Oecologia (1995) 102:277–284

ORIGINAL PAPER

Robin A. Harrington · James H. Fownes
Frederick C. Meinzer · Paul G. Scowcroft

Forest growth along a rainfall gradient in Hawaii: *Acacia koa* stand structure, productivity, foliar nutrients, and water- and nutrient-use efficiencies

Received: 15 July 1994 / Accepted: 5 January 1995

Abstract We tested whether variation in growth of native koa (*Acacia koa*) forest along a rainfall gradient was attributable to differences in leaf area index (LAI) or to differences in physiological performance per unit of leaf area. Koa stands were studied on western Kauai prior to Hurricane Iniki, and ranged from 500 to 1130 m elevation and from 850 to 1800 mm annual precipitation. Koa stands along the gradient had basal area ranging from 8 to 42 m^2/ha, LAI ranging from 1.4 to 5.4, and wood increment ranging from 0.7 to 7.1 tonnes/ha/year. N, P, and K contents by weight of sun leaves (phyllodes) were negatively correlated with specific leaf mass (SLM, g m^{-2}) across sites; on a leaf area basis, N increased whereas P and K decreased with SLM. LAI, aboveground woody biomass increment, and production per unit leaf area (*E*) increased as phyllode $\delta^{13}C$ became more negative. The $\delta^{13}C$ data suggested that intrinsic water-use efficiency (ratio of assimilation to conductance) increased as water availability decreased. In five of the six sites, phyllode P contents increased as LAI increased, but biomass increment and *E* were not correlated with phyllode nutrient contents, suggesting that productivity was limited more by water than by nutrient availability. Because vapor pressure deficits increased with decreasing elevation, actual water-use efficiency (ratio of assimilation to transpiration) was lower at drier, low-elevation sites. There was a trade-off between intrinsic water-use efficiency and production per unit of canopy N or P across the gradient. In summary, koa responds to water limitation both by reducing stand LAI and by adjusting gas exchange, which results in increased intrinsic water-use efficiency but decreased *E*.

Key words Carbon isotope composition · Leaf area index · Nitrogen-use efficiency · Phosphorus-use efficiency · Specific leaf mass

Introduction

Koa (*Acacia koa* Gray) is one of the two predominant endemic tree species of Hawaiian forests. Koa's wood is quite valuable, while koa forest provides key habitat for many other native and endemic organisms (Whitesell 1990). We need to understand the environmental constraints to koa growth both for ecosystem restoration and, potentially, for sustainable forest management. Koa ranges from lowland dry forest to montane wet forest (Wagner et al. 1990; Whitesell 1990), but is absent from very wet rainforests (Mueller-Dombois 1987). Reduced growth of koa on dry sites could be caused by a reduction in leaf area, or a reduction in growth per unit leaf area (*E*), or both. We measured growth rates and leaf area index (LAI), calculated *E*, and used leaf nutrient concentrations and stable carbon isotope ratios to determine if adjustments to koa growth along a rainfall gradient were primarily due to differences in stand canopy development (LAI) or to differences in physiological performance (*E*, nutrient-use and water-use efficiency).

Drought stress has been shown to affect canopy development, by decreasing maximum LAI and increasing leaf senescence in *Hordeum vulgare* (Legg et al. 1979) and *Eucalyptus maculata* (Pook 1986). LAI of Pacific Northwest forests correlated with indices of site water balance (Grier and Running 1977; Gholz 1981). In addition to reducing leaf area, water stress can reduce *E*. At LAI of 1.0, removal of competing understory vegetation increased *E* in *Pinus ponderosa* by 50%, although the gain was less at higher LAI (Waring 1983). Irrigation, fertilization, and irrigation plus fertilization each increased *E* in *Pinus sylvestris* while reducing allocation to roots (Waring 1983). Water stress was implicated in lower *E* for *Pinus contorta* growing on southern exposures (Kaufmann and Ryan 1986). In *Salix viminalis*, greater

R.A. Harrington (✉) · J.H. Fownes
Department of Agronomy and Soil Science,
University of Hawaii at Manoa, Honolulu, HI 96822, USA

F.C. Meinzer
Hawaiian Sugar Planters' Association,
P.O. Box 1057, Aiea, HI 96701, USA

P.G. Scowcroft
Institute of Pacific Islands Forestry,
U.S. Forest Service, Honolulu, HI 96813, USA

biomass accumulation under higher water and nutrient availabilities was attributed to greater efficiency of leaf area in utilizing intercepted radiation (Cannell et al. 1987). We hypothesized that as rainfall decreased, koa forest would have lower LAI, lower *E*, or both.

Physiological processes underlying variation in *E* could potentially be inferred from changes in foliar characteristics. Greater *E* could result from greater photosynthetic rates on an area basis, achieved by increasing specific leaf mass (SLM) and/or nutrient content (Ellsworth and Reich 1993). However, foliar nutrient concentrations of *Metrosideros polymorpha* were observed to be greater on dry sites than on wet sites on the island of Hawaii (Vitousek et al. 1992). If water supply is limiting, and gas exchange is restricted by reduced stomatal conductance, then *E* could be reduced even at high nutrient contents.

Discrimination against the naturally occurring stable isotope ^{13}C during photosynthesis is determined largely by the ratio of intercellular (p_i) to atmospheric (p_a) partial pressure of CO_2 (Farquhar et al. 1982a,b; Evans et al. 1986; Farquhar et al. 1989). The ratio p_i/p_a is also directly related to the ratio of instantaneous photosynthesis (A) and leaf conductance (g) (Farquar and Richards 1984; Farquhar et al. 1989), a measure of intrinsic water-use efficiency (WUE). Variation in annual tree ring $\delta^{13}C$ of *Fagus sylvatica* was correlated with basal area growth and annual water deficits (Dupouey et al. 1993). Along a gradient of elevation and precipitation on the island of Hawaii, $\delta^{13}C$ of *Metrosideros polymorpha* became less negative with increasing elevation independent of water status (Vitousek et al. 1988), and apparently responded to other factors in addition to p_i/p_a (Vitousek et al. 1990). Among populations on the island of Kauai, *M. polymorpha* leaves had less negative $\delta^{13}C$ values where water uptake was restricted by drought or waterlogging, but $\delta^{13}C$ was closely correlated with p_i/p_a (Meinzer et al. 1992).

Although phyllode $\delta^{13}C$ provides an integrated estimate of intrinsic WUE (photosynthesis/conductance), actual WUE (photosynthesis/transpiration) is influenced by the leaf-to-air vapor pressure gradient, which varied along our elevation gradient. We hypothesized that actual WUE would increase in proportion to intrinsic WUE, so we calculated actual WUE from phyllode $\delta^{13}C$ values and estimates of the leaf-to-air vapor pressure gradient.

Within a species, nutrient-use efficiency may be compromised as WUE increases in response to reduced water availability (Lajtha and Whitford 1989; Gutierrez and Meinzer 1994). If the WUE of koa increased as a result of reduced stomatal conductance, rather than from increased photosynthetic capacity per unit leaf area, it would exhibit such a trade-off in resource-use efficiencies. In a fertilization experiment on *Picea abies*, N addition increased intrinsic WUE in a dry year but not in wet years, suggesting that the effect was that of increased LAI leading to more rapid depletion of soil water and thus stomatal closure rather than increased photosynthetic capacity (Högberg et al. 1993). We hypothesized that in koa, intrinsic WUE would be negatively correlated with biomass increment per unit of canopy nutrient mass, an integrated index of nutrient-use efficiency.

We set out to test the above hypotheses in natural stands of *Acacia koa* growing along an elevation/precipitation gradient on the island of Kauai, Hawaii. Unfortunately, Hurricane Iniki damaged our study sites only 6 months after establishment of our permanent measurement plots, making it impossible to complete the 3-year study as planned. Therefore, the results presented are based on a single measurement of pre-hurricane LAI and growth rates measured over a 6-month interval. Although preliminary, our results indicated that koa forest showed both developmental and physiological adjustments in response to water stress and that nutrient-use efficiency was traded off against intrinsic WUE.

Materials and methods

Sites

Study sites were located on the island of Kauai along an elevational gradient ranging from 500 m to 1130 m running across Puu Ka Pele Forest Reserve, Na Pali Kona Forest Reserve, and Kokee State Park (Fig. 1, Table 1). Annual precipitation along this gradient ranged from approximately 850 mm at the lowest elevation to 1800 mm at the highest elevation (Giambelluca et al. 1986). The corresponding mean daily temperature decreased approximately 5°C from the lowest to the highest elevation (Table 1).

Six study sites were established along the gradient in 1992 (Table 1). The sampling area at the sites was circular, 20 m in diameter, except for Makaha 1 (500 m) and Milolii (800 m), where a 12-m-diameter area was used to allow sufficient gap-free border. At the lowest elevation, Makaha 1 (500 m), the koa trees were low in stature, and stem form was convoluted and prostrate. Understory vegetation consisted primarily of *Styphelia tameiameiae*, *Scaevola* sp., and the exotic *Lantana camara*. At Makaha 2 (640 m), koa trees had a spreading growth form, there was a subcanopy of *Metrosideros polymorpha* and *Dodonaea viscosa*, and an understory of *L. camara* and *Styphelia tameiameiae*. The koa at the two mid-elevation sites, Milolii (800 m) and Puu Opae (900 m), had a spreading growth form, relatively open canopies with some individuals of *M. polymorpha*, and the understory was dominated by *Styphelia tameiameiae*, and *D. viscosa*. Puu Opae (940 m) was also invaded by the exotic species *Psidium guajava*. The two high-elevation stands, Kumuwela (1100 m) and Halemanu (1130 m), appeared to be in a state of gap phase regeneration, possibly as a result of Hurricane Iwa in 1982. Halemanu had a sub-dominant canopy of *M. polymorpha* and *D. viscosa*. Both high-elevation sites had a sparse understory of *Hedyotis* sp. and were invaded by the exotic species *Rubus argutus*.

Weather data

In 1992, weather stations were set up at 500, 800 and 1100 m along the gradient (Fig. 1). Air temperature (T, °C) and relative humidity (RH) were measured at 15-s intervals using a temperature and relative humidity probe (HMP35C, Campbell Scientific Inc. Logan, Utah). Hourly average, daily maximum and daily minimum T and RH were stored in a datalogger (model CR10, Campbell Scientific). Long-term mean annual rainfall was estimated by interpolation based on rain-gauges at known elevations in the vicinity of our site gradient (Giambelluca et al. 1986). Vapor pressure deficit (VPD) was calculated from T and RH data recorded at each weather station using the saturation vapor pressure equation of Murray (1966). Values for the 640, 900, and 1130 m sites were estimated by interpolation based on elevation.

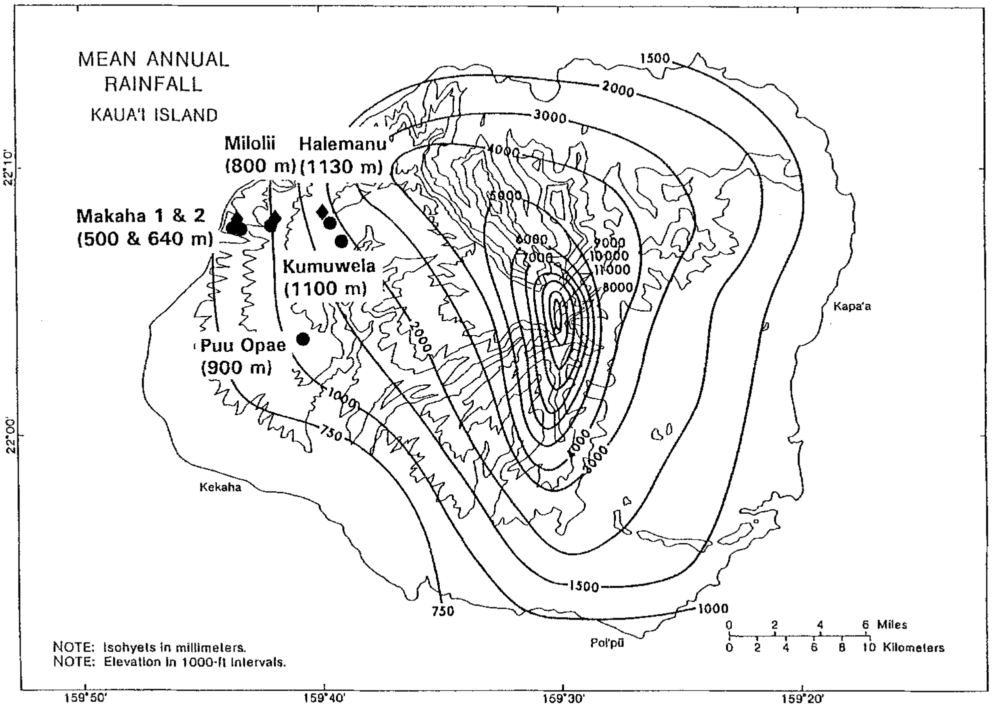

Fig. 1 Location of study sites (●) and weather stations (◆) in *Acacia koa* forests along an elevation/precipitation gradient on western Kauai, Hawaii

Table 1 Site and stand characteristics of *Acacia koa* forests growing along an elevation gradient on western Kauai, Hawaii: elevation, aspect, slope, mean monthly temperature (*T*) in January and July 1993, long-term mean annual rainfall, mean annual maximum vapor pressure deficit in 1993 (VPD_{max}), stem density of *A. koa*, mean tree diameter of *A. koa* at 1.3 m (*DBH*), percentage of total stand basal area (*BA*) which is *A. koa*, soil pH (1:1 water), and soil N, P, and K

Elevation (m)	Aspect (°)	Slope (°)	Jan T (°C)	July T (°C)	Rain (mm)	VPD_{max} (mbar)	Stem density (#/ha)	Mean DBH (cm)	% BA	Soil pH	Soil N (%)	Soil P (ppm)	Soil K (ppm)
500	265	10	16.8	22.1	850	14.8	4686	4.00	92.5	5.3	0.38	11.0	180
640	310	25	15.9	21.2	1000	14.2	1210	10.83	72.4	5.1	0.43	2.4	260
800	280	12	14.8	20.2	1165	13.6	6012	3.71	95.5	4.8	0.38	11.0	120
900	20	10	13.9	19.2	1270	12.4	1878	9.44	95.0	4.7	0.94	4.8	160
1100	210	17	12.1	17.3	1750	10.0	2992	9.98	66.7	4.0	0.75	2.0	120
1130	170	10	11.8	16.7	1800	9.6	8244	4.99	85.3	4.3	1.15	5.2	200

Tree and stand measurements

Total stand LAI was estimated nondestructively using a LI-COR LAI-2000 plant canopy analyzer (LI-COR 1992). In previous tests, optical estimates agreed well with harvest and allometric estimates of LAI in plantations of phyllodinous *Acacia auriculiformis* and other tropical tree species (Harrington and Fownes 1995). Above-ground woody biomass (*W*, kg) was calculated from measurements of stem diameter at breast height (*D*, cm) using the allometric equation:

$$W = 0.0668D^{2.418}$$

(K. Grace and J. Fownes, unpublished data). Stand woody biomass increment (ΔW, Tonnes ha^{-1} $year^{-1}$) was estimated from two measurements of *D* over a 6-month interval, and was used with measurements of LAI to calculate *E* (kg m^{-2} $year^{-1}$). ΔW and *E* were not calculated for Milolii (800 m) because this site had been measured only once before Hurricane Iniki hit Kauai (September 1992). Litterfall data were incomplete because of the hurricane and are not presented. Soil samples were taken at 5-m intervals along a transect running up and down slope and composited for analysis.

Foliage sampling and analysis

Fully expanded sun phyllodes were sampled from ten trees at each site and pooled to make up a single sample from each site. Leaf area was measured on fresh samples with an area meter (LI-COR LI-3100). The samples were then dried at 70°C, weighed and finely ground. Samples were analysed for nutrient content by the University of Hawaii Agricultural Diagnostic Service Center. We calculated canopy nutrient-use efficiencies as the above-ground woody biomass produced per unit of canopy N (CNUE) or P (CPUE).

Phyllode samples were taken during both wet and dry seasons for analysis of $\delta^{13}C$ (Boston University Stable Isotope Laboratory), and the two values were averaged.We calculated intrinsic WUE and actual WUE for koa phyllodes at each site from phyllode $\delta^{13}C$ values and estimates of the prevailing leaf-to-air VPD. Phyllode $\delta^{13}C$ values were first used to calculate isotopic discrimination (Δ) as

$$\Delta = (\delta_a - \delta_p)/(1+\delta_p)$$

where δ_p is the isotopic composition of the plant and δ_a is the isotopic composition of the air (Farquhar et al. 1982b). The $\delta^{13}C$ value of the air was taken as −8‰, the value at Mauna Loa, Hawaii (Anonymous 1984). The following relationships

$$\Delta = a + (b-a)p_i/p_a$$

and

$$p_i = p_a - 1.6A/g$$

where a is the discrimination resulting from slower diffusion of $^{13}CO_2$ than $^{12}CO_2$ in air (4.4‰), b is discrimination associated with carboxylation by Rubisco (29‰), and p_i/p_a is the ratio of intercellular (p_i) to ambient (p_a = 347 μbar) partial pressure of CO_2, were combined to yield the equation

$$A/g = 0.625p_a(1-(\Delta-a)/(b-a))$$

for the estimation of intrinsic WUE (A/g). Actual WUE (A/T; μmol mmol^{-1}) was calculated as

$$A/T = (A/g)/(\mathrm{VPD}/P)$$

where P is atmospheric pressure and VPD is the average maximum VPD at each site (Table 1). Phyllode temperature was assumed to be equal to air temperature for these calculations because previous measurements in koa stands on the island of Oahu indicated that phyllode-air temperature differentials were typically less than 1°C (F.C. Meinzer, R.A. Harrington and J.H. Fownes, unpublished observations).

Results

Stand characteristics along the gradient

Stand basal area, canopy height, LAI, and wood increment generally increased with elevation and therefore with precipitation (Fig. 2). In some cases the trends were relatively weak, and in each case, Makaha 2 (640 m) fell above and Milolii (800 m) fell below the regression lines (Fig. 2). Despite the scatter evident in these relationships, the functional relationship between wood increment and LAI was stronger (Fig. 3).

Phyllode characteristics

Phyllode nutrient content and SLM were not correlated with site elevation. However, phyllode N, P, and K concentrations (weight basis) were negatively correlated with SLM across sites (Fig. 4a). The low elevation sites were highest in nutrient content and Milolii (800 m) was lowest (Fig. 4a). There was no correlation between phyllode nutrient concentrations and surface soil nutrient pools (Table 1). Phyllode N per unit leaf area increased, whereas P and K per unit area decreased with increasing SLM, reflecting the fact that on a relative basis, P and K concentrations decreased more than SLM increased (Fig. 4b).

Phyllode $\delta^{13}C$ values generally became more negative with increasing elevation and precipitation, although the correlation with elevation was weak (Fig. 5). With the exception of Makaha 1 (500 m), there was a trend for nutrients to increase and SLM to decrease as $\delta^{13}C$ became more negative (Fig. 6).

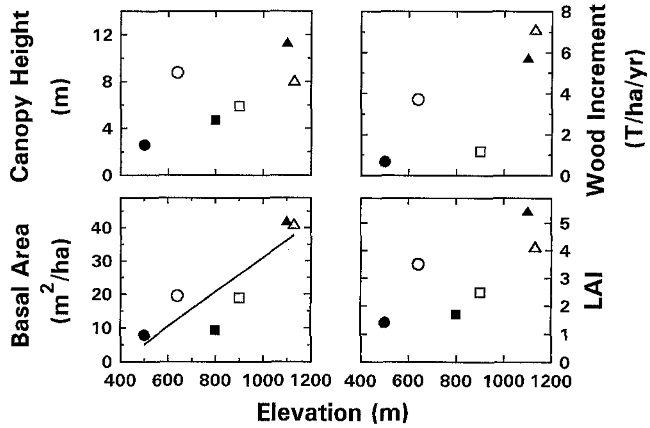

Fig. 2 Basal area (m^2/ha), canopy height (m), leaf area index (*LAI*), and wood increment (tonnes/ha per year) versus elevation for *Acacia koa* forest stands growing along an elevation/precipitation gradient on western Kauai, Hawaii. *Symbols* represent each of the six study sites: Makaha 1 at 500 m (●), Makaha 2 at 640 m (○), Milolii at 800 m (■), Puu Opae at 900 m (□), Kumuwela at 1100 m (▲), Halemanu at 1130 m (△). *Solid line* indicates significant (P < 0.05) regression (Basal area = –20.817 + 0.0519 elevation, r^2 = 0.69, P = 0.0250)

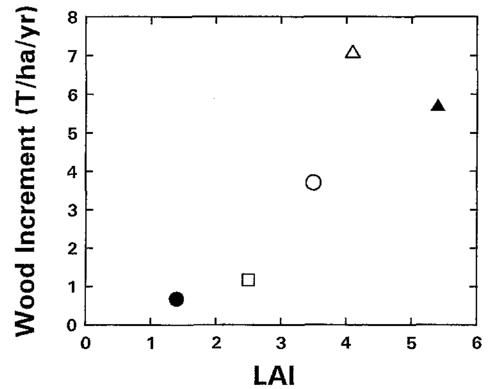

Fig. 3 Stand woody biomass increment (tonnes/ha per year) versus stand leaf area index (LAI) for *Acacia koa* forest stands along an elevation/precipitation gradient on western Kauai, Hawaii. *Symbols* represent each of the six study sites: Makaha 1 at 500 m (●), Makaha 2 at 640 m (○), Milolii at 800 m (■), Puu Opae at 900 m (□), Kumuwela at 1100 m (▲), Halemanu at 1130 m (△)

Resource-use efficiency and stand growth

Stand LAI, woody biomass increment, and E increased as $\delta^{13}C$ became more negative (Fig. 7). CNUE and CPUE generally increased with increasing elevation (Fig. 8), and $\delta^{13}C$ generally decreased with elevation (Fig. 5), suggesting that there was a trade-off between canopy nutrient-use efficiency (CNUE and CPUE) and intrinsic WUE (Fig. 9). Actual WUE (*A*/*T*) increased with elevation (Fig. 8) There was thus no significant correlation between actual WUE (*A*/*T*) and intrinsic WUE ($\delta^{13}C$) across sites (Fig. 9).

Discussion

Water limitation of stand development and growth

Stand basal area, canopy height, LAI and wood increment generally increased, and phyllode $\delta^{13}C$ generally

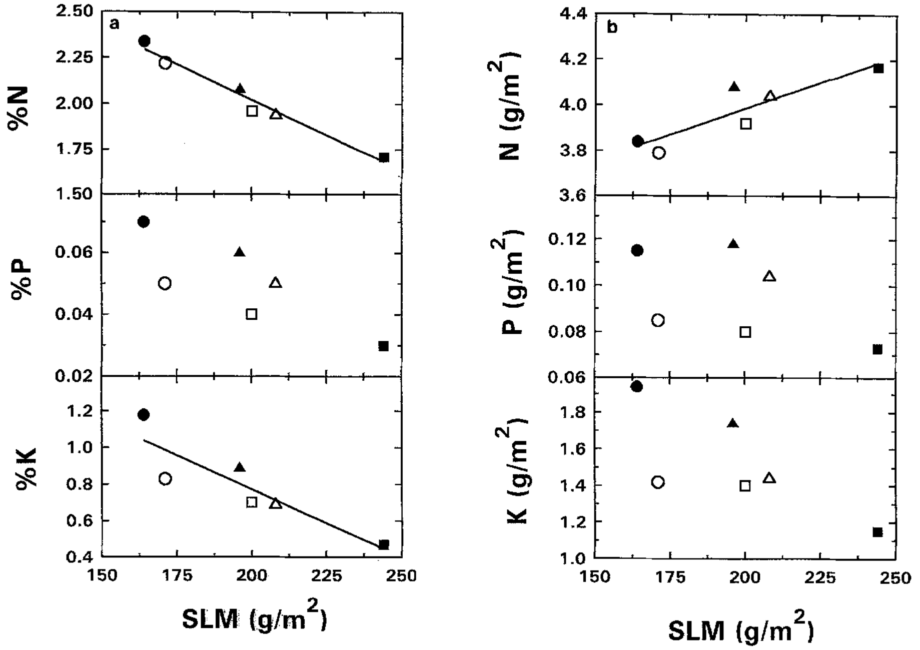

Fig. 4a,b Nutrient content **a** per unit leaf weight (%N, %P, %K), and **b** per unit leaf area (N, P, K g/m^2) of *Acacia koa* phyllodes versus specific leaf mass (*SLM*; g/m^2) sampled from forest stands growing along an elevation/precipitation gradient on western Kauai, Hawaii. *Symbols* represent each of the six study sites: Makaha 1 at 500 m (●), Makaha 2 at 640 m (○), Milolii at 800 m (■), Puu Opae at 900 m (□), Kumuwela at 1100 m (▲), Halemanu at 1130 m (△). *Solid lines* represent significant ($P < 0.05$) regressions ($\%N = 3.5497 - 0.0765\ SLM$, $r^2 = 0.96$, $P = 0.0004$; $\%K = 2.2492 - 0.7386\ SLM$, $r^2 = 0.74$, $P = 0.0177$; $NA = 0.3059 + 0.004632\ SLM$, $r^2 = 0.76$, $P = 0.0146$)

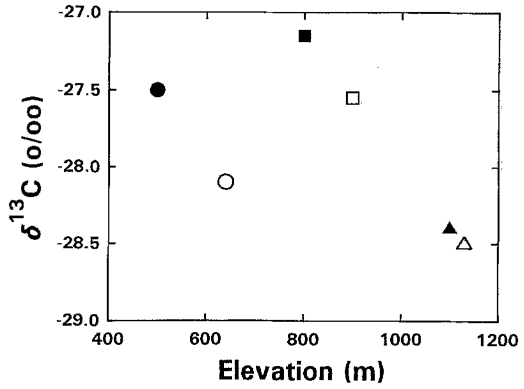

Fig. 5 Phyllode δ^{13}C versus elevation for *Acacia koa* stands growing along an elevation/precipitation gradient on western Kauai, Hawaii. *Symbols* represent each of the six study sites: Makaha 1 at 500 m (●), Makaha 2 at 640 m (○), Milolii at 800 m (■), Puu Opae at 900 m (▲), Kumuwela at 1100 m (▲), Halemanu at 1130 m (△)

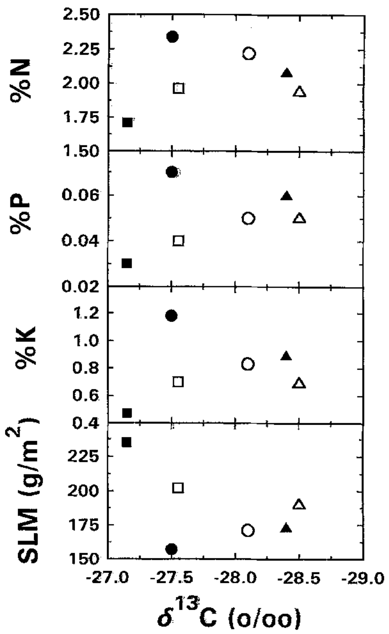

Fig. 6 Phyllode nutrient contents (%N, %P, %K) and specific leaf mass (*SLM*, g/m^2) versus phyllode δ^{13}C for *Acacia koa* stands growing along an elevation/precipitation gradient on western Kauai, Hawaii. *Symbols* represent each of the six study sites: Makaha 1 at 500 m (●), Makaha 2 at 640 m (○), Milolii at 800 m (■), Puu Opae at 900 m (□), Kumuwela at 1100 m (▲), Halemanu at 1130 m (△)

became more negative, with increasing elevation and therefore with increasing precipitation. However, differences in site microclimate at a given elevation may have diminished the correlations of these parameters with elevation. Makaha 2 is on a steep northwest-facing slope and had much greater stand basal area, LAI, canopy height, and wood increment than would be expected based on its low elevation (640 m). Makaha 2 also yielded more negative phyllode δ^{13}C than a simple regression against elevation would predict, suggesting that water availability may be higher than expected based on precipitation. Conversely, Milolii is on an exposed, west-facing ridge, and exhibited lower stand basal area, LAI and canopy height, than would be expected from its elevation (800 m). Here, phyllode δ^{13}C values were less negative than expected based on elevation, suggesting a relatively high intrinsic WUE and thus lower water availability than would be predicted from precipitation. Patterns along the elevation gradient may also have been clearer had we been able to collect longer-term observations before Hurricane Iniki.

Despite the scatter evident in the relationships between stand characteristics and elevation, we observed strong functional relationships among stand characteristics, and between stand characteristics and phyllode

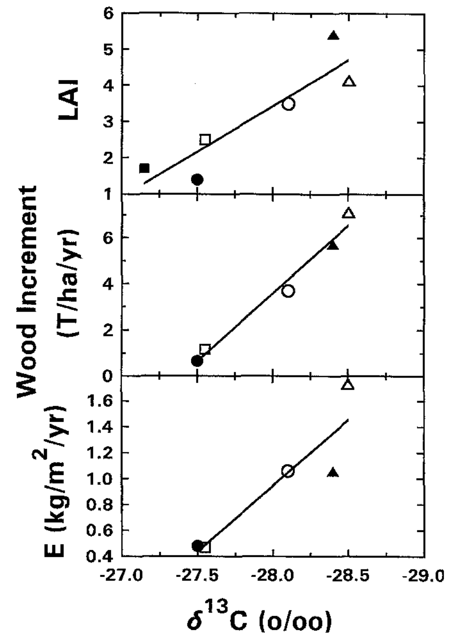

Fig. 7 Stand leaf area index (LAI), woody biomass increment (tonnes/ha per year) and woody biomass production per unit leaf area (*E*) versus phyllode $\delta^{13}C$ for *Acacia koa* stands growing along an elevation/precipitation gradient on western Kauai, Hawaii. Symbols represent each of the six study sites: Makaha 1 at 500 m (●), Makaha 2 at 640 m (○), Milolii at 800 m (■), Puu Opae at 900 m (□), Kumuwela at 1100 m (▲), Halemanu at 1130 m (△). *Solid lines* are significant ($P < 0.05$) regressions (LAI = –67.487–2.533 $\delta^{13}C$, $r^2 = 0.77$, $P = 0.0131$; wood increment = –161.05–5.8804 $\delta^{13}C$, $r^2 = 0.97$, $P = 0.0012$; E = –27.526–1.0169 $\delta^{13}C$, $r^2 = 0.79$, $P = 0.0270$)

$\delta^{13}C$. Our findings are consistent with the correlation between LAI and site water balance reported for Pacific Northwest forests (Grier and Running 1977; Gholz 1981) and the correlation between LAI and biomass increment (Waring 1983). Our finding that E was reduced under conditions of lower water availability (as suggested by less negative phyllode $\delta^{13}C$), agrees with observations in *Pinus sylvestris* (Waring 1983) and *P. contorta* (Kaufmann and Ryan 1986). The less negative $\delta^{13}C$ values and the lack of correlation with phyllode nutrient concentration indicate that the reduction in *E* was primarily caused by stomatal closure. However, the high SLM and high phyllode N on an area basis at Milolii suggest that both decreased stomatal conductance and increased photosynthetic capacity may have contributed to the high intrinsic WUE at this site. *Metrosideros polymorpha* on Kauai had less negative leaf $\delta^{13}C$ at sites with apparently low water availability and these higher values were associated with both decreased stomatal conductance and with increased biochemical capacity for photosynthesis (Meinzer et al. 1992).

In our study, actual WUE of koa increased with rainfall, because the 10% decrease in intrinsic WUE between 500 and 1100 m was more than compensated by a 33% decrease in average maximum leaf-to-air VPD. Interpretation of carbon isotope composition as a measure of actual WUE is thus subject to error if differences in VPD

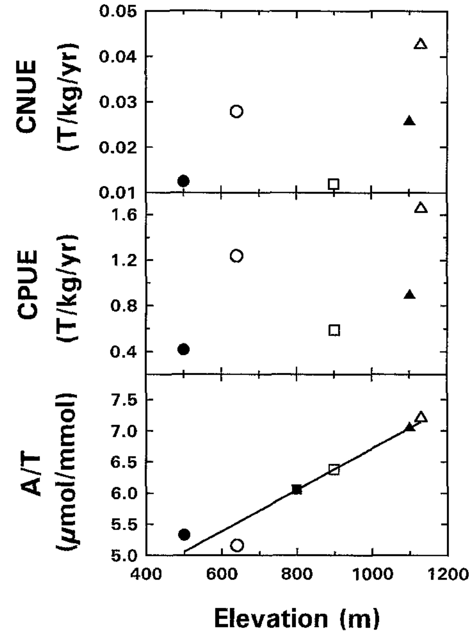

Fig. 8 Canopy nitrogen-use efficiency (*CNUE*), canopy phosphorus-use efficiency (*CPUE*), and photosynthesis/transpiration (*A/T*) versus elevation for *Acacia koa* stands growing along an elevation/precipitation gradient on western Kauai, Hawaii. Symbols represent each of the six study sites: Makaha 1 at 500 m (●), Makaha 2 at 640 m (○), Milolii at 800 m (■), Puu Opae at 900 m (□), Kumuwela at 1100 m (▲), Halemanu at 1130 m (△). *Solid line* is significant ($P < 0.05$) regression (3.4006 + 0.00331 elevation, $r^2 = 0.93$, $P = 0.0013$)

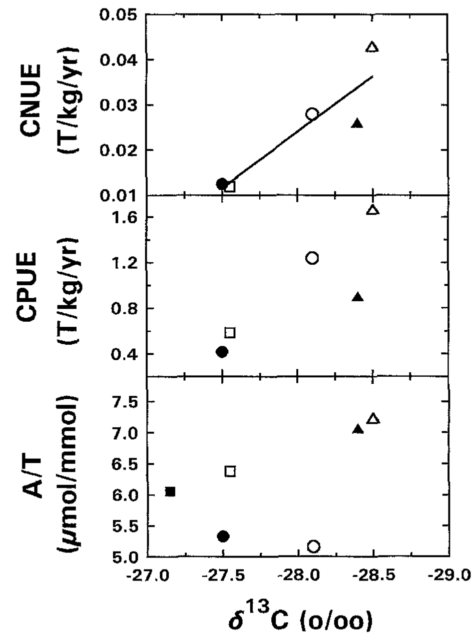

Fig. 9 Canopy nitrogen-use efficiency (*CNUE*), canopy phosphorus-use efficiency (*CPUE*), and photosynthesis/transpiration (*A/T*) versus phyllode $\delta^{13}C$ for *Acacia koa* stands growing along an elevation/precipitation gradient on western Kauai, Hawaii. Symbols represent each of the six study sites: Makaha 1 at 500 m (●), Makaha 2 at 640 m (○), Milolii at 800 m (■), Puu Opae at 900 m (□), Kumuwela at 1100 m (▲), Halemanu at 1130 m (△). *Solid line* is significant ($P < 0.05$) regression (*CNUE* = –0.6707–0.0248 $\delta^{13}C$, $r^2 = 0.76$, $P = 0.0310$)

are great (Farquhar et al. 1988). Although these results point to both leaf area and physiological responses to drought in koa, the increased LAI with increased phyllode P concentration (except at Makaha 1) suggests the possibility that productivity was also related to nutrient availability.

Nutrient limitation versus water limitation

Decreasing nutrient concentration with increasing phyllode SLM in koa resembles the pattern observed in *M. polymorpha* along an elevational gradient on the island of Hawaii (Vitousek et al. 1988; Vitousek et al. 1990). In *M. polymorpha*, these trends resulted in roughly constant nutrient content per unit leaf area (Vitousek et al. 1988), while we observed increasing N and decreasing P and K per unit leaf area with increasing SLM in koa.

Trees at the Makaha 1 (500 m) site had low stature and growth, low SLM, and yet relatively high phyllode nutrient concentrations. A similar pattern of leaf characteristics was found in *M. polymorpha* leaves on the island of Hawaii, where comparisons at the same elevations and substrate types but different annual rainfall rates showed higher nutrients and lower SLM at the drier sites (Vitousek et al. 1992). Nutrient concentrations could be higher at dry sites because soils developed from similar parent material have higher cation and P availability on dry than on wet sites (Jackson and Sherman 1953; Jenny 1980; Fox et al. 1991). Higher soil pH and extractable soil P and K concentrations at drier sites along our gradient are consistent with this pattern (Table 1). High phyllode nutrients but low LAI and less negative $\delta^{13}C$ at Makaha 1 suggest that limited water availability was more important than nutrient limitation there.

At the other five sites, phyllode nutrients, particularly P, increased as LAI increased and $\delta^{13}C$ became more negative. Such a pattern could arise from more rapid production and decomposition of organic matter at the wetter sites. The higher soil N at the higher sites (Table 1) supports this hypothesis. However, biomass increment and *E* were not correlated with phyllode nutrient contents, suggesting that growth was not primarily limited by nutrient availability. Although koa is known to fix atmospheric nitrogen, our attempts to quantify N fixation rates using the ^{15}N natural abundance method were inconclusive, but showed no evidence of a trend in fixation along the gradient.

Lower phyllode P concentrations at the drier sites would support the idea that increased intrinsic WUE was achieved primarily through stomatal closure rather than increased photosynthetic capacity. Although the highly weathered soil in this area is low in P (Table 1) and forest ecosystems in nearby but wetter areas are limited by P and not other elements (Herbert and Fownes 1995), we feel that the evidence, taken together, implicates water availability as the primary factor controlling production in koa stands distributed along an elevational gradient.

Resource-use efficiencies

Our estimates of CNUE and CPUE support the hypothesis that integrated nutrient-use efficiency is traded off against intrinsic WUE in koa. Similar trends have also been observed for instantaneous measurements: instantaneous WUE and photosynthetic NUE have been reported to be negatively correlated across species (Field et al. 1983) and across treatments in *Larrea tridentata* (Lajtha and Whitford 1989). Results varied, however, when instananeous nutrient-use efficiencies were compared with integrated estimates of WUE as estimated by foliar $\delta^{13}C$ values. Integrated WUE and photosynthetic NUE were negatively correlated across species (DeLucia and Schlesinger 1991) and across a span of plant age in *Coffea arabica* (Gutierrez and Meinzer 1994). However, among populations of *Metrosideros polymorpha* on Kauai, maximum photosynthetic NUE did not differ with site water availability and was independent of foliar $\delta^{13}C$ (Meinzer et al. 1992). In our study, integrated estimates of CNUE and CPUE were not traded off against actual WUE (A/T) because of the much lower VPD at the higher-elevation, wetter sites. These wetter stands had low intrinsic WUE, but relatively high actual WUE, because lower evaporative demand allowed for high rates of CO_2 uptake relative to water loss.

The use of integrated annual canopy nutrient-use efficiencies corresponds well to the use of $\delta^{13}C$ as an integrated index of intrinsic WUE. However, our sampling methods may underestimate CNUE and CPUE because only sun phyllodes were sampled, so the SLM values we obtained are probably higher than the canopy average (Boardman 1977). This error would lead to overestimation of canopy mass and thus underestimation of production per unit of canopy N or P. This effect would be greater at sites with high LAI, which correspond to our high-elevation, low-intrinsic WUE sites. This potential error does not weaken our conclusion: the slopes of the CNUE and CPUE versus intrinsic WUE relationships would actually be steeper than those presented.

Conclusion

Under conditions of reduced water availability, *Acacia koa* exhibited reduction of stand LAI and thus growth, as well as physiological adjustments that increased intrinsic WUE but reduced biomass production per unit of leaf area. Although phyllode nutrient contents generally increased as LAI increased, biomass increment and *E* were not correlated with phyllode nutrient contents, suggesting that water limitation was more important than nutrient limitation along the gradient. There appeared to be a trade-off between canopy nutrient-use efficiencies and intrinsic WUE. However, there was no trade-off between canopy nutrient-use efficiencies and actual WUE. Intrinsic WUE was apparently increased primarily through partial stomatal closure, but the actual WUE was strongly influenced by leaf-to-air VPD, and was therefore higher at the cooler, wetter high-elevation sites.

Acknowledgements This research was funded by the USDA NRI Competitive Research Grants Program (no. 91–37101–6673). We thank T. Suchocki for assistance in the field and in the laboratory. We thank M. Erickson and the staff of the Kokee Natural History Museum's J.M. Souza Jr. Training Center and Field Station for logistical support. We thank E. Petteys, the Kauai District Manager of the Hawaii Division of Forestry and Wildlife, and W. Souza, the Kauai District Supervisor of the Hawaii State Parks Division, for access to field sites. We also thank D. Bartholomew, G. Goldstein, P. Vitousek, and two anonymous reviewers for thoughtful comments on earlier drafts of this manuscript. This paper is Hawaii Agricultural Experiment Station Journal Series Number 4016.

References

Anonymous (1984) Modeling $\delta^{13}C$. In: Harris JM, Nickerson EC (eds) Geophysical monitoring for climatic change, no. 12. U.S. Department of Commerce, Boulder, Colo, pp 95–96

Boardman NK (1977) Comparative photosynthesis of sun and shade plants. Annu Rev Plant Physiol 28:355–377

Cannell MGR, Milne R, Sheppard LJ, Unsworth MH (1987) Radiation interception and productivity of willow. J Appl Ecol 24:261–278

DeLucia EH, Schlesinger WH (1991) Resource-use efficiency and drought tolerance in adjacent great basin and Sierran plants. Ecology 72:51–58

Dupouey JL, Leavitt S, Choisnel E, Jourdain S (1993) Modelling carbon isotope fractionation in tree rings based on effective evapotranspiration and soil water status. Plant Cell Environ 16:939–947

Ellsworth DS, Reich PB (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96:169–178

Evans JR, Sharkey TD, Berry JA, Farquhar GD (1986) Carbon isotope discrimination measured concurrently with gas exchange to investigate CO_2 diffusion in leaves of higher plants. Aust J Plant Physiol 13:281–292

Farquhar GD, Richards RA (1984) Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Aust J Plant Physiol 11:539–552

Farquhar GD, Ball MC, Von Cammerer S, Roksandic Z (1982a) Effect of salinity and humidity on ^{13}C value of halophytes – evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO_2 under different environmental conditions. Oecologia 52:121–124

Farquhar GD, O'Leary MH, Berry JA (1982b) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust J Plant Physiol 9:121–137

Farquhar GD, Hubick KT, Condon AG (1988) Carbon isotope fractionation and plant water-use efficiency. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecological research. Springer, Berlin Heidelberg New York, pp 21–40

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol 40:503–537

Field C, Merino J, Mooney HA (1983) Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. Oecologia 60:384–389

Fox RL, de la Pena RS, Gavenda RT, Habte M, Hue NV, Ikawa H, Jones RC, Plucknett DL, Silva JA, Soltanpour P (1991) Amelioration, revegetation, and subsequent soil formation in denuded bauxitic materials. Allertonia 6:128–184

Gholz HL (1981) Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology 63:469–481

Giambelluca TW, Nullet MA, Schroeder TA (1986) Rainfall atlas of Hawaii. Department of Land Natural Resources, State of Hawaii

Grier CC, Running SW (1977) Leaf area of mature northwestern coniferous forests: relation to site water balance. Ecology 58:893–899

Gutierrez MV, Meinzer FC (1994) Carbon isotope discrimination and photosynthetic gas exchange in coffee hedgerows during canopy development. Aust J Plant Physiol 21:207–219

Harrington RA, Fownes JH (1995) Radiation interception and growth of planted and coppice stands of four fast-growing tropical trees. J Appl Ecol 32:1–8

Herbert DA, Fownes JH (1995) Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. Biogeochemistry (in press)

Högberg P, Johannisson C, Hällgren J-E (1993) Studies of ^{13}C in the foliage reveal interactions between nutrients and water in forest fertilization experiments. Plant Soil 152:207–214

Jackson ML, Sherman GD (1953) Chemical weathering of minerals in soils. AdvAgron 5:219–318

Jenny H (1980) The soil resource: origin and behavior. (Ecological studies 37) Springer, Berlin Heidelberg New York

Kaufmann MR, Ryan MG (1986) Physiographic, stand, and environmental effects on individual tree growth efficiency in subalpine forests. Tree Physiol 2:47–59

Lajtha K, Whitford WG (1989) The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. Oecologia 80:341–348

Legg J, Day W, Lawlor DW, Parkinson KJ (1979) The effects of drought stress on barley growth: models and measurements showing the relative importance of leaf area and photosynthetic rate. J Agric Sci 92:703–716

LiCor Inc (1992) LAI-2000 plant canopy analyzer operating manual. LiCor Inc., Lincoln

Meinzer FC, Rundel PW, Sharifi MR (1992) Carbon isotope composition in relation to leaf gas exchange and environmental conditions in Hawaiian *Metrosideros polymorpha* populations. Oecologia 91:305–311

Mueller-Dombois D (1987) Forest dynamics in Hawaii. Trends Ecol Evol 2:216–220

Murray FW (1966) On the computation of saturation vapor pressure. J Appl Meteorol 6:203–204

Pook EW (1986) Canopy dynamics of *Eucalptus maculata* Hook. IV. Contrasting responses to two severe droughts. Aust J Bot 34:1–14

Vitousek PM, Matson PA, Turner DR (1988) Elevational and age gradients in Hawaiian montane rainforest: foliar and soil nutrients. Oecologia 77:565–570

Vitousek PM, Field CB, Matson PA (1990) Variation in foliar ^{13}C in Hawaiian *Metrosideros polymorpha*: a case of internal resistance? Oecologia 84:362–370

Vitousek PM, Aplet G, Turner D, Lockwood JJ (1992) The Mauna Loa environmental matrix: foliar and soil nutrients. Oecologia 89:372–382

Wagner WL, Herbst DR, Sohmer SH (1990) Manual of the flowering plants of Hawaii. Bishop Museum, Honolulu, Hawaii

Waring RH (1983) Estimating forest growth and efficiency in relation to canopy leaf area. Adv Ecol Res 13:327–354

Whitesell CD (1990) *Acacia koa* Gray. In: Burns RM, Honkala BH (eds) Silvics of North America, vol 2. Hardwoods. Agriculture Handbook 654, USDA, Washington DC, pp 17–25