Symbiotic Nitrogen Fixation by *Acacia koa* at the Keauhou Ranch Reforestation Area

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Introduction

The rate at which *Acacia koa* (koa) stands develop has important implications for koa plantation forestry and the use of koa in ecosystem restoration. How quickly individual trees grow, how growth rate changes over time, and how stands self-thin is not well understood.

Development of koa stands may differ from that of other trees because koa is a nitrogen-fixing species. Like most legumes, koa is able to convert atmospheric nitrogen to a plant-usable form. In many Hawaiian forests, nitrogen is the nutrient that limits plant production, so koa may play an important role in ecosystem processes. The questions that I'll address include What is the rate of biomass and nitrogen accumulation in koa stands of different ages?, and How does nitrogen fixation by koa change as stands age?

Site description

Keauhou Ranch is the site of the largest and most complete age sequence of koa stands in Hawai'i. The Ranch, which is owned by Kamehameha Schools/ Bernice Pauahi Bishop Estate (KSBE), is located on the slope of Mauna Loa above Kilauea Caldera on the Big Island. Of the Ranch's 11,000 ha (27,180 acres), 3723 ha (9200 acres) have been withdrawn from cattle lease, and over 486 ha (1200 acres) are part of the koa reforestation project (Peter Simmons, pers. comm.).

Beginning in 1977, KSBE began to reforest land that had previously supported logging and grazing. The approach is to fence an area of 20–40 ha (50–100 acres) and to scarify the soil by bulldozing. Many seedlings sprout from the seed bank, and bare spots are planted with seedlings by KSBE students and staff. Over the years, intensity of scarification has decreased, and more seed trees and pockets of native forest have been left (Peter Simmons, pers. comm.). Stands are heavily dominated by koa; the ground cover is largely exotic grasses.

The completeness of this stand-age sequence presents a unique opportunity to look at koa stand development. In December 1995 I established four plots each in the 1977, 1984, 1988, and 1991 stands in relatively homogeneous areas of koa; plots are circular and 10 m in diameter. Although the reforestation area lies on a mixture of different-aged lava flows, my plots are all on 2000–3000 year old a'a. Mean annual precipitation in the area is 1900 mm (75 inches) (Giambelluca et al. 1986) and elevation is 1800 m (5900 ft).

What is the rate of koa biomass accumulation?

To estimate how quickly koa biomass accumulates over time, I measured diameter at breast height (DBH, 1.4 m) of all koa trees in the study plots and used allometric equations to calculate aboveground koa biomass. Allometric equations were developed by the USDA Forest Service based on harvests at Keauhou. In summer 1994 the Forest Service harvested 54 trees in the 1977–1979 stands; DBHs ranged from 8 to 30 cm. In November 1995 the Forest Service and I harvested an additional 25 trees in younger stands (1987 and 1991) to provide accurate data for trees from 1.5 to 8 cm DBH. Whole trees divided into stem, branches, twigs, and leaves were weighed in the field. Tissue subsamples were dried in the lab. Tree DBH is related to aboveground dry weight as shown in Figure 1.

Estimates of aboveground koa biomass in stands ranging from 5 to 19 years in age show that biomass accumulates relatively quickly for the first 12 years but slows substantially between 12 and 19 years (Figure 2).

What is the rate of koa nitrogen accumulation?

To estimate aboveground nitrogen accumulation in koa leaves, branches, and stemwood over time, I used allometric equations to calculate biomass of these pools and multiplied by tissue percent nitrogen. Nitrogen analyses (Kjeldahl digestion) were done at Stanford University.

Stem and branch wood nitrogen accumulates relatively rapidly during the first 12 years of tree growth and more slowly for the next seven years (Figure 3). Total mass of leaf nitrogen, on the other hand, increases for the first eight years of stand development and then declines. On a per-hectare basis, leaf biomass is similar

Figure 1. The relationship between aboveground biomass and DBH for 79 sample trees in Keauhou Ranch Reforestation Area. $f(x) = -0.109x + 0.233x^2 + 0.002x^3$; $R2 = 0.969$.

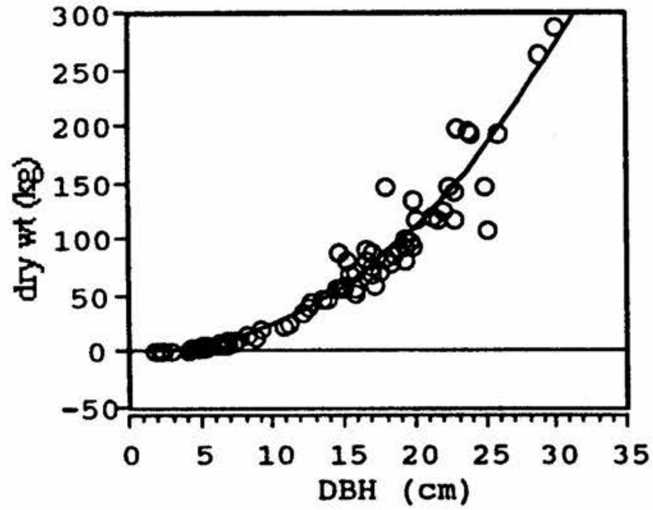


Figure 2. Accumulation of aboveground koa biomass in an age sequence of koa stands at Keauhou Ranch Reforestation Area (mean ± standard error).

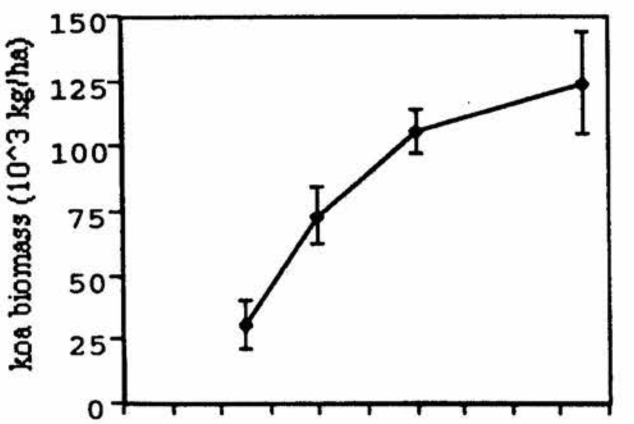


Figure 3. Accumulation of aboveground koa nitrogen in an age sequence of stands at Keauhou Ranch Reforestation Area.

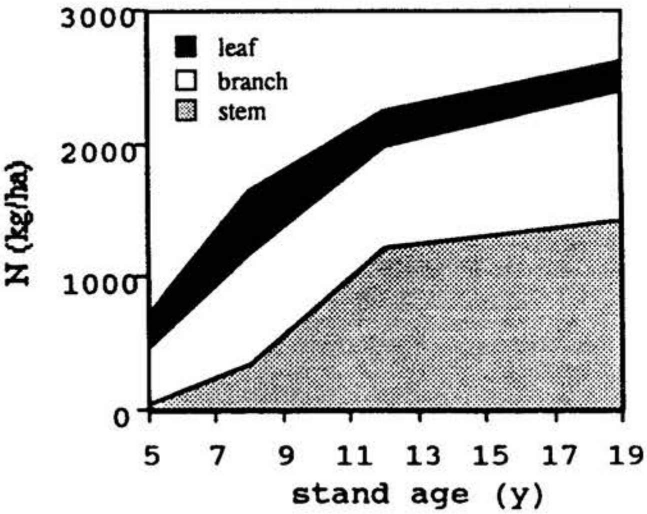
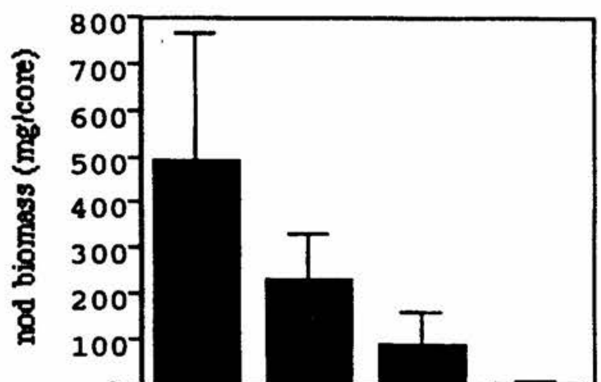


Figure 4. Nodule biomass per unit area of soil in an age sequence of koa stands at Keauhou Ranch Reforestation Area, Feb. 1996 (mean ± standard error). Cores were $0.05\ m^2$, 30 cm deep; n = 8 per stand age.



in the 5-year-old and the 19-year-old stands, which may have important implications for stand development.

How does nitrogen fixation by koa change as stands age?

There are three major sources of the nitrogen that become incorporated into koa biomass: the soil, atmospheric deposition (i.e., dry deposition and precipitation), and symbiotic nitrogen fixation. I estimated the amount of nitrogen that koa fixes in stands of different ages.

Nitrogen is fixed by bacteria (*Bradyrhizobium* spp.) that live in nodules on the tree roots. Nitrogen input to the ecosystem depends on both the rate of the enzymatic reaction in nodules and the abundance of nodules. Using an enzymatic assay (acetylene reduction), I found that reaction rate did not vary significantly between nodules in old and young stands. Thus, the important variable to consider is nodule abundance.

To measure abundance of nodules in the field, I dug soil cores in study plots. Nodules were sorted from the soil, dried, and weighed.

I found a striking pattern in nodule abundance: while young trees are heavily nodulated, nodule biomass declines quickly, and by 19 years of age trees have essentially no nodules (Figure 4). Thus, nitrogen input to the ecosystem via fixation is important only in the early years of stand development.

Discussion

Why these declines in tree growth rate and nitrogen fixation occur is not obvious. In natural mixed-species forests, koa trees of greater size and age than those in the oldest stand here continue to fix nitrogen (pers. observation), so some feature of these stands or this site must be responsible for the decline that we observed.

I think that the explanation involves energy. Tree growth and nitrogen fixation are both dependent on energy supply—carbon is fixed by photosynthesis in the leaves and transported to other parts of the plant, including nodules. Leaf biomass decreases relative to wood biomass as stands age (Figure 3). With a decline in rate of carbon accumulation relative to tissue respiratory costs, trees may not be able to spare carbon to support growth and nitrogen fixation.

The idea of a photosynthesis-respiration imbalance has been used to explain the general phenomenon of a decline in aboveground net primary production with stand age. This hypothesis has recently been called into question because sapwood respiration comprises a small part of stand carbon budgets and increases little after canopy closure (Gower et al. 1996, Ryan and Waring 1992). Other proposed mechanisms of decreasing nutrient (especially nitrogen) availability and photosynthetic rate over time seem to be relatively more important (Gower et al. 1996). However, the importance of sapwood respiration increases with temperature and if sapwood biomass continues to increase over time (Gower et al. 1996, Ryan et al. 1995). Thus, in the case of these koa stands, a limitation of growth and nitrogen fixation by carbon supply seems plausible: sapwood volume is increasing substantially over this short age sequence; temperatures are relatively warm year-round; and nitrogen availability increases, rather than decreases, over time (H.L. Pearson, unpublished data), presumably because koa is a nitrogen-fixer.

I am currently testing this explanation in a thinning experiment at Keauhou. The experiment will tell me whether trees sustain higher growth and nitrogen-fixation rates for a longer period of time if they are widely spaced.

I have worked in only one site so I cannot make generalizations for all the places in which koa grows. I expect, however, that these patterns will be found in other dense koa stands, but that rates of tree growth and the decline in nitrogen fixation will differ. Climate, soil fertility, and other ecosystem characteristics would be expected to influence stand development.

The results of this study are interesting from both scientific and land-management perspectives. Effective use of koa in plantation forestry and ecosystem restoration requires an understanding of how koa stands develop and why they develop that way.

Conclusions

The patterns of koa stand development that I found at Keauhou Ranch are as follows:

1. Rates of koa biomass and nitrogen accumulation decline substantially after the first decade of tree growth.

2. Nitrogen fixation by koa also declines as stands age, so that input of nitrogen via fixation is negligible in stands older than 12 years.

Acknowledgements

I thank T. Casey, K. Figueira, P. Kealoha, R. Lindsey, and P. Simmons of Kamehameha Schools Bernice Pauahi Bishop Estate for access to the field site and/or logistic support; P. Simmons for helpful discussions; J. Ewel, D. Goo, P. Scowcroft, and A. Urakami of the USDA Forest Service, Institute of Pacific Islands Forestry, for collaboration on allometric harvests; M. Nordborg and D. Pearson for field assistance; T. Benning and J. Burns for map-making; and my advisor, P. Vitousek, for support of this work.

Literature cited

Giambelluca, T.W., M.A. Nullet, and T.A. Schroeder. 1986. Rainfall atlas of Hawai'i. Department of Land and Natural Resources, State of Hawai'i, Honolulu, Hawaii, USA.

Gower, S.T., R.E. McMurtrie, and D. Murty. 1996. Aboveground net primary production decline with stand age: potential causes. Trends in Ecology and Evolution 11:378–382.

Ryan, M.G., S.T. Gower, R.M. Hubbard, R.H. Waring, H.L. Gholz, W.P. Cropper Jr., and S.W. Running. 1995. Woody tissue maintenance respiration of four conifers in contrasting climates. Oecologia 101:133–140.

Ryan, M.G., and R.H. Waring. 1992. Maintenance respiration and stand development in a subalpine lodgepole pine forest. Ecology 73:2100–2108.

Smith, V.H. 1992. Effects of nitrogen:phosphorus supply ratios on nitrogen fixation in agricultural and pastoral ecosystems. Biogeochemistry 18:19–35.

Questions

Q: Your data indicate there's stagnation occurring in the stand, and what is your proposed thinning percentage?

A: I should point out that in the stagnation, the decline in koa biomass accumulation rate, there can be two things going on: one is density changes, and one is growth-rate changes. What I'm finding is that tree density changes, falls off dramatically over time, but that growth rate of dbh increases, continues to increase. Most of that biomass pattern can be explained by decline in density over time. What I've done in the thinning experiment is to reduce basal area by about 50 percent. I did that by removing trees that were smaller and that were misshapen, and I tried to pick out ones that I thought a forester would leave. But the density that I have left is probabaly much higher than we'll see in, say, a 40-year-old stand.

Q: Could you describe the soils in that area and their productivity? How do they compare with other soils throughout the islands?

A: Yes, I didn't present any of the soils data at all. It's a two-to three-thousand-year-old a'a flow that's been bulldozed. It's a jumble of rocks, a very rocky substrate. I think available phosphorus as quite low at that site. I expect that will increase, but not in the time scales we're looking at. Available N . . . I can't compare that off the top of my head to other sites, but one interesting thing I've found is that as the stands get older, nitrogen availability increases. Which is the pattern we'd expect to see with a nitrogen-fixer.

Q: What was the original plant spacing on those sites?

A: After the scarification, a lot of seedlings came up out of the seed bank, and then bare spots were filled in with seedlings. I know the original density of seedlings put in was tremendous, about 80,000 seedlings per acre in the first allotments. Then in later years, in the eighties and nineties, that density was down. Still, thousands of seedlings per acre.