Water-Use Efficiency in Hawaiian Trees:

An Eco-physiological Approach and Methodology

by Sharifa Gulamhussein, MFS 2005

Background

The ultimate causes of deforestation are manifold, often involving social, political, and economic motivations for the region in question. In the case of Hawaii, vast tracts of tropical forest were cleared in the 1830's for timber extraction of *Santalum* and *Acacia* trees and to make way for a booming cattle industry (Elevitch and Wilkinson 2000). In the past few decades, however, Hawaii's economy has shifted heavily toward agriculture and tourism, resulting in subsequent abandonment of these lands. Today, an estimated two-thirds of state's original forests have been cleared and only 10% of Hawaii's dry tropical forests now remain (Juvik and Juvik 1998).

Natural forest regeneration in Hawaii is severely impeded due to the synergistic effects of dry, nutrient-depleted soil conditions and the growing threat of intractable invasive species (Reiners et al. 1994; Scowcroft et al. 2004; Vitousek et al. 1987). Although reforestation efforts were first attempted in the 1920's by the Hawaiian Territorial Forestry officials and the private, non-profit Hawaiian Sugar Planters' Association, they involved the systematic introduction of exotic tree genera such as *Araucaria*, *Casuarina*, and *Eucalyptus* on Forest Reserve lands (Woodcock 2003). Among Hawaiians today, there is growing concern for implementing more environmentally friendly approaches, such as reforesting using native species (Dewar 2002; Elevitch and Wilkinson 2000; Kelly 2003). The tremendous environmental benefits of planting native species include ameliorating degraded soil conditions, encouraging forest regeneration, providing habitat for endangered species, preventing watershed erosion and flash floods, and maintaining ecosystem integrity and health in the long term (Harrington and Ewel 1997; Hobbs and Norton 1996; Montagnini 2001). Public and private institutions, local communities, and individuals are asking, "Which native species will grow well? Where should I plant them? How will reforesting my land benefit me, my community, or institution and the environment at large?" Investigating how plants will physiologically respond to degraded, water-stressed site conditions and whether they will survive in the long-term can help address these questions.

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An Eco-physiological Approach

Plant eco-physiology is the science of understanding how plants respond to the abiotic and biotic factors that affect their growth and development in a given environment (Larcher 2003). Eco-physiological research provides a keen understanding of whole plant functions while simultaneously contributing useful information about forest health by identifying "stressful" growth environments for plants such as limiting light, water, or nutrients. In the past, reforestation studies focused on simply restoring degraded soils by planting native species. The assumption was that if it grew there in the past, it can grow there now

(Elevitch and Wilkinson 2000). It is apparent, however, that as landuse changes through time, so do the growing conditions available at a particular site (Scowcroft et al. 2004). The power in conducting eco-physiological research resides in its practical premise: determining *how* and *why* native plant species grow well on certain sites and *what* limits their growth including factors such as resource competition for water, light, nutrients, and space with other organisms.

Eco-physiological Methods

Many eco-physiological studies begin their investigations with the tree's leaf. Leaves are the most vital organs of the vegetative plant body. Their primary function is the collection and transformation of sunlight, carbon dioxide, and water into sugars for energy and growth (Ashton and Berlyn 1992; Kerstetter and Poethig 1998). Indeed, leaf structure has evolved through time to maximize function while compensating for environmental stressors such as low-moisture availability (Kaplan 2001). For example, leaves posses tiny pores on their surface called "stomata," deriving from the Greek word for "mouth." Acting like miniature gates, these stomata regulate the amount of carbon dioxide and water entering and leaving trees at any given time (Willmer and Fricker 1996). The total number of stomata per leaf area and their size can restrict the amount of air and water entering a tree from the atmosphere, hence ultimately affecting tree growth. Eco-physiologists often conduct light-microscopic studies determining stomatal number, size, and density per leaf surface. Measuring these parameters can help elucidate the structural constraints of plant carbon intake and water-use overtime (Berlyn and Miksche 1976).

In addition to leaf anatomical methodologies, it is useful to research tree water-use using carbon chemistry. On Earth, there are two naturally existing elemental forms of carbon: abundant ^{12}C (98.9%) and its heavier isotope ^{13}C (1.1%), which contains an extra neutron in its atomic nucleus (Farquhar et al. 1989). By examining the distribution of these two types of carbon in nature and their transformation and fixing into organic compounds like sugars during photosynthesis, plant function and plant water-use can be modeled (Dawson et. al, 2002; Farquhar et al. 1989).

Water-use Efficiency in Trees

Water-use efficiency (WUE) is an eco-physiological measure quantifying the ratio of net CO_2 uptake from the atmosphere during photosynthesis versus net H_2O loss (Larcher 2003). WUE can be measured directly throughout a day as a plant conducts photosynthesis, allowing CO_2 into a leaf and water vapor out through the stomata. Although instantaneous measures of water-use efficiency are important for understanding short-term plant water use, it is often useful to model water-use and loss over the longer time scales using $\delta^{13}C$ stable isotopes. $\delta^{13}C$ integration into a tree and subsequent kinetic fractionation, that is selective discrimination against $\delta^{13}C$ uptake by the enzyme Rubisco, occurs during CO_2 carbon fixation, leaving the heavier $\delta^{13}C$ isotope behind inside the leaf. Hence, measuring the isotopic levels of $\delta^{13}C$ in plant leaves can be used as a standardized measure of water-use and loss through time (Dawson et al. 2002; Warren et al. 2001). In addition to leaf analysis, other methods of measuring tree WUE have been developed to quantify $\delta^{13}C$ in wood cellulose of tree rings to account for water-use through multiple growing seasons over a tree's life-time (Brendel et al. 2000; Ferrio and Voltas 2005; Leavitt and Long 1986). Stable isotopic modeling in tree rings has been used in climate change research to reconstruct paleoclimates to extrapolate CO_2 levels in our atmosphere pre-industrial revolution (Barber et al. 2004).

On the scale of entire watersheds, eco-physiologists today are modeling the flow of water and carbon through forests using methodologies from both the fields of plant physiology and stable isotopic chemistry. This integrative approach allows for tracing the source and fate of water and carbon dioxide at the ecosystem level. One hot topic in eco-physiological research involves tracing from *where* a tree receives its water using the stable isotopes of $\delta^{18}O$ and deuterium δD. This isotopic approach teases apart the various sources of water entering a tree be it from shallow soils, deep ground water, or from precipitation (Dawson et al. 2002; Yakir and Sternberg 2000).

Eco-physiological Studies in Hawaii

Currently, one of the most promising approaches for reforestation in Hawaii is replanting degraded landscapes with native tree species such as *Acacia koa* (Gray) which could potentially ameliorate dry, degraded soil conditions encouraging forest regeneration. Within the past 20 years tree eco-physiological studies with koa have steadily increased. Walters and Bartholomew (1984, 1999) investigated tree anatomical response to gas exchange, water use, and light in a greenhouse setting. Meinzer et al. (1996) found that WUE could be attributed to physiological responses of stomata closing under stressed environmental conditions. Harrington et al. (1995) investigated how moisture determines leaf area index (LAI) and water-use of koa along a precipitation gradient on the island of Kauai. Ares and Fownes (1999) sampled leaves along an elevation gradient in order to determine koa stand structure, productivity, and water use on the big island of Hawaii. Still others have investigated the role of substrate type, nutrient availability, and role of temperature and geographic location on native trees (Pearson and Vitousek 2002; Scowcroft et al. 2004). Determining the environmental factors which limit tree growth and establishment in the wild, then, is a vital piece of the larger effort in understanding how native trees grow and interact with the Hawaiian environment at large.

Although eco-physiological studies are crucial for elucidating plant function from tiny leaf to whole watersheds, it is important to use an interdisciplinary team to present decision makers on the ground with the most accurate, integrative model and recommendations for sustainable forest management. Successful reforestation of degraded landscapes is collaborative task in Hawaii. My Tropical Resources Institute summer research involved quantifying *Acacia koa* $\delta^{13}C$ isotopic content and leaf stomata characteristics to determine water-use efficiency on the slopes of Mauna Loa volcano on the Big Island of Hawaii. Through collaborative planning with the University of Hawaii, Manoa, the United States Forest Service, Hawaii Volcano National Park, and private landowner Kamehameha Schools, results will inform reforestation management recommendations in Hawaii.

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