The measured $\delta^{13}\text{C}$ values were rather similar ($r^2=0.55$, $P=0.09$) to $\delta^{13}\text{C}$ values predicted from pi/pa following the model $\delta^{13}\text{C}=-8-22.6(\text{pi}/\text{pa})$ (Farquhar et al. 1982).

Dry matter production and partitioning in the greenhouse

Biomass accumulation, leaf area, and LAR of koa seedlings decreased with decreasing water supply (Fig. 6A–C) but these variables along with RSR were not correlated to $\delta^{13}\text{C}$. The increase in LAR pointed to a change in biomass allocation (i.e., a leafier plant) following increased water supply. At the leaf level, SLW increased with decreasing water supply ($r^2=0.23$, $P=0.01$).

Discussion

Along an elevational and rainfall gradient on the island of Hawaii, koa showed adjustments in stand structure, productivity rate, and canopy development. The consistent pattern of decreasing basal area with increased elevation on both aa and pahoehoe reinforced the idea that this variable could be useful to characterize site potential

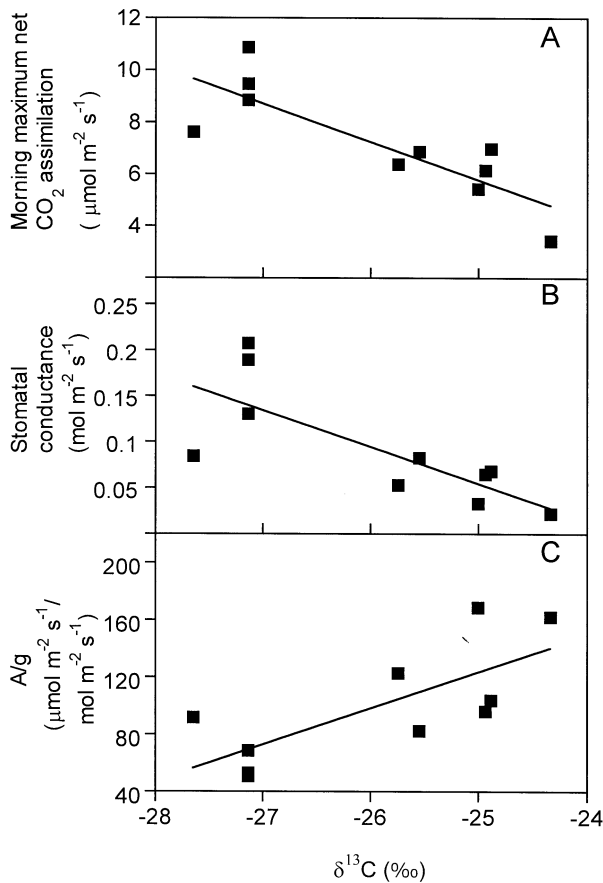


Fig. 5 Carbon isotope discrimination versus net CO₂ assimilation (A, $r^2=0.69$, $P=0.003$) (A), stomatal conductance (g , $r^2=0.58$, $P=0.01$) (B), and intrinsic water use efficiency ($WUE=A/g$) ($r^2=0.55$, $P=0.01$) (C) for koa seedlings in the greenhouse

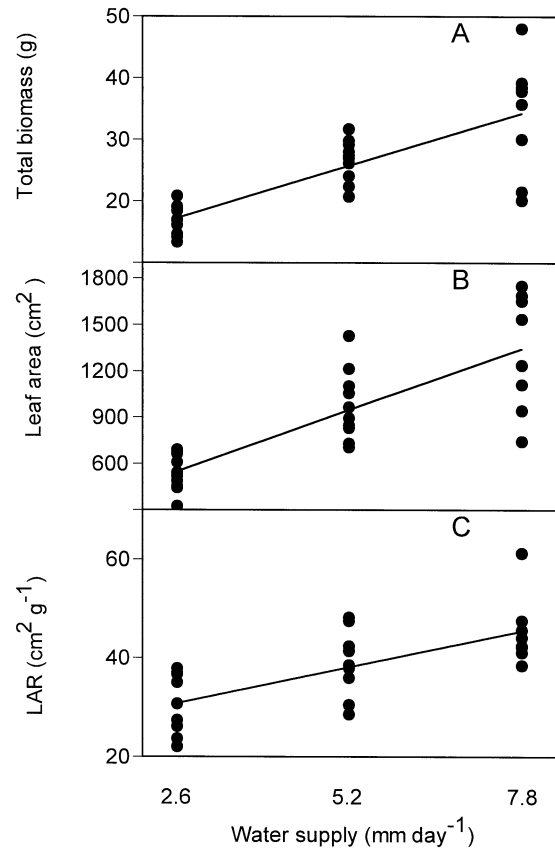


Fig. 6 Water supply versus total biomass ($r^2=0.62$, $P=0.00001$) (A), leaf area ($r^2=0.64$, $P=0.00001$) (B) and leaf area ratio (LAR) ($r^2=0.47$, $P=0.001$) (C) of koa seedlings in the greenhouse

for koa production. Basal area is a convenient, common measure of forest stand structure and stocking that can also be an index of successional status (Held and Winstead 1975), site growth potential (Fralish 1987), and stand composition (Fralish 1988). On the island of Hawaii, analysis of long-term growth data showed that maximum or asymptotic stand basal area was able to reflect how site quality affected recruitment, growth, and mortality of koa (Grace 1995). Hence, comprehensive screening of basal area in mature stands within the remaining koa populations in Hawaii could generate site productivity estimates and growth simulations on a regional basis. Along the gradient, the decrease in basal area (and likely of productivity) with elevation appeared steeper in koa stands on aa than on pahoehoe, probably due to increased water limitation caused by lower water-holding capacities of aa compared to pahoehoe flows.

Changes in stand canopy development along the gradient were revealed in the decrease in LAI both on aa and pahoehoe. Stand LAI closely relates to vital processes such as light interception, photosynthesis and transpiration, and subsequently to stand growth (Fownes and Harrington 1990). On the other hand, no conclusive trend emerged for the productivity-LAI relationship (i.e.,

E) which was measured on a reduced number of koa stands along the gradient. The stands may have differed in other features such as maintenance respiration that may have affected aboveground growth per unit leaf area. Although E was sometimes found not to change in parallel to changes in LAI in forest stands (Jose and Gillespie 1996), both LAI and E of koa decreased with decreasing rainfall across an elevational gradient in the island of Kauai (Harrington et al. 1995).

Among the potential causes of declining koa productivity with elevation, light could not limit productivity directly because solar radiation tended to increase with elevation, but it may affect productivity indirectly through effects on vapor pressure deficits and water stress. Furthermore, the decline in koa productivity along the gradient was not caused by a direct temperature effect, as previous studies have indicated that koa productivity increased with elevation across altitudinal ranges similar to that in our study (Grace 1995; Harrington et al. 1995). Additionally, on the studied stands on young organic soils, there was no evidence of noticeable nutrient effects on koa productivity across the gradient. Increased foliar Ca and Mg with elevation very likely reflected less leaching at high-elevation, drier sites. Overall, this study

did not provide evidence of any major constraint for koa along the gradient other than increased water limitation with elevation.

The soils under the koa stands were extremely gravelly and stony and had very low water-holding capacity and hydraulic conductance. These features added to high surface and subsurface run-off, and uneven rainfall may have contributed to water shortages in the soil despite relatively high rainfall. Thus, lower stand LAI and productivity with increasing elevation were likely the consequence of periodic water shortages. In addition, water vapor pressure deficits tended to increase with elevation and may have also affected koa stomatal response.

Koa showed increased $\delta^{13}\text{C}$ and, therefore, decreased carbon isotope discrimination along the field gradient. This suggested that stomatal conductance was reduced to a greater extent than CO_2 assimilation, resulting in increased intrinsic WUE in response to reduced soil water availability. Such behavior agreed with other studies in which discrimination decreased in dry sites compared to relatively wet ones (Garten and Taylor 1992; Jaindl et al. 1995). In mixed stands, increased $\delta^{13}\text{C}$ of koa suggested that koa likely faced competition for water from tropical ash.

Nevertheless, the $\delta^{13}\text{C}$ pattern we observed in the field could potentially be ascribed to other factors such as increased solar radiation or reduced temperature which varied in parallel along the gradient. Alternatively, the carbon isotope composition of plant tissues may simply decrease with elevation because of changes in CO_2 and O_2 partial pressures (Körner et al. 1991). The previously reported changes (1.1% in $\delta^{13}\text{C}$ every 1000 m), however, cannot explain per se the range of values we observed. In addition, $\delta^{13}\text{C}$ has been found to relate to leaf phenotypic characteristics such as mass or thickness (expressed either as SLW or specific leaf area, SLA, i.e., the inverse of SLW) (Sparks and Ehleringer 1997; Nageswara Rao and Wright 1994) with SLA being proposed as a surrogate for isotope discrimination (Nageswara Rao and Wright 1994). In this study, koa SLW was correlated to $\delta^{13}\text{C}$ along the gradient but, again, increased SLW is a typical response to many environmental factors known to vary with elevation such as increased UV-B (Searles et al. 1995) or solar radiation (Chen et al. 1996).

Providing complementary evidence of water limitation for koa, the $\delta^{13}\text{C}$ response of koa seedlings to decreased water supply in the greenhouse followed a similar trend to that in the field both in direction and magnitude. The difference in the absolute values was not surprising as the sources of C were different. The ratio of instantaneous measurements of net assimilation and stomatal conductance agreed with long-term estimates of WUE and reaffirmed our interpretation of $\delta^{13}\text{C}$ indicating increased stomatal limitation (lower pi/pa) with increased water supply. This pattern, sometimes referred as two-step carbon isotope discrimination has been described for drought-avoiding tree species and differs from that for some drought-tolerant species which keep

their stomata opened and show a non-stomatal limitation to assimilation (Picon et al. 1996). Increased SLW of koa phyllodes with decreased water supply agreed with findings for other phyllodinous species such as *A. auriculiformis* (Phillips and Riha 1993). Nonetheless, in contrast to the pattern for the field gradient, SLW of koa phyllodes did not correlate to $\delta^{13}\text{C}$ or instantaneous measures of WUE, implying that WUE regulation was not simply mediated by changes in phyllode morphology.

In addition to the decrease in dry matter and leaf area of koa seedlings following reduced water supply, we also observed changes in the fractional biomass partitioning to leaves. Changes in LAR, however, were not related to $\delta^{13}\text{C}$, and nor was RSR, suggesting that water supply effects on $\delta^{13}\text{C}$ operated primarily via the gas exchange process instead of through plant morphological changes.

The relationships between WUE and estimates of stand productivity or seedling growth remained elusive probably because of differences in respiration rates or biomass partitioning. Discrepancies between carbon isotope discrimination and dry matter production have not been unusual in studies with agricultural (Jefferies and Mackerron 1997) and forest (Zhang and Cregg 1996) crops.

This study provided complementary evidence that long-term structural and growth adjustments as well as changes in WUE are important mechanisms of the response of koa to water limitation. Further research would examine whether WUE is also genetically controlled in koa.

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