Indicators of forest ecosystem productivity and nutrient status across precipitation and temperature gradients in Hawaii

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Abstract: Precipitation and temperature are known to have important effects on forest productivity, but these effects may be strongly mediated through their influence on soil and leaf nutrients. We measured indicators of forest productivity and soil and leaf nutrients across independent gradients of precipitation and elevation/temperature in lower montane Hawaiian forests dominated by a single overstorey species, *Acacia koa*, situated on 1500–3000-y-old soils that were mixtures of volcanic ash and basalt. Stand basal area was highest at the wettest site, 2000 mm mean annual precipitation (MAP), and leaf N and P were lowest at the driest site, 1000 mm MAP. Soil N availability and leaf N concentration declined across an 850-m elevation gradient, but this was not correlated with stand basal area or soil organic matter content. Across all stands, basal area was negatively correlated with the exchangeable soil P fraction. As well, the soil C:N ratio was negatively correlated with both soil P availability and the size of the primary mineral P fraction. Soil P availability and weathering appear to be important determinants of soil organic matter quantity and quality. Overall, precipitation is the major driving force for forest productivity, but P weathering and availability play important roles in limiting productivity in wetter sites and in controlling soil organic matter dynamics in these N-fixing forests.

Key Words: *Acacia koa*, carbon, elevation, forest, nitrogen, phosphorus, precipitation, productivity, leaves, soils, temperature

INTRODUCTION

The structure and function of forest ecosystems derive from interactions among climate, soils, the biotic community, and disturbance or management history. Over broad spatial scales, incoming solar radiation and evapotranspiration strongly influence ecosystem energy and water balance, which gives rise to changes in the structure and function of the dominant vegetation community (Holdridge 1967). At smaller spatial scales, topography, soil depth, mineralogy, and physical and chemical properties influence the supply and access of plants to soil water and nutrients, as well as the cycling of organic matter and nutrients (Montagnini & Jordan 2005).

In the islands of the Hawaiian archipelago, in the Pacific Ocean, there are strong gradients of precipitation and temperature associated with the dominant trade wind circulation patterns crossing volcanic mountains that range up to 4600 m in height. The dominant soil parent materials are deposits of ash and basalt that are relatively homogeneous in composition (Wright & Helz 1987). The native forest canopy is dominated by two tree species: *Metrosideros polymorpha* Gaud. and *Acacia koa* Gray. Both have broad ecological ranges, but *M. polymorpha* is a slow-growing, stress-tolerant tree that is a major primary successional, as well as a climax, species. *Acacia koa*, by contrast, is a fast-growing N-fixing tree that does not generally disperse well onto fresh lava or ash deposits but is a pioneering species during secondary succession.

Studies across environmental gradients in Hawaii have provided important insights into climatic influences on forest ecosystem structure and function. Increasing elevation generally leads to a decline in above-ground net primary productivity (ANPP) (Aplet & Vitousek 1994, Raich et al. 1997), litter decomposition (Vitousek et al. 1994), leaf nutrient concentration (Vitousek et al. 1988), and the accumulation of soil organic matter (SOM) and N during primary succession on young soils (Raich et al. 1997, Vitousek et al. 1988).
Ecosystem productivity shows an optimal response to increasing precipitation. In Hawaii, the above-ground net primary productivity (ANPP) of A. koa generally increases with mean annual precipitation (MAP) from 750–2500 mm (Ares & Fownes 1999, Harrington et al. 1995). Litter decomposition and nutrient cycling rates are also depressed at low precipitation, but soil nutrient availability and leaf nutrient concentration may actually be higher due to an overarching water limitation to plant productivity (Vitousek et al. 1992, 1994). As MAP increases above 2500 mm, there is a reduction in the soil oxygen level and redox status. This reduces litter decomposition, N mineralization, and N availability which results in lower stand biomass and ANPP (Kitayama et al. 1998, Schuur 2001, Schuur & Matson 2001). Thus, at low precipitation, forest productivity is primarily limited by water. As precipitation increases, this limitation is reduced, and forest productivity is increasingly limited by nutrient availability and supply rates.

Although effects of changes in MAP on A. koa forests have been investigated previously (Ares & Fownes 1999, Harrington et al. 1995), these studies have not addressed effects on soil properties or processes. In addition, the precipitation gradients investigated have been arrayed across elevation gradients associated with the orographic precipitation patterns common in Hawaii. This has introduced a confounding factor in the analysis and prevented the investigation of an independent temperature effect. Because A. koa is a nitrogen-fixing tree, productivity and nutrient responses to climatic variation may not be completely congruent with patterns found for M. polymorpha, especially on younger soils where N is limiting to the productivity of M. polymorpha. For A. koa, P rather than N may be the major limiting nutrient to productivity, even on relatively young soils (Pearson & Vitousek 2001, Scowcroft et al. 2007).

The objective of this study was to determine the effects of temperature and precipitation on basic indicators of forest productivity, nutrient availability, and plant nutrition in regenerating A. koa forests of Hawaii. Secondarily, we were interested in the degree of climate versus nutrient control over forest structure and productivity. We measured the basal area, leaf nutrient concentration, leaf mass per area, soil nutrient availability, soil organic matter, soil N mineralization potential and soil P fractions of forests dominated by A. koa that were distributed across independent elevation and temperature gradients on the Island of Hawaii. Relationships of site variables to the climatic gradients and to each other were used to provide insight into climatic and nutrient controls over forest productivity and nutrient status. We expected productivity to be more strongly related to precipitation than elevation and for soil and leaf P rather than N to be more sensitive to changes in precipitation and elevation.

Figure 1. Location of Acacia koa study plots on the Island of Hawaii. Thinner contour lines correspond to 500-m elevation increments. Thicker lines correspond to 500-mm increments of mean annual precipitation. Study site locations: Keauhou Ranch (KR), : Hawaii Volcanoes National Park (HAVO), ○: Honomalino (HONO), ●.

MATERIALS AND METHODS

Study site descriptions

This study was conducted on the Island of Hawaii, the largest and youngest in the Hawaiian archipelago (Figure 1). The A. koa forests selected were all regenerated in abandoned pastures and degraded forest that had been used for livestock grazing since the mid-1800s. Prior to that, they were most likely mixed A. koa–M. polymorpha forests, although few historical records exist of unaltered forest communities. We chose stands that had regenerated into almost pure A. koa forests after livestock exclusion and ungulate removal. Three sites were selected along the slopes of the Mauna Loa Volcano that varied in mean annual precipitation (MAP) from 1000–2000 mm. The driest site (1000 mm MAP) was at Honomalino (HONO), part of the larger Kona Hema Preserve owned and managed by The Nature Conservancy. Stands of A. koa were regenerated in 1978 after the cessation of grazing by deliberate scarification of the soil surface to stimulate seed regeneration. The moderate precipitation site (1500 mm MAP) was in the Hawaii Volcanoes National Park (HAVO), owned and managed by the US National Park Service. Acacia koa regenerated mainly from root sprouts after cessation of grazing and fencing and removal of all ungulates in
the early 1970s. The site with the greatest precipitation (2000 mm MAP) is part of Keauhou Ranch, owned and operated by Kamehameha Schools, a non-profit trust foundation. Livestock were removed from a degraded mixed *Acacia koa*–*M. polymorpha* forest near the top of the ranch (1600–1800 m). Beginning in 1977, separate 80-ha blocks were clearcut-harvested and scarified to remove all overstorey vegetation and to stimulate seed regeneration of *A. koa*. We chose to study the stand regenerated in 1978.

At each site, stands were selected between 1600 and 1650 m asl in order to control for variation in mean annual temperature (MAT). At HAVO, we selected additional stands that ranged from 1200–2050 m in elevation in order to establish an elevation/temperature gradient that was independent of the precipitation gradient. The stands were classified mainly as subtropical lower-montane wet and moist forests (Tosi et al. 2002), although stands at HONO, the driest site, were near the border of the dry forest transition. Stand age varied from 25–30 y at the time of the study (2003–2004). Stand density ranged from 1100–4250 trees ha$^{-1}$ (Table 1). *Acacia koa* represented 100% of the basal area in each stand selected for the study.

All but one of the stands were situated on soils derived from surface lava flows and ash deposits that ranged in age from 1500 to 3000 y (Lockwood et al. 1988). The stand at 1200 m at HAVO was on a 3000–5000-y-old mixture of ash and lava. The soils were classified as either Andisols or as Histosols with andic properties reflective of the volcanic parent material: low bulk density, high organic matter content, and high water-holding capacity (Soil Survey Staff, http://soils.usda.gov/technical/classification/osd/index.html).

Mean annual precipitation and temperature for each site was estimated by overlaying rainfall isohyets (Giambelluca et al. 1986) onto a map of site locations based on GPS coordinates. Mean annual temperature was estimated for each site from MAT data collected from NOAA weather stations distributed across the Island of Hawaii from near sea level to ∼4000 m. Climate summaries were obtained from the Western Regional Climate Center website (http://www.wrcc.dri.edu/index.html). Mean annual temperature at sea level and an empirical adiabatic lapse rate were estimated by plotting the 30-y (1971–2000) average MAT for each station against its published elevation and developing a linear regression equation. Mean annual temperature at sea level was estimated as the y-intercept at 0 m, 23.2°C, and the empirical adiabatic lapse rate was estimated as the slope of the regression line, 5.0°C per 1000 m.

### Stand inventory and productivity

Three plots, 10 × 10 m each, were selected in each stand. At the beginning of the study, tree stem diameter at breast height (dbh) was measured for all trees greater than 1 cm dbh and 1 m in height. Tree ferns were excluded from these measurements. Basal area was calculated as the sum of total tree cross-sectional area per unit ground area (m$^2$ ha$^{-1}$). One year later, the inventory was repeated to determine if there was a significant increase in stand basal area. Basal area was selected as an indicator of site productivity, assuming these 25–30-y-old stands had achieved or were approaching their maximum basal area (Gmax). Maximum basal area has been used for several decades to complement tree height at a standard base age, i.e. site index, as a predictor of stand volume and overall productivity (Assmann 1970). Conceptually, Gmax is related to the crown growing space requirement for trees of a certain stem diameter at breast height (dbh). As the individual tree crowns fill the available growing space, this sets the upper limit for the proportional stem basal area that the site can support. Further stem dbh growth requires the death of competing trees to free up the necessary growing space for the expanding tree crowns.

More productive sites can support trees with proportionally smaller crowns, which results in a higher Gmax (Baker & Scowcroft 2005). Gmax is typically well-correlated with tree height at a standard base age (i.e. site index) as an indicator of site productivity (Fralish 1994). The advantage of measuring basal area rather than height is that stands approach Gmax much earlier than maximum height (Sterba & Monserud 1993). The time to reach Gmax depends upon initial stem density and tree growth rates. Therefore, in stands that are assumed or known to be approaching Gmax, basal area can serve as a rapid index for comparison of site productivity, even in

### Table 1. Site characteristics for *Acacia koa* stands on the Island of Hawaii.

<table>
<thead>
<tr>
<th>Site</th>
<th>Elevation (m)</th>
<th>MAP (mm)</th>
<th>MAT (°C)</th>
<th>Stand age (y)</th>
<th>Soil age (y)</th>
<th>Density (stems ha$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>HONO 1600</td>
<td>1000</td>
<td>15.2</td>
<td>25</td>
<td>1500–3000</td>
<td>3400</td>
<td></td>
</tr>
<tr>
<td>HAVO 1200</td>
<td>1500</td>
<td>17.0</td>
<td>30</td>
<td>3000–5000</td>
<td>1630</td>
<td></td>
</tr>
<tr>
<td>HAVO 1350</td>
<td>1500</td>
<td>16.4</td>
<td>30</td>
<td>1500–3000</td>
<td>3530</td>
<td></td>
</tr>
<tr>
<td>HAVO 1600</td>
<td>1500</td>
<td>15.2</td>
<td>30</td>
<td>1500–3000</td>
<td>4250</td>
<td></td>
</tr>
<tr>
<td>HAVO 1900</td>
<td>1500</td>
<td>13.7</td>
<td>30</td>
<td>1500–3000</td>
<td>2600</td>
<td></td>
</tr>
<tr>
<td>HAVO 2050</td>
<td>1500</td>
<td>13.0</td>
<td>30</td>
<td>1500–3000</td>
<td>1100</td>
<td></td>
</tr>
<tr>
<td>KR 1650</td>
<td>2000</td>
<td>15.0</td>
<td>25</td>
<td>1500–3000</td>
<td>1330</td>
<td></td>
</tr>
</tbody>
</table>

*Stand age at HAVO approximate based on time of complete ungulate removal.*
stands with different stem density or somewhat different ages. In our sites, there was no significant increase in stand basal area between the two inventory periods; thus, we concluded that they were approaching Gmax. Basal area is reported as the average over the two successive inventories.

**Soil nutrient availability**

We used ion-exchange resin membrane (IEM) probes to estimate soil nutrient availability in the field, known commercially as PRS-probes (Western Ag Innovations, Saskatoon, Canada). The IEM probes consist of separate, semi-permeable cation and anion exchange resin membranes, each with a 17.5-cm² surface area encapsulated in a 3 × 15.5-cm plastic probe. The IEM is meant to act as an infinite sink for labile soil nutrients. In the field, however, IEM probes may act as dynamic exchangeers instead (Cooperband & Logan 1994). Despite these potential limitations, IEM probes have been used successfully in field and laboratory analyses. Extraction of P in laboratory incubations using IEM correlated highly (R² = 0.99) with extraction using more traditional ion exchange resin beads (Myers et al. 2005). In a growth chamber study, N adsorption by IEM probes correlated significantly and positively with crop N uptake grown in a range of soil types (Qian & Schoenau 2005). Adsorption on the IEM probes is sensitive to differences in nutrient availability associated with variability in soil water content (Johnson et al. 2005), season of the year (McGrath et al. 2000) soil depth (Drohan et al. 2005), and litter decay rates (Cooperband & Logan 1994), with incubation times ranging from 14 to 90 d (Drohan et al. 2005). More importantly for this study, they have been used successfully in tropical Andisols to determine plant-available P (Hernandez-Moreno & Negrin 1998).

For our study, IEM probes were inserted into the soil of each plot at a 45° angle to a depth of 5–10 cm below the soil surface and replaced every 3 mo for 1 y. Trials before the start of the study showed that the resin membrane surface was not saturated with the more available ions, e.g. Ca²⁺ and NO₃⁻, during this time interval, and results from probes used during the study confirmed this. After removal from the field, probes were washed in deionized water and sent back to the manufacturer for analysis. Nutrients are eluted from the resin surface in a solution of 0.5 M HCl and analysed for ammonium and nitrate on an autoanalyser. Other nutrient cations and anions are analysed using an ICP-emission spectrometer. Results are reported as micrograms of the cation or anion adsorbed per cm² of resin membrane surface. Data are reported as the average over each 3-mo period.

After the end of the field study, soil samples were collected from each plot for standard laboratory extraction, incubation and analysis for available N and P. Three samples from the 0–15-cm depth were collected in each plot and combined for analysis. Samples were kept on ice during transport to the laboratory and then refrigerated at 4°C. Soil was sieved field-moist through a 2-mm sieve to remove coarse fragments, roots and particulate organic matter.

A sample of the sieved soil was oven-dried at 105°C for at least 48 h to determine water content. Then a 10-g oven-dry equivalent sample was extracted in 100 ml of 2 M KCl by shaking on a shaker table for 1 h. Extracts, including a blank KCl solution sample, were filtered through Whatman cellulose filter paper and frozen. Samples were sent to the University of Hawaii-Manoa, Agricultural Diagnostic Service Center (ADSC) for analysis of ammonium (NH₄⁺) and nitrate (NO₃⁻) on an autoanalyser.

Additional samples were subjected to both aerobic and anaerobic incubations to measure N mineralization potential. An aerobic N mineralization potential (Nₐₐr) was chosen for comparison to previous studies in M. polymorpha (Vitousek et al. 1988) and A. koa (Pearson & Vitousek 2001) forests. Soils were wetted to field capacity and placed in flasks covered with parafilm to allow gas exchange but prevent water loss. Soils were incubated in the dark at room temperature, ~25°C, for 28 d. Field capacity was determined by saturating field-moist samples with distilled water on filter paper inside freely draining funnels. The soils were allowed to drain overnight (~16 h), and then they were weighed and oven-dried to determine water content. This was used to determine the amount of water to add to field-moist samples to bring them to field capacity prior to incubation.

The anaerobic N mineralization potential (Nₐₐa) was also determined to estimate the N contained in soil microbial biomass and overcome any potential N immobilization during aerobic incubation. For the anaerobic incubation, soils were saturated with water and kept for 7 d at 40°C in sealed flasks. After incubation, the samples were extracted and analysed for NH₄⁺ and NO₃⁻ as described above. Mineralization potential for both aerobic and anaerobic incubations was estimated as the difference in available N before and after incubation.

Soil P fractions were analysed using the Hedley et al. (1982) sequential extraction method as modified by Tiessen & Moir (1993). This procedure extracts P from more to less available pools with sequentially stronger chemical extractants. The anion exchange resin membrane probe was used to extract labile P (Resin-Pi). Next, 0.1 M NaOH was added to extract non-occluded
inorganic (NaOH-Pi) and organic (NaOH-Po) phosphorus, typically considered to be the exchangeable and mineralizable P pools, respectively. Finally, 1 M HCl was added to dissolve primary mineral P (HCl-Pi).

The initial NaOH extraction was acidified to precipitate the soluble organic matter; however, this was not sufficient to remove all visible traces in solution. We added acid-washed charcoal to the NaOH extracts and shook them gently for 10 min on a shaker table to adsorb all the remaining soluble organic matter (Olsen & Sommers 1982). After centrifugation, the supernatant was recovered for inorganic P analysis. Tests showed no significant addition or removal of inorganic P due to the charcoal filtration procedure.

Total soil P in the NaOH fraction was determined by digesting the extract with ammonium persulphate (Tiessen & Moir 1993). Extracts from all fractionation and digestion steps were analysed for inorganic P using the citric acid-molybdate colorimetric procedure on a UV-visible spectrophotometer (Murphy & Riley 1962). Organic P in the NaOH fraction was calculated as the difference between total P and NaOH-Pi.

Soil organic matter, C and N content

Soil organic matter content was determined via loss on ignition in a muffle furnace. Oven-dried soil samples were weighed into acid-washed crucibles that had previously been heated to 500 °C to remove any surface organic contaminants. The samples were then slowly brought up to 500 °C over a 4-h period in the muffle furnace and allowed to combust for an additional 4 h. The samples were cooled to ~200 °C, placed in a desiccator until they cooled to room temperature and then reweighed. Organic matter content was calculated as the change in mass before and after combustion. Total soil C and N content were determined from oven-dried samples in a Carlo Erba NA 2500 elemental analyser.

Leaf mass per area and nutrient concentration

A pruning pole with extensions was used to clip terminal branches in the upper canopy that contained fully expanded A. koa phyllodes, the swollen rachis of the compound leaf that replaces true leaves on mature plants. In each plot, five phyllodes were collected from each of three different trees and combined in a paper bag for a total of 15 leaves per plot and 45 leaves per site. Leaf mass per area (LMA, g m⁻²) was determined on fresh leaf samples using a flat-bed scanner. Leaves for nutrient analysis were oven-dried at 70 °C and ground through a Wiley mill to pass a 1-mm mesh screen. Leaves were sent to ADSC for analysis of N using an elemental analyser and for P via ICP-emission spectroscopy. Leaf nutrient concentration is reported on a leaf-mass (mg g⁻¹) and leaf-area (g m⁻²) basis.

Data analyses

Although replicate plots were randomly established within each stand, the stands themselves represented unique geographical locations. Thus, the replicate plots were not randomly distributed in space. This raises the problem of pseudoreplication (Hurlbert 1984), in which differences across the gradients may be due to uncontrolled sources of variation inherent to the particular geographic location of each stand rather than to differences in elevation or precipitation. For our study, the most likely sources of uncontrolled variation included genetic differences among the populations of A. koa and the thinner ash deposition on the soil at the driest site, HONO.

Despite these limitations, we chose to compare stands along the precipitation gradient by one-way analysis of variance (Proc ANOVA), using SAS software, Version 9.1 (SAS Institute, Inc., Cary, NC). Where significant differences were indicated, we used Tukey’s means separation test to distinguish significant differences among the sites. A significance level of 95% (P < 0.05) was used for the ANOVA and means separation tests.

We chose a regression approach to analyse differences along the elevation gradient at HAVO. Basal area and plant and soil nutrients were regressed against elevation using a linear regression approach in SAS (Proc REG). Again, significance was determined at the 95% level, and the strength of the correlation was reported as the R²-value. This avoids the problem of pseudoreplication but lacks the inferential power of ANOVA. We also regressed basal area and leaf and soil nutrient values against each other to explore their interrelationships.

RESULTS

Precipitation gradient

Basal area, leaf and soil nutrients arrayed across the precipitation gradient are summarized in Table 2. Basal area was significantly greater at KR (57.4 m² ha⁻¹) than at HAVO (20.8 m² ha⁻¹) but not at HONO (28.0 m² ha⁻¹). Leaf mass per area (g m⁻²) increased with decreasing precipitation from 191 g m⁻² at KR (2000 mm MAP) to 253 g m⁻² at HONO (1000 mm MAP), but differences among the sites were not significant (P = 0.12). Leaf N per mass decreased with precipitation from 2.30% at KR to 1.53% at HONO. Leaf N at HONO was significantly lower than at HAVO or KR. Leaf P per mass ranged from a low of 0.057% at HONO to 0.110% at HAVO. The
difference between these two sites was significant. When expressed per unit leaf area (g m$^{-2}$), leaf N per area was not significantly different among the sites. Leaf P per area at HAVO was significantly greater than at both HONO and KR.

Soil N availability as measured by the IEM probes did not differ significantly across the precipitation gradient. Average values over the 90-d periods were within ~10% of each other across all three sites (range = 22.3–25.0 µg cm$^{-2}$). Available N was dominated by NO$_3^-$ relative to NH$_4^+$, averaging 95% or more of the total at all three sites (data not shown). Soil P availability, however, was significantly different among the sites and decreased in the order HAVO > HONO > KR. Soil net N mineralization potential for both the aerobic and anaerobic laboratory incubations was significantly greater at HONO than at HAVO or KR. The N$_{ana}$ potential at KR was also significantly greater than at HAVO. The P fractions showed complex patterns across the precipitation gradient. Labile Resin-Pi was significantly greater at HONO (2.61 µg g$^{-1}$) than at KR (0.08 µg g$^{-1}$). There were no significant differences in the exchangeable NaOH-Pi or mineralizable NaOH-Po fractions. Primary mineral P, as indicated by the HCl-Pi fraction, was significantly greater at HAVO (251 µg g$^{-1}$) than at HONO (153 µg g$^{-1}$) and KR (78.6 µg g$^{-1}$).

Soil organic matter was high in all the soils but decreased significantly in the order KR (58.4%) > HONO (47.7%) > HAVO (28.7%). Soil C and N content, however, decreased significantly in the order HONO > KR > HAVO. The C:N ratio at KR (14.0) was significantly greater than at HAVO (11.8).

### Elevation/temperature gradient

The significance and strength of the correlations between elevation and A. koa basal area, leaf and soil nutrients across the 850-m gradient at HAVO are summarized in Table 3. Basal area varied across the elevation gradient from a high of 57.3 m$^2$ ha$^{-1}$ at 1350 m to a low of 20.9 m$^2$ ha$^{-1}$ at 1600 m, but there was no significant relationship with elevation. Similarly, LMA varied inconsistently across the elevation gradient, ranging from a low of 21.1 g m$^{-2}$ at 1350 m to a high of 274 g m$^{-2}$ at 1900 m. Leaf N per mass was significantly negatively correlated with elevation (R$^2$ = 0.89, P < 0.05), declining from 2.25% at 1200 m to 1.59% at 2050 m. Leaf P varied little across the gradient, ranging from 0.093% at 1200 m to 0.117% at 1350 m.

Soil N availability as indexed by the IEM probes declined significantly with elevation (R$^2$ = 0.86, P < 0.05) from 33.4 to 15.7 µg cm$^{-2}$. Soil P availability generally declined with elevation, but the correlation was not significant (P = 0.07). Aerobic and anaerobic N mineralization potentials showed no consistent patterns with elevation. Some of the soil P fractions did correlate significantly with elevation. Resin-Pi declined with

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**Table 2. Basal area and soil and leaf nutrients across a Mean Annual Precipitation (MAP) gradient for A. koa stands at 1600–1650 m elevation. Mean ± SE. Values within a row followed by the same letter do not differ significantly (P < 0.05). HONO = Homonalino Forest; HAVO = Hawaii Volcanoes National Park; KR = Keauhou Ranch.**

<table>
<thead>
<tr>
<th>MAP (mm)</th>
<th>HONO</th>
<th>HAVO</th>
<th>KR</th>
</tr>
</thead>
<tbody>
<tr>
<td>1000</td>
<td>1500</td>
<td>2000</td>
<td></td>
</tr>
<tr>
<td>Basal area (m$^2$ ha$^{-1}$)</td>
<td>28.0ab ± 6.45</td>
<td>20.8b ± 9.35</td>
<td>54.7a ± 6.96</td>
</tr>
<tr>
<td>LMA (g m$^{-2}$)</td>
<td>253a ± 11.4</td>
<td>225a ± 26.8</td>
<td>193a ± 24.4</td>
</tr>
<tr>
<td>Leaf N (%)</td>
<td>1.53b ± 0.139</td>
<td>2.12a ± 0.110</td>
<td>2.30a ± 0.01</td>
</tr>
<tr>
<td>Leaf P (%)</td>
<td>0.057b ± 0.006</td>
<td>0.110a ± 0.017</td>
<td>0.083ab ± 0.006</td>
</tr>
<tr>
<td>(g m$^{-2}$)</td>
<td>3.88a ± 0.353</td>
<td>4.46a ± 0.404</td>
<td>4.43a ± 0.664</td>
</tr>
<tr>
<td>Soil N (µg cm$^{-2}$)</td>
<td>24.7a ± 4.70</td>
<td>25.0a ± 9.33</td>
<td>22.3a ± 0.652</td>
</tr>
<tr>
<td>Soil P (µg cm$^{-2}$)</td>
<td>0.073b ± 0.002</td>
<td>0.129a ± 0.002</td>
<td>0.052c ± 0.004</td>
</tr>
<tr>
<td>N mineralization (µg g$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>aerobic</td>
<td>221a ± 26.9</td>
<td>45.6b ± 7.20</td>
<td>37.9b ± 35.9</td>
</tr>
<tr>
<td>anaerobic</td>
<td>309a ± 5.91</td>
<td>133c ± 19.4</td>
<td>214b ± 27.6</td>
</tr>
<tr>
<td>P fractions (µg g$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Resin-Pi</td>
<td>2.61a ± 0.34</td>
<td>0.98ab ± 0.44</td>
<td>0.08b ± 0.05</td>
</tr>
<tr>
<td>NaOH-Pi</td>
<td>86.2a ± 10.6</td>
<td>103.0a ± 0.70</td>
<td>70.3a ± 5.11</td>
</tr>
<tr>
<td>NaOH-Po</td>
<td>313a ± 65.7</td>
<td>167a ± 37.1</td>
<td>617a ± 135</td>
</tr>
<tr>
<td>HCl-Pi</td>
<td>153b ± 3.90</td>
<td>251a ± 35.8</td>
<td>78.6b ± 9.17</td>
</tr>
<tr>
<td>SOM (%)</td>
<td>47.7b ± 1.35</td>
<td>28.7c ± 3.06</td>
<td>58.4b ± 2.65</td>
</tr>
<tr>
<td>Soil C (%)</td>
<td>31.2a ± 3.62</td>
<td>15.2c ± 3.17</td>
<td>23.7b ± 1.33</td>
</tr>
<tr>
<td>Soil N (%)</td>
<td>2.28a ± 0.46</td>
<td>1.29c ± 0.14</td>
<td>1.69b ± 0.07</td>
</tr>
<tr>
<td>C:N</td>
<td>13.6ab ± 0.76</td>
<td>11.8b ± 0.18</td>
<td>14.0a ± 0.21</td>
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</tbody>
</table>
Table 3. Stand productivity and soil and leaf nutrients from 1200–2050 m asl at Hawaii Volcanoes National Park (HAVO). Strength of significant regression relationships with elevation are shown. Mean ± SE.

<table>
<thead>
<tr>
<th>Elevation (m)</th>
<th>1200</th>
<th>1350</th>
<th>1600</th>
<th>1900</th>
<th>2050</th>
<th>P-value</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal area (m² ha⁻¹)</td>
<td>55.1 ± 6.04</td>
<td>57.3 ± 12.4</td>
<td>20.9 ± 9.35</td>
<td>39.0 ± 22.8</td>
<td>27.9 ± 8.37</td>
<td>ns</td>
<td>0.76</td>
</tr>
<tr>
<td>LMA (g m⁻²)</td>
<td>218 ± 8.25</td>
<td>214 ± 10.5</td>
<td>211 ± 13.0</td>
<td>274 ± 2.50</td>
<td>264 ± 13.0</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>Leaf N (%)</td>
<td>2.25 ± 0.03</td>
<td>2.09 ± 0.13</td>
<td>2.12 ± 0.06</td>
<td>1.63 ± 0.01</td>
<td>1.59 ± 0.07</td>
<td>&lt;0.05</td>
<td>0.89</td>
</tr>
<tr>
<td>Leaf P (%)</td>
<td>4.91 ± 0.11</td>
<td>4.47 ± 0.34</td>
<td>4.46 ± 0.05</td>
<td>4.36 ± 0.10</td>
<td>4.23 ± 0.39</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>Leaf N per mass (%)</td>
<td>0.093 ± 0.003</td>
<td>0.117 ± 0.07</td>
<td>0.110 ± 0.001</td>
<td>0.100 ± 0.01</td>
<td>0.103 ± 0.003</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>Soil N (µg cm⁻²)</td>
<td>33.4 ± 3.02</td>
<td>32.6 ± 3.46</td>
<td>18.7 ± 2.27</td>
<td>13.1 ± 3.63</td>
<td>15.7 ± 2.62</td>
<td>&lt;0.05</td>
<td>0.86</td>
</tr>
<tr>
<td>Soil P (µg cm⁻²)</td>
<td>0.147 ± 0.025</td>
<td>0.168 ± 0.58</td>
<td>0.118 ± 0.003</td>
<td>0.123 ± 0.004</td>
<td>0.081 ± 0.012</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>N mineralization (mg g⁻¹)</td>
<td>58.6 ± 4.54</td>
<td>17.0 ± 5.18</td>
<td>45.6 ± 7.20</td>
<td>41.3 ± 22.8</td>
<td>36.4 ± 11.8</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>aerobic</td>
<td>229 ± 29.8</td>
<td>88.5 ± 27.9</td>
<td>133 ± 19.4</td>
<td>58.4 ± 12.4</td>
<td>112 ± 27.2</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>anaerobic</td>
<td>2.55 ± 0.482</td>
<td>0.976 ± 0.333</td>
<td>0.980 ± 0.440</td>
<td>0.521 ± 0.394</td>
<td>0.126 ± 0.002</td>
<td>0.05</td>
<td>0.76</td>
</tr>
<tr>
<td>Resin-P</td>
<td>52.8 ± 4.01</td>
<td>57.0 ± 22.3</td>
<td>103 ± 10.6</td>
<td>73.0 ± 0.697</td>
<td>80.2 ± 11.4</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>NaOH-Pi</td>
<td>133 ± 16.1</td>
<td>214 ± 23.8</td>
<td>182 ± 61.6</td>
<td>167 ± 37.1</td>
<td>212 ± 37.2</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>NaOH-Po</td>
<td>409 ± 12.3</td>
<td>377 ± 15.2</td>
<td>353 ± 24.5</td>
<td>251 ± 35.8</td>
<td>241 ± 20.9</td>
<td>&lt;0.01</td>
<td>0.96</td>
</tr>
<tr>
<td>HCl-Pi</td>
<td>24.0 ± 0.493</td>
<td>20.4 ± 1.69</td>
<td>28.7 ± 3.06</td>
<td>21.3 ± 1.39</td>
<td>23.2 ± 1.64</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>SOM (%)</td>
<td>12.8 ± 0.764</td>
<td>12.1 ± 0.732</td>
<td>15.2 ± 1.83</td>
<td>10.4 ± 0.893</td>
<td>13.6 ± 2.37</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>Soil C (%)</td>
<td>1.09 ± 0.047</td>
<td>1.07 ± 0.037</td>
<td>1.29 ± 0.135</td>
<td>0.843 ± 0.046</td>
<td>1.03 ± 0.207</td>
<td>ns</td>
<td>0.06</td>
</tr>
<tr>
<td>Soil N (%)</td>
<td>11.7 ± 0.322</td>
<td>11.3 ± 0.509</td>
<td>11.8 ± 0.179</td>
<td>12.4 ± 0.390</td>
<td>13.5 ± 0.567</td>
<td>&lt;0.05</td>
<td>0.77</td>
</tr>
</tbody>
</table>

From 2.51 to 0.126 µg g⁻¹ (R² = 0.76, P = 0.05). Likewise, HCl-Pi declined significantly with elevation from 409 to 241 µg g⁻¹ (R² = 0.96, P < 0.01). Soil organic matter, C and N content did not vary consistently across the elevation gradient. However, the soil C:N ratio increased significantly with elevation from a low of 11.3 at 1350 m to a high of 13.5 at 2050 m (R² = 0.77, P < 0.05).

Across both the elevation and precipitation gradients, there were significant correlations among the measurements of forest productivity and soil and leaf nutrients. Leaf N per mass was significantly negatively correlated with LMA (Figure 2a), but leaf N per area was not (Figure 2b). The N₃₅₅ potential was significantly positively correlated with soil C content (Figure 2c). Basal area was significantly negatively correlated with the NaOH-Pi fraction (Figure 3a). Available soil P was significantly positively correlated with the HCl-Pi fraction (Figure 3b) but negatively correlated with the soil C:N ratio (Figure 3c). The NaOH-Po fraction was significantly positively correlated with SOM (Figure 3d) and the HCl-Pi fraction was significantly negatively correlated with the soil C:N ratio (Figure 3e).

**DISCUSSION**

The pattern of increasing A. koa productivity with precipitation has been observed in previous studies across local precipitation gradients (Ares & Fownes 1999, Harrington et al. 1995). A separate study of A. koa populations distributed across the Island of Hawaii showed that trees in drier sites had larger crown growing space requirements, as well (Baker & Scowcroft 2005). Thus, productivity and Gmax are both lower in drier sites.

We did not find a significant relationship of A. koa basal area with elevation, but basal area was lower at 1600–2050 m (21–40 m² ha⁻¹) than at 1200 and 1350 m (55.1 and 57.3 m² ha⁻¹, respectively). Previous studies have generally found a decrease in ANPP with increasing elevation (Kitayama & Aiba 2002, Raich et al. 1997, Weaver & Murphy 1990) but not necessarily stand basal area, biomass or soil organic matter (Raich et al. 1997, Weaver & Murphy 1990). Singh et al. (1994) found no consistent differences in stand basal area, biomass, or ANPP in Himalayan forests of Nepal from 300–3000 m. Only in subalpine and alpine ecosystems above 3000 m were there any noticeable declines in biomass and productivity.

Raich et al. (1997) suggested that declines in ANPP with elevation were directly related to the effects of temperature on nutrient cycling and availability. In our study, we found a significant negative relationship between N availability and elevation, but there was no relationship between N availability and basal area or leaf N concentration. This is not unexpected, since A. koa is an N-fixing tree. An earlier study with N fertilization at KR showed no effect on stem diameter growth, stand basal area, or extractable soil N (Pearson & Vitousek 2001).
Leaf N per mass did decrease significantly with precipitation and temperature, but this is likely a consequence of changes in LMA across the environmental gradients. Based on a common garden experiment with A. koa seedlings collected across a precipitation gradient, Ares et al. (2000) concluded that LMA is a developmental adaptation of A. koa phyllodes to prevailing environmental conditions and does not inherently vary among populations.

Because leaf N per area did not vary significantly across the environmental gradients, we hypothesize that variation in LMA is likely the result of changing leaf density due to the build-up of non-photosynthetic tissues (Niinemets 2001). This would reduce leaf N per mass but not necessarily leaf N per area. Greater leaf density may result in increased internal CO₂ diffusion resistance, which would reduce photosynthetic rates (Niinemets et al. 2006). This relationship has not been investigated for A. koa.

The negative correlation between stand basal area and the exchangeable soil inorganic P pool (NaOH-Pi) may be a result of greater rate of P immobilization in A. koa woody biomass relative to weathering of primary mineral P. Pearson & Vitousek (2001) estimated an immobilization of ~50 kg P ha⁻¹ in the plant biomass of 20-ye-old A. koa stands at KR. Using their allometric equations and P concentrations for A. koa stems and branches, we estimate that there was ~80 kg ha⁻¹ of P immobilized in woody tissues in the stands we studied at KR, 22 kg ha⁻¹ at 1600 m at HAVO and 21 kg ha⁻¹ at HONO. Phosphorus weathering rates in Hawaiian soils with an average ash depth of 50 cm and an MAP of ~2500 mm were estimated as ~0.85 kg ha⁻¹ over the first 2100 y (Crews et al. 1995). Since the ash depth in our soils was ~20 cm and MAP ranged from 1000–2000 mm, weathering inputs are likely insufficient to match the P immobilization in regenerating A. koa tree biomass. If so, then scavenging of the exchangeable inorganic P pool would be necessary to maintain rapid P immobilization, and we would expect to see an inverse relationship between the P immobilization rate (i.e. A. koa productivity) and the size of the NaOH-Pi pool.

Differences in soil P availability across the climatic gradients appear to be more directly related to soil properties, such as primary mineral P and the soil C:N ratio, than to direct influences of temperature or precipitation. The soil C:N ratio has been used as an indicator of SOM quality, with lower ratios associated with a larger and more active microbial community (Friedel et al. 2006) and higher rates of N mineralization and nitrification (Bengtsson et al. 2003, Ross et al. 2004). It has also been related to soil P status in leguminous pastures (Parfitt et al. 2005). Parfitt et al. (2005) hypothesized that P limitation resulted in lower-quality litter production which then led to an increase in

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**Figure 2.** Influence of leaf mass per area and soil C on measurements of leaf and soil N. Leaf N per mass as a function of leaf mass per area (LMA) (a). Leaf N per area as a function of LMA (b). Anaerobic N mineralization potential (Nₐₐₙₐ) as a function of soil C (c). Keahou Ranch (KR), ▲; Hawaii Volcanoes National Park (HAVO), ○; Honomalino (HONO), ●.

Thus, elevation may have had a significant impact on N cycling rates, but this does not appear to be important to overall A. koa productivity.
the soil C:N ratio. We found a similar negative correlation between available P and the soil C:N ratio, suggesting that soil P may influence the quality of plant litter and SOM.

Available P was also positively correlated with the primary mineral P (HCl-Pi) pool. This suggests that weathering from this pool is important for supplying P for plant uptake. Kitayama et al. (2000) found a similar
relationship between labile and primary mineral P across an elevation gradient in tropical forests of Borneo. Elevation had an overriding influence on ANPP, but P use efficiency was related to the size of the actively cycling P pool.

It is unclear how climate may be influencing P availability and the primary P pool size across the environmental gradients in our study. In general, increasing temperature and precipitation increase biological and chemical reaction rates. This would drive greater soil weathering rates (Chadwick et al. 2003), which should result in a decline in primary mineral P. These patterns have been detected across gradients of precipitation (Miller et al. 2001) and elevation (Kitayama et al. 2000) in tropical forests on much older soils (≥105 y old). However, we found the highest primary mineral P and the highest P availability to the IEM probes in the middle of our precipitation range and a decline in primary mineral P with increasing elevation. Our only hypothesis is that due to the relatively young age of these soils, site-specific differences in recent ash deposition may be influencing the mineral P content of these soils in a manner that is inconsistent with the expected influence of temperature or precipitation.

In reviewing the sites in our study, it appears that even though stand basal area is highest at the wettest site, KR, it may be experiencing the greatest P limitation. It had the lowest soil P supply to the IEM probes; the lowest Resin-Pi, NaOH-Pi and HCl-Pi fractions; and the highest soil C:N ratio. By contrast, HAVO, the moderate-precipitation site, has in general the highest soil P supply, largest P pool sizes, and the lowest soil C:N ratio. We are uncertain why there is a decline in these values with increasing elevation. Despite the lower leaf N and P in the stands at HONO, available P was greater than at KR, and the Resin-Pi fraction was significantly larger than at KR or HAVO. Thus, the stands at HONO are probably limited mainly by water rather than available P. In contrast, the stands at KR are probably P-limited, as evidenced by their response to P fertilization in conjunction with thinning and understorey grass control (Scowcroft et al. 2007). The elevation gradient had a significant influence on N availability and leaf N concentration at HAVO, but neither was significantly related to stand basal area. As well, we cannot separate the direct effect of temperature from the indirect effect of variable ash deposition and soil depth on changes in P availability and supply across the elevation gradient. Given the dominant influence of N on SOM and nutrient cycling rates, the interactions of N and P across these environmental gradients and their influence on productivity, SOM, and nutrient cycling in these secondary A. koa forests deserve further study.

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LITERATURE CITED


