2017 ERDKUNDE Vol. 71 · No. 1 · 77–92

TOWARDS ESTABLISHING A NEW ENVIRONMENTAL ARCHIVE – ANNUAL GROWTH PERIODICITY, STABLE CARBON ISOTOPE VARIABILITY AND RECONSTRUCTION POTENTIAL OF 'AKOKO (*EUPHORBIA OLOWALUANA*), A NATIVE HAWAIIAN TREE WITH C_4 PHOTOSYNTHETIC PATHWAY

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With 8 figures, 2 tables and 3 photos
Received 16 November 2016 · Accepted 27 February 2017

Summary: Tree ring patterns provide one of the best records of pre-instrumental environmental and climate variability. To date, tree ring chronologies were explored from woody plant species with C_3 photosynthetic pathway, only. For the first time, we have studied wood growth periodicity and stable carbon isotope ratios of tree ring cellulose of a tree species with C_4 photosynthesis and compared these data to those of a C_3 tree species from the same habitat. The investigated species, Māmane (*Sophora chrysophylla*, C_3) and 'Akoko (*Euphorbia olowaluana*, C_4), are small endemic Hawaiian trees sampled from a rather dry, high elevation site on the ridge between Mauna Loa and Mauna Kea on the island of Hawai'i, USA. A relatively strong correlation in ring patterns was found within the 'Akoko and the Māmane individuals as well as with ring-width patterns from a nearby population of introduced Deodar cedar (*Cedrus deodara*) trees that serve as a reference. This correlation is evidence that the C_4-plant 'Akoko may form annual growth rings. In addition to being the first demonstration of annual growth rings in a C_4 plant, our findings have important implications for future climate change research in Hawai‘i. Unlike plants with a C_3-photosynthetic pathway, C_4 plants do not show strong discrimination against ^{13}C during the photosynthetic fixation of CO_2. Thus, 'Akoko may provide a record of past atmospheric CO_2 concentration (CO_2atm) that can be compared with, and possibly supplement, the well-known Keeling curve produced by the nearby Mauna Loa Atmospheric Observatory. Regression analysis indicates a significant relationship between 'Akoko δ^{13}C averages and atmospheric δ^{13}C values. Furthermore, time series of tree ring data from both species provide long-term information on the response of C_3 and C_4-plants to increasing atmospheric CO_2 concentrations and climate change. Trends in δ^{13}C (intrinsic water-use efficiency, iWUE) of the two species show similar responses in that both demonstrate an increase in iWUE over time and with increased CO_2atm. 'Akoko and Māmane iWUE curves are different however, in that the 'Akoko (C_4) curve is non-linear and a significant increase could only be observed post 1975, while the Māmane curve shows a distinct linearly increasing trend throughout the observation period.

Zusammenfassung: Jahrringe von Bäumen werden seit Jahrzehnten als Klima- und Umweltarchiv genutzt, um natürliche und anthropogene Veränderungen der letzten 1000 Jahre oder mehr zu rekonstruieren. Bis heute wurden Jahrringchronologien ausschließlich von Holzpflanzen mit dem C_3-Photosynthesemechanismus erstellt. In dieser dendrochronologischen Studie wurden zum ersten Mal Untersuchungen zur Periodizität des Holzzuwachses und den Verhältnissen der stabilen Isotope des Kohlenstoffs an einer Baumart durchgeführt worden, welche dem C_4-Photosyntheseweg folgt. Die erhobenen Daten wurden mit solchen von C_3 Bäumen verglichen, welche im gleichen Lebensraum wachsen. Die untersuchten Arten, Māmane (*Sophora chrysophylla*, C_3) und 'Akoko (*Euphorbia olowaluana*, C_4), sind kleine Bäume von einem trockenen Hochlagenstandort zwischen Mauna Loa und Mauna Kea der Insel Hawai‘i (Big Island), USA. Die individuellen Holzzuwachsmuster beider Arten zeigten hohe Korrelationen sowohl untereinander, als auch mit einer robusten Referenz-Chronologie von Himalaya Zedern (*Cedrus deodara*), welche vor mehr als 100 Jahren auf Hawai‘i eingeführt wurden. Die starken statistischen Zusammenhänge lassen erstmals den begründeten Schluss zu, dass die Zuwachsringe der untersuchten C_4-Baumart jährlich sind und tatsächlich als Jahrringe bezeichnet werden können. Es können somit jahrgenau datierbare Chronologien des Holzzuwachses dieser C_4-Pflanzen erstellt werden, welche als wertvolle Grundlage für künftige Untersuchungen zur zeitlichen Dynamik des globalen Wandels in der Region dienen können. Die Analyse der stabilen Isotope des Kohlenstoffs in den Jahrringen, erlaubt Rückschlüsse über die pflanzlichen Reaktionen auf Umwelt- und Klimaveränderungen zu ziehen. Pflanzen mit C_4-Photosynthesemechanismus nehmen das atmosphärische CO_2 ohne große Veränderungen des ^{13}C/^{12}C-Verhältnisses in ihre Biomasse auf, wodurch C_4-Bäume eine Möglichkeit bieten die Veränderungen des atmosphärischen CO_2 vor der Zeit direkter Messungen (1958) jahrgenau zu rekonstruieren. Der deutliche Zusammenhang zwischen Veränderungen im CO_2 der Atmosphäre und δ^{13}C in Jahrringen der C_4-Baumart `Akoko konnte in dieser Studie belegt werden. Darüber hinaus haben die, aus den$\delta^{13}$C-Werten abgeleiteten Trends der intrinsischen Wassernutzungseffizienz (iWUE) einen deutlichen Anstieg gezeigt, der auf ansteigende $CO_2$ Konzentrationen der Atmosphäre zurückgeführt werden kann. Für `Akoko (C_4) seit ca. 1975 und für Māmane (C_3) bereits seit Beginn des Untersuchungszeitraums im Jahr 1960. Während der Trendverlauf

https://doi.org/10.3112/erdkunde.2017.01.05 ISSN 0014-0015 http://www.erdkunde.uni-bonn.de

bei Māmane einen deutlich linearen Anstieg über die gesamte Untersuchungsperiode zeigt, ist bei `Akoko ein nicht-linearer Trend in der iWUE zu beobachten. Von 1960 bis 1975 sind für die C_4-Baumart keine bis schwache Veränderungen festzustellen. Ein deutlicher Anstieg der iWUE wurde erst nach 1975 gemessen. Die hier vorgestellten ersten Ergebnisse belegen das Potential von Vergleichsstudien zur Langzeit-Variabilität von Wachstum und Wassernutzungseffizienz von Holzpflanzen mit C_3 und C_4 Photosynthese. Sie können einen wichtigen Beitrag zu Beantwortung der Frage der Anpassungsfähigkeit von C_3 und C_4 Pflanzen an den Klimawandel leisten.

Keywords: Euphorbia, C_4, Growth rings, Hawaiian tree, 'Akoko, Māmane, dendrochronology

1 Introduction

Tree ring analysis has been widely used to reconstruct the climate and stand history of temperate forests (Abrams et al. 1995; Swetnam and Baisan 2003; Rentch et al. 2003), but because growth ring patterns are caused by annual variations in climate and imply the need for seasonality, it is a common assumption that tropical trees lack annual rings (Lang and Knight 1983; Bruening 1996). This however, is not always true. Work conducted by Worbes et al. (2003) or Lisi et al. (2008), has shown that tropical trees do in fact produce annual growth rings in areas where there are fluctuating extremes in temperature or rainfall or distinct wet/dry seasons. Many other studies have validated these findings and have raised important implications for the future of management decisions involving tropical forests (e.g. Worbes 1989; 1995; 1999; 2002; Stahle 1999; Dünisch and Montóia 2003; Fichtler and Clark 2003; Brienen and Zuidema 2005; Brienen and Zuidema 2006; Therrell et al. 2006; Baker and Bunyavejchewin 2006; Bräuning et al. 2009; Lewis et al. 2009; Rozendaal et al. 2009; Brienen et al. 2010; Hérault et al. 2010; Rozendaal et al. 2010; Trouet et al. 2010; Rozendaal and Zuidema 2011; Wils et al. 2011; Dong et al. 2012; Zuidema et al. 2012; Locosselli et al. 2013; Altman et al. 2013; De Ridder et al. 2013; Zuidema et al. 2013; Groenendijk et al. 2014; Locosselli et al. 2016; Colombaroli et al. 2016; Volland et al. 2016).

Sub-alpine locations in the tropics, such as those found on Hawai'i Island's Mauna Kea and Mauna Loa volcanoes, are good potential areas for tree-ring studies because they often demonstrate seasonal patterns in rainfall and temperature. For example, drought events, and frost in winter months are commonly found in these regions (Woodcock 1974; Ashlock and Gange 1983; Lindsay et al. 1997). Maintaining the subalpine forest ecosystem of Hawai'i and understanding how trees are responding to climate change is of vital importance as it is home to the largest remaining stand of Māmane (*Sophora chrysophylla)*, which is the primary food and habitat source for the native Hawaiian bird Palila (*Loxioides bailleui*) (Hess et al. 1999). The Māmane and Naio (*Myoporum sandwicense*) co-dominated forests of Mauna Kea serve as critical habitat for other rare and endangered native Hawaiian birds, such as the Akiapola'au (*Hemignathus wilsoni*), as well (Berger 1972).

We hypothesize that the tree ring patterns of native tree individuals found at the sub-alpine sites of Hawai'i may correspond to these extreme climatic events or "signals". The demonstration of annual growth rings in native Hawaiian trees shall allow us to assign calendar dates to each ring and correlate ring width patterns with existing climate data so that inferences about historical climate conditions and forest responses can be made (Frank et al. 2008; Francisco et al. 2015). In the future, our work shall help to better interpret tree-ring data on how native trees have responded to El Niño events and other extreme climates in the past and shall allow scientists to better predict how the growth and structure of native Hawaiian forests will react to climate change and global warming (Jin et al. 2003; Frank et al. 2008).

Once the dendrochronological dates can be determined, it is possible to perform precise stable isotope analysis in order to better assess isotopic fractionation and underlying ecophysiological processes, particularly, in the C_4 arboreal system.

1.1 C_4 woody plants as a potential proxy record for atmospheric $\delta^{13}CO_2$

As the concentration of atmospheric carbon dioxide, $[CO_2]_{atm}$, increases due to persistent fossil fuel burning and land-use change, $^{13}C/^{12}C$ ratios ($\delta^{13}C$) decrease (e.g., Freyer and Belacy 1983; Leavit and Long 1986; Leavitt and Lara 1994). This is because the organic matters that comprise fossil fuels have much less ^{13}C than atmospheric CO_2 due to plants' strong discrimination against

^{13}C during photosynthetic uptake (Brugnoli et al. 1988; Farquhar et al. 1989). The photosynthetic pathways of C_3 and C_4 plants differ in their incorporation of CO_2 as well as with the way in which they convert CO_2 into organic matter (Edwards and Walker 1983). Plants with the C_3 photosynthetic pathway discriminate much more strongly against the atmospheric $^{13}CO_2$ than plants with C_4 photosynthesis (Cernusak et al. 2013). ^{13}C discrimination during photosynthetic uptake of CO_2 is much lower in C_4 plants, which assimilate CO_2 carbon isotopes in proportion to their atmospheric availability. This has important implications for the use of woody C_4 plants for analyzing historical $^{13}C/^{12}C$ ratios because C_4 tree-ring carbon isotopes potentially allow dating of post-industrial (after 1850) $\delta^{13}CO_{2atm}$ and CO_2 concentrations to before the start of Charles Keeling's regular measurements in 1958 at the Mauna Loa Observatory (Keeling (1978)). δ^{13}C records from C_4 tree rings could provide regionally resolved pre-instrumental records of atmospheric CO_2 independent from measurements of air bubbles in southern hemispheric Antarctic ice cores that provide rather poor time resolution and dating.

As a prerequisite, it has to be demonstrated that woody C_4 plants can provide annually resolved tree ring sequences and long-lived or (sub-)fossil individuals can be found.

1.2 Hawaiian 'Akoko as a model species for demonstrating annual C_4 plant responses to increased $[CO_2]_{atm}$

Major crops like maize, millet or sugar cane are annual C_4-plants. With respect to the rapidly increasing atmospheric CO_2 and temperature in the past 150 years, the future of C_4 plants has become questionable (Anand et al. 2014). The fact that these crops do not lay annual rings makes it difficult to gain valuable information about past developments for assessing their future response to climate change. However, the wood of long-living C_4-trees contains highly valuable long-term data about the general adaptation potential of C_4-plants to climate change and CO_2 rise. The challenge is to extract this information and assign it with exact calendar dates.

Time series data from C_4 'Akoko (*Euphorbia olowaluana*) allow for comparisons to be made between C_3 and C_4 responses to increasing atmospheric CO_2 concentrations and environmental change. The 'Akoko at our Hawai'i Island study sites are of particular interest because woody C_4 'Akoko is associated with woody C_3 Māmane (*Sophora chrysophylla*) and Naio (*Myoporum sandwicense*) allowing for comparitive studies under the same conditions.

In this study, ring width patterns of the 'Akoko, a native Hawaiian C_4 tree (Pearcy and Troughton 1975), were crossdated with those of Māmane and Deodar cedar (*Cedrus deodara*), both of which lay annual rings and grow on Mauna Kea relatively near to 'Akoko (Francisco et al. 2015). Additionally, stable carbon isotope data (δ^{13}C), has been collected from 'Akoko and Māmane growth rings. Demonstrating annual periodicity and identifying the isotopic compositions of growth rings in 'Akoko, under the varying conditions found at Hawai'i's sub-alpine forests, will allow for a better assessment of how increasing atmospheric CO_2 concentrations will affect a number of factors including carbon balance, nutrient and water cycling, and potentially the fate of these native Hawaiian forests as habitats for native and endangered wildlife (Raich and Schlesinger 1992).

1.3 Hypotheses

H1: The ring structures of C_4 and C_3 trees are positively correlated and show similar response variable patterns to environmental factors.

The growth ring patterns of 'Akoko were crossdated with those of Māmane individuals and with the growth ring patterns of a population of nearby Deodar Cedar. High correlation values are a strong indication of annual rings (Cook and Kairiukstis 1990; Worbes 1995). Additionally, high correlations between the δ^{13}C trend in 'Akoko growth rings and that of atmospheric carbon dioxide (1960–1987; McCarroll and Loader 2004) would also support annual periodicity.

H2: Carbon isotope ratios in 'Akoko **growth rings are correlated with past trends in atmospheric CO_2 from Keeling Curve (i.e., a potential for climate reconstructions exists).**

Investigating the carbon isotope ratios in 'Akoko growth rings may allow for the reconstruction of past trends in atmospheric CO_2 concentrations (Leavitt and Long 1983). Although carbon isotope ratios in 'Akoko have not previously been investigated, it is reasonable to suspect that the isotopic signatures will follow theory in that they will display an inverse relationship with rising CO_2 concentrations in the atmosphere. It is hypothesized that the δ^{13}C values found in 'Akoko growth rings can be accurately calibrated with climate data resulting in the production of an 'Akoko $\delta^{13}C$ curve that can be extrapolated back in time and which can be converted into a curve of estimated historic atmospheric CO_2 concentrations. If this can be done, we may say that 'Akoko has climate reconstruction potential.

H3: There is a positive relationship between ^{13}C discrimination (intrinsic water-use efficiency) and atmospheric carbon dioxide concentration for both 'Akoko and Māmane.

Studies have reported increased ^{13}C discrimination in various tree species under elevated CO_2 conditions (Feng 1999; Gagen et al. 2011; Saurer et al. 2004; Cernusak et al. 2013) (or iWUE in C_3 plants). Because the rate, and sometimes the direction, of change varies among species and regions (Gagen et al. 2011; Saurer et al. 2004), it is possible that Māmane (C_3) may have a higher rate of change than 'Akoko (C_4). In which case, we might determine that increased iWUE of Māmane in response to rising atmospheric CO_2 concentration allows it to better compete with the 'Akoko (C_4) photosynthetic strategy, which by definition is more efficient in water use. While ^{13}C fractionation in C_3 plants is controlled by the stomata-regulated ratio of intercellular to ambient CO_2 concentrations (ci/ca; Eq 2), variation in C_4 bundle-sheath leakiness can either dampen or amplify the effects of ci/ca, so that $\delta^{13}C$ measurements cannot be used to precisely assess water-use efficiency in C_4 plants, although they exhibit some relationship (Cernusak et al. 2013).

2 Material and methods

2.1 Study site

The subalpine woodland of Mauna Kea, Big Island, Hawai'i, USA is ecologically significant in that it encompasses critical habitat of the endangered Hawaiian honeycreeper known as the Palila (*Loxiodes bailleui*) (Scott et al. 1986). Maintaining this subalpine forest ecosystem and understanding how trees are responding to climate change is of vital importance as it is home to the largest remaining stand of Māmane, which is the primary food and habitat source for the Palila (Hess et al. 1999). The Māmane and Naio (*Myoporum sandwicense*) co-dominated forests of Mauna Kea serve as critical habitat for other rare and endangered native Hawaiian birds, such as the Akiapola'au, as well (Berger 1972).

Our study site, at the Pōhakuloa Training Area, is located above the inversion layer at the burn site of a fire that occurred in August 2009 on the southern slope of Mauna Kea, Hawai'i (Fig. 1). This area is approximately 24-25 kilometers from the Mauna Loa Atmospheric Observatory. Samples were gathered at approximately 2,000m to 2,200m elevations within a Māmane and Naio (*Myoporum sandwicense*) dominated subalpine forest stand (Scowcroft and Sakai 1983). The soils are medium textured and comprised of sandy loams derived from volcanic ash, sand and cinder (Scowcroft and Sakai 1983). They are described as course and low in organic matter, which results in a low water-retention capacity (Scowcroft and Conrad 1992). Additionally, Deodar cedar (*Cedrus deodara*) samples were gathered at the Pu'u La'au hunter cabin site located on the western slope of Mauna Kea. 'Akoko samples and Deodar cedar sites are approximately 14.7 kilometers apart from one another.

The climate of the subalpine woodland on Mauna Kea is highly variable yet it is generally considered to be harsh for plant growth, with drought events and frost in winter months commonly occurring in these regions (Woodcock 1974; Ashlock and Gange 1983; Lindsay et al. 1997). Temperatures range from nighttime lows near freezing to daytime highs above 20°C (van Riper 1980; Scowcroft 1983). Mean annual temperatures typically range from 9°C to 13°C and mean annual rainfall is approximately 511 mm, with fog-drip contributing to additional precipitation (Juvik et al. 1993). Rainfall occurs primarily during heavy winter storms (Juvik et al. 1993). The wet season typically occurs from November to April and the dry season from May to October (van Riper 1980; Scowcroft 1983).

2.2 Study species

'Akoko (*Euphorbia olowaluana* (Sherff) Croizat and O. Deg)

'Akoko is an endemic Hawaiian C_4 tree found primarily in high elevation, dry forests on Maui and Hawai'i islands (Pearcy and Troughton 1975) (Photo 1, left). It is in the Euphorbiaceae family and is considered increasingly rare with a declining population trend (Bruegmann and Caraway 2003). 'Akoko has an important role in the native Hawaiian ecosystem in that it serves as critical habitat for a rare species of Hawaiian yellow-faced bee, appropriately named, *Hylaeus akoko* (Magnacca 2007). At both our Pōhakuloa Training Area study site and Pu'u Wa'awa'a

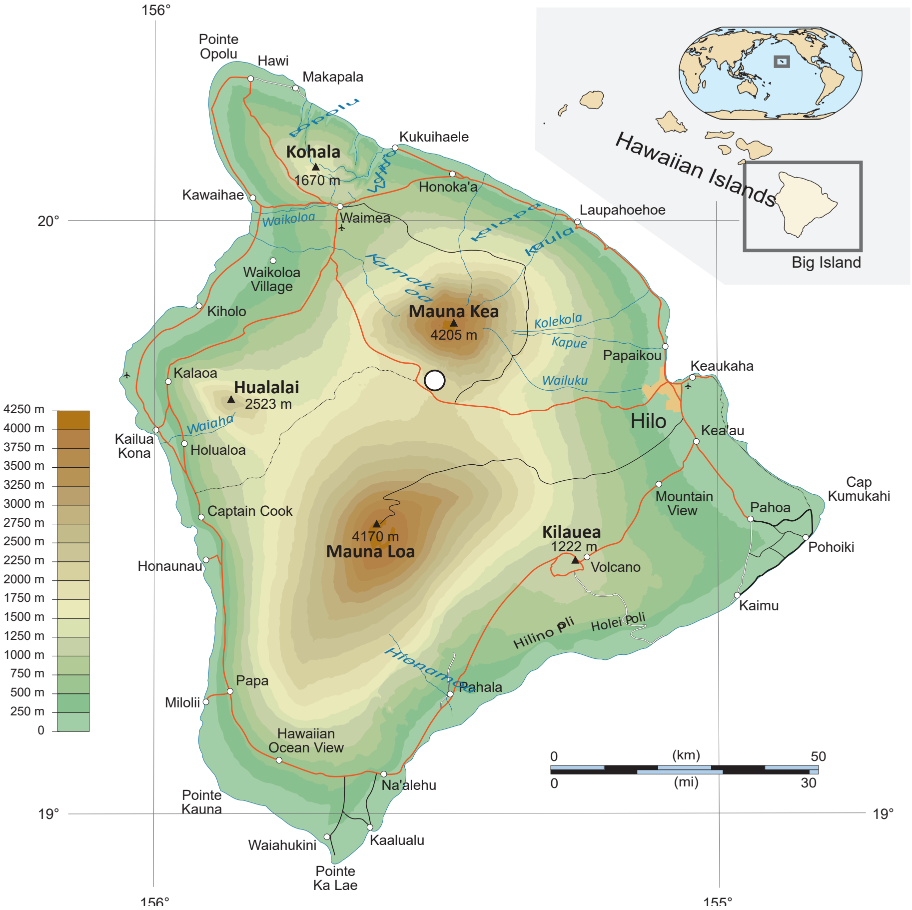

Fig.1: Sampling site (white circle) of 'Akoko *(Euphorbia olowaluana)* and Māmane *(Sophora chrysophylla)* on the southern slope of Mauna Kea in the Māmane/Naio Forest on Big Island, Hawai'i, USA.

Wildlife Sanctuary, isolated 'Akoko trees appear to be supporting large populations of an assorted group of *Hylaeus* spp. that are rarely found in other areas (Magnacca 2007). Two species, *H. dimidiatus* and *H. paradoxicus* are only found at these locations, suggesting that the conservation of 'Akoko in our Pōhakuloa Training Area study site in particular, is important to the survival of native bees, even if other populations of the trees remain (Magnacca 2007).

'Akoko is a species of interest to dendrochronologists as it is a rare C_4 tree. Thus, it offers the opportunity for studies comparing C_3 and C_4 photosynthetic responses to climate change over time (Pearcy and Troughton 1975). There are however, major gaps in the knowledge concerning 'Akoko growth periodicity and age structure dynamics.

Māmane (*Sophora chrysophylla* (Salisb.) Seem.)

Māmane is a C_3 woody tree species endemic to Hawai'i (Photo 1, right). It can be found from near sea level up to an elevation near 3,000 m (Francisco et al. 2015). Māmane is a dominant species in subalpine compositions on East Maui and Hawai'i. Māmane is a hard wood, making it very dense and durable. It is ecologically significant in that it serves as critical habitat for the endangered, endemic honeycreeper, Palila (*Loxioides bailleaui*) (Francisco et al. 2015).

Deodar Cedar (*Cedrus deodara* (D. Don) G. Don)

Deodar cedar is a fast growing, needle leaf evergreen tree with an average height of 12 to 19 meters (Gilman and Watson 1993). Deodar cedar grows in full sun and tolerates clay, loam, sandy and/or well drained soils (Gilman and Watson 1993).

2.3 Sample collection and processing

Live 'Akokos were not used in this study due to their cultural and ecological significance. Prior investigations have revealed that it can be difficult to distinguish ring boundaries on increment cores of native

Hawaiian tropical tree species and thus cores were not used to examine 'Akoko growth rings. Instead, we examined the growth formations of 'Akoko using cross-sectional disks, which were cut approximately 10-15 cm in thickness from dead, fallen individuals. Two cross-section samples were obtained from each of 20 'Akoko individuals.

Each cross-section was cut with a chainsaw above any buttresses, near the base of the main tree trunk. Samples were leveled using a hand planer and sanded until smooth (Photos 2 and 3). Sanding was done using a belt sander and by hand using sandpaper course grit sizes 50, 80, and 120. Samples were then polished with an orbital sander using sandpaper fine grit sizes 320, 400, 600 (Francisco et al. 2015).

Two Deodar cedar cores were taken from each of 10 live individuals using an increment borer. The cores were then stored in plastic straws. In order to avoid any alteration of the fresh wood samples by fungi or bacteria, cores were dried in the laboratory immediately after field work. Next, the cores were mounted on wood blocks using wood glue. After 2-3 days, once the glue was dry, the cores were sanded using the same method as was used for the 'Akokos.

Māmane samples were obtained from a prior collection gathered at the Pōhakuloa Training Area by Kainana Francisco (Francisco et al. 2015). Three Māmane samples were chosen for isotope analysis. These samples were chosen because they were those most likely to overlap with the 'Akoko in terms of ring years.

2.4 Tree-ring analysis

Upon examination of 'Akoko wood thin sections, it seemed as though light colored bands correspond to less dense wood with thinner cell walls and larger lumen. Dark colored bands correspond to more dense wood with thicker cell walls and smaller lumen. This signifies density changes that may indicate a period of dormancy in growth. Thus, we define a growth increment as one light colored band followed by one dark colored band. Each 'Akoko ring boundary was visually identified and marked using a pencil along three radii starting from the pith at the first distinguishable ring and moving toward the bark. The radii were drawn through the least disturbed portions of the

Photo 1: Woody C_4 tree 'Akoko *(Euphorbia olowaluana)* (left) and C_3 species Māmane *(Sophora chrysophylla)* (right) at the Pōhakuloa Training Area on the southern slope of Mauna Kea (Nov 2011). Trees are 3-5m tall and have stem diameters of up to 25 cm.

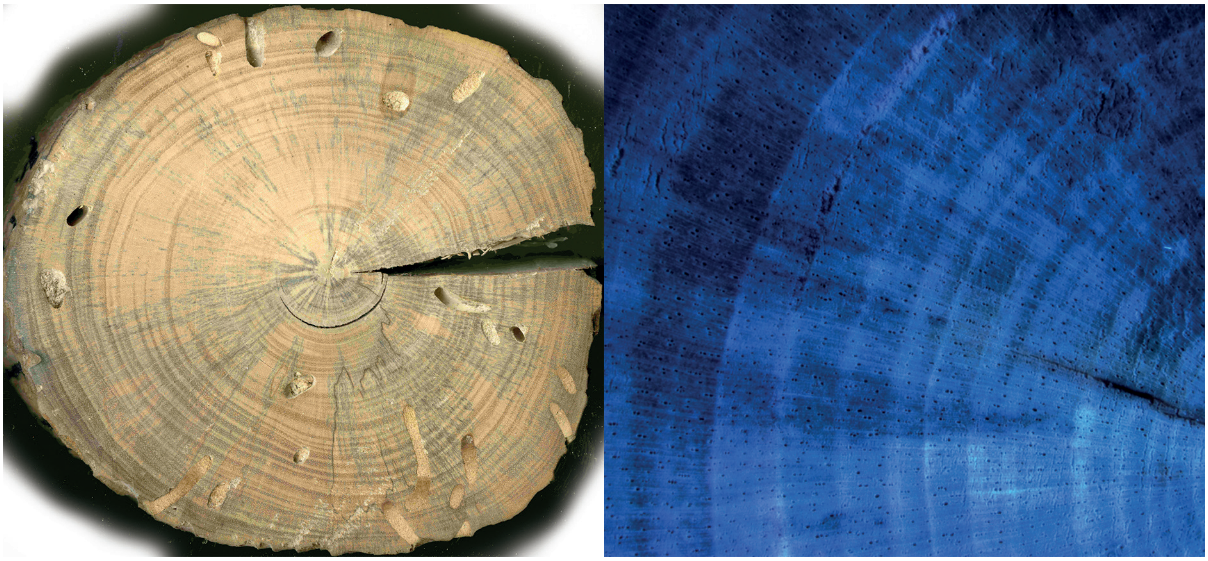

Photo 2: Stem disk of 'Akoko (diameter ca. 15 cm). Tree rings are difficult to identify using normal incident light (right). UV light drastically improves the visibility of wood structures (left).

wood. Consecutive ring widths, beginning at the center and moving towards the bark, were digitally measured at a precision of 0.001 mm, using a VELMEX Measuring System (Velmex, Inc.) and MeasureJ2X computer software program (Speer 2010). The method for identifying and measuring cedar growth rings were the same as for the 'Akoko with one difference; two cores were taken from each cedar individual in order to serve as two separate radii.

The raw ring width measurements were then crossdated using a statistical software program, COFECHA (Grissino-Mayer 2001), which is used to numerically confirm that crossdating is accurate. Well crossdated 'Akoko samples provide evidence for annual rings if correlation values meet the statistical threshold (Pearson correlation; critical correlation: 99% confidence level at r = 0.5155), when compared to cedar samples (Cook and Kairiukstis 1990; Worbes 1995).

2.5 Stable carbon isotope analysis

Growth rings were dissected from three 'Akoko and three Māmane samples using a scalpel. Each dissected sample was >3-4 mg and approximately 3-4 mm width (in tangential direction) and ~10 mm in height (vertical direction). The dissected wood was then chopped into small pieces (<1 mm thickness); this increased the contact surface for solvents in order to make cellulose extraction more efficient. Cellulose extraction and homogenization were performed according to Boettger et al. (2007), Laumer et al. (2009), Wieloch et al. (2011) and Schollän et al. 2014.

Once extraction was complete and samples were homogenized, 180-220µg of each cellulose sample were packed into tin capsules. This involved placing the cellulose into the capsule and folding the capsule around the sample to create a solid packaging free of rips or tears. Stable carbon isotopes were measured by combustion using an elemental analyser (Model NA 1500; Carlo Erba, Milan, Italy) coupled online via open split to an Isoprime IRMS (Isoprime Ltd, Cheadle Hulme, UK). The operating temperature of

Photo 3: Stem disk of Māmane (diameter ca. 18.5 cm). Tree rings, as well as sap wood and heart wood boundaries are easy to distinguish.

the combustion oven was set to 1080°C. The analytical precision ($2\sigma \pm 0.1‰$ for $\delta^{13}C$) was monitored constantly by measurements of internal and external reference material: IAEA CH-6, IAEA CH-3 and IAEA CH-7 scale, certificated value are -10,449‰, -24,724‰ and -32,151‰, respectively. Three of these standards were run after every 10th sample. For all analyses, Helium 5.0 was used as carrier gas. The isotope ratios are given in the delta (δ) notation, relative to the standards VPDB (Vienna-PDB) (Craig 1957).

2.6 ^{13}C discrimination and intrinsic water-use efficiency

The $\delta^{13}C$ values found within the growth increment wood of the Māmane individuals, as well as the 'Akoko individuals, were averaged for each year. We then calculated iWUE for each growth year in Māmane (C_3) and 'Akoko (C_4) in order to produce an iWUE curve for each species.

It is important to note that intrinsic water-use efficiency (iWUE) cannot be estimated precisely from $\delta^{13}C$ of C_4 plants because trends are generally muted and in opposite direction to that for C_3 plants (Cernusak et al. 2013). However, the ^{13}C isotope discrimination (Δ) can be obtained from either C_3 (Δ_3) or C_4 (Δ_4) organic material of interest and directly be compared. Please refer to Farquhar et al. (1989) and Cernusak et al. (2013) and citations therein for further information regarding the bases for the discrimination of C_4 plants.

2.7 Statistics

2.7.1 Determination of periodicity

Classical tree ring analysis methods coupled with stable carbon isotope data were used to determine the periodicity of 'Akoko growth rings. Using COFECHA and a statistical series intercorrelation minimum of 0.5155, we analyzed raw ring width data in order to determine if 'Akoko ring boundaries were properly identified.

Ring width site chronologies were produced using ARSTAN, a statistical software program that standardizes the data by removing age-dependent and non-climate trends (Cook and Kairiukstis 1990; Schweingruber 1996). The tree-ring series were detrended using a Friedman variable span smoother growth curve with tweeter sensitivity set at the least sensitive level (level 9). A robust (biweight) mean using bootstrap confidence limits was employed in calculating mean chronologies. The chronologies were then compared statistically in order to determine whether or not significant relationships exist. Pearson's product-moment correlation coefficient, which tests the linear relationship between quantitative data sets, was also used in evaluating the chronologies (Grissino-Mayer 2001).

Highly correlated chronologies allow for the assumption that they are mainly influenced by the same factor and provide evidence for annual rings (Cook and Kairiukstis 1990; Worbes 1995).

2.7.2 Quality of the chronology

The statistical quality of our chronologies was evaluated using the following parameters: *EPS* (Expressed Population Signal), *RBAR* (average of running correlations), series intercorrelation, and mean sensitivity. Additionally, quality was assessed further by visually observing the presence of pointer years and the synchronocity of the peaks in our tree-ring series "spaghetti" plots (Fig. 2 and Fig. 3). EPS is used as a measure of common variability within a chronology, taking sample depth into account. EPS values greater than 0.85 are considered satisfactory – this means that the series has strong correlation and there are enough trees for cross-dating to be accurate (Wigley et al. 1984). RBAR and EPS are considered some of the best measures of the common growth "signal" in a series. RBAR values greater than 0.3 are considered satisfactory, and greater than 0.4 are very good (Wigley et al. 1984). Series intercorrelation indicates how well a chronology records a common signal. A high series intercorrelation indicates a strong common signal.

2.7.3 Evaluation of potential for reconstruction of changes in atmospheric CO_2

The potential for 'Akoko to be used as a viable species for atmospheric CO_2 reconstructions was determined by a multiple regression analysis correlating the 'Akoko $\delta^{13}C$ chronology and CO_2 data. The data include atmospheric $\delta^{13}C$ values and CO_2 concentrations from the Mauna Loa Atmospheric Observatory (Keeling et al. 2001). Regression analyses demonstrating climate data as a significant predictor of 'Akoko $\delta^{13}C$, identify 'Akoko as a potential species for atmospheric CO_2 reconstruction.

3 Results

3.1 Crossdating

3.1.1 Deodar Cedar

A 98-year continuous time span chronology (Fig. 2), dating from 1916 to 2013 (an 89-year portion from 1925 to 2013 with two or more series) was developed using 20 samples taken from 10 Deodar cedar individuals (n=10, ten individuals with 2 radii for all samples but one (Cedar4), from which only one radii was taken). The chronology included 1,452 rings, had a series intercorrelation of 0.840, a mean sensitivity of 0.558 and an autocorrelation of 0.421.

3.1.2 'Akoko

A 59-year long chronology (Fig. 3) was established from seven of the 20 'Akoko trees sampled at the Pōhakuloa burn area on Mauna Kea. This chronology included 743 rings, a series intercorrelation of 0.553, mean sensitivity of 0.408 and a 0.216 autocorrelation. Because the exact death dates of the 'Akoko samples are unknown, we first measured the ring-widths haphazardly using a generic start of 1000 to create a "floating chronology" with no real defined dates (undated). Since the Cedar chronology was produced using live cores and thus the rings were dated, we were able to use Cofecha to verify crossdating between the undated 'Akoko samples and the dated Cedar samples. This resulted in an 'Akoko chronology dating from 1933-1991.

3.2 Quality of the chronology

The series intercorrelations for the Cedar and 'Akoko chronologies are above the significance threshold of 0.5155 (Tab. 1). Cedar series intercorrelation = 0.840 ; 'Akoko series intercorrelation = 0.553. EPS values are greater than the satisfactory threshold of 0.85 (Figs. 2 and 3) – this means that the series has strong correlation and there are enough trees for cross-dating to be accurate. RBAR values are greater than the satisfactory threshold of 0.3 (Figs. 4 and 5).

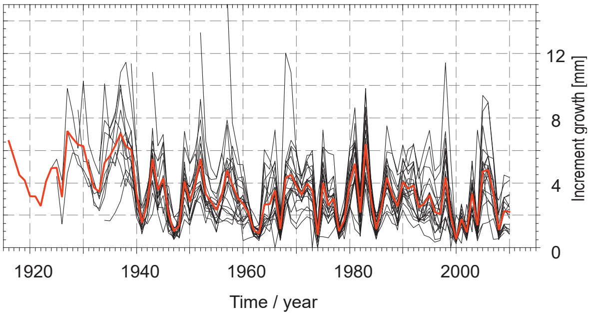

Fig. 2: Raw tree-ring series (black) and the mean of all series (red) from 10 Cedar *(Cedrus deodara)* individuals. Samples are from the Pu'u La'au hunter cabin, Hawai'i.

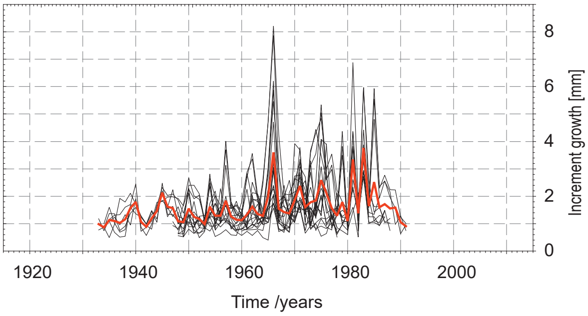

Fig. 3: Raw tree-ring series (black, n = 19) and the mean of all series (red) from seven cross-sections of 'Akoko *(Euphorbia olowaluana)* from Pōhakuloa, Hawai'i. (1933–1991).

3.3 Dating 'Akoko tree rings and support for annual periodicity

'Akoko tree rings were dated through crossdating with live cedar cores. Correlation values met the statistical threshold when compared to cedar samples (Tab. 2). This serves as evidence for 'Akoko laying annual rings (Cook and Kairiukstis 1990; Worbes 1995) and supports hypothesis 1. Additionally, synchronicity of the peaks can be seen in figure 2 and 3. The most notable peaks are those occurring in 1981 and 1983. These peaks are obvious and present in both the cedar and 'Akoko "spaghetti" plots (Figs. 2 and 3).

3.4 Isotope analysis and evaluation of climate reconstruction potential

A significant relationship was identified between $\delta^{13}C$ from 'Akoko tree rings and atmospheric $\delta^{13}C$ (Fig. 6). The p-value of this analysis was 5.517e-08, with an adjusted R-squared of 0.673. Because these two factors are highly correlated (r=0.83), 'Akoko is determined to be a viable species for atmospheric CO_2 reconstructions. This supports hypothesis 2.

Tab. 1: General summary statistics from Cofecha of Cedar (*Cedrus deodara*) and 'Akoko (*Euphorpia olowaluana*) tree-ring chronologies from Mauna Kea, Hawai'i.

Parameter	Cedar	'Akoko
Time span	1925–2013	1933–1991
Number of cores or radii (individuals)	20 (10)	19 (7)
Number of rings in series	1,452	743
Average number of years in a series	76.42	39.11
Series intercorrelation	0.840	0.553
Standard deviation	1.866	0.888
Auto-correlation	0.421	0.216
Average mean sensitivity	0.558	0.408

3.5 Comparing intrinsic water-use efficiencies between 'Akoko and Māmane

For both 'Akoko and Māmane, intrinsic water-use efficiency (iWUE) increased over time and thus, increased as atmospheric CO_2 concentrations increased (Figs. 7 and 8). This finding supports hypothesis 3. Additionally, it supports other studies that have also reported increased iWUE in various tree species under elevated CO_2 conditions (Feng 1999; Gagen et al. 2011; Saurer et al. 2004). The relationships between increased iWUE and year were positive and significant for both 'Akoko (P = 7.833e-08; df = 26; F = 54.4) and Māmane (P = 4.552e-10; df = 23; F =105.6). The slopes of these relationships were 1.48 and 1.08 for 'Akoko and Māmane respectively, indicating that the rate of change of 'Akoko iWUE is higher than that of Māmane.

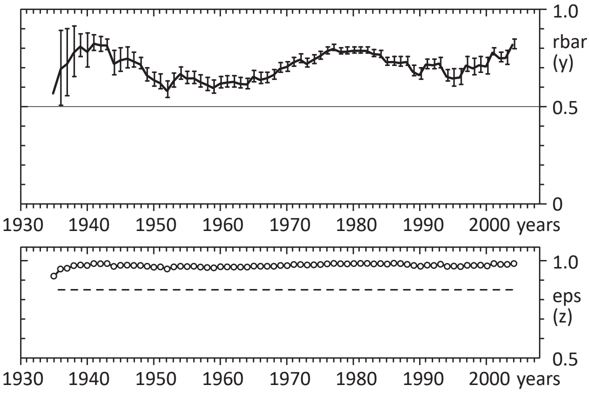

Fig. 4: (Top) Detrended RBar, using a 20-year window and a 19-year overlap, (Bottom) Expressed Population Signal (EPS) values of an 89-year long chronology (1925–2013) of Cedar (*Cedrus deodara*) from Pu'u La'au hunter cabin, Hawai'i. This chronology is based on 19 live Cedar cores (n=10, ten individuals with 2 radii for all individuals but one (Cedar4), from which only one radii was taken). RBAR is the running mean correlation among trees in a series. It is considered one of the best measures of the common growth "signal" in a series. Values greater than 0.3 are considered satisfactory, and greater than 0.4 are very good. EPS (expressed population signal) is used as a measure of common variability within a chronology, taking sample depth into account. EPS values greater than 0.85 (red line) are considered satisfactory – this means that the series has strong correlation and there are enough trees for cross-dating to be accurate.

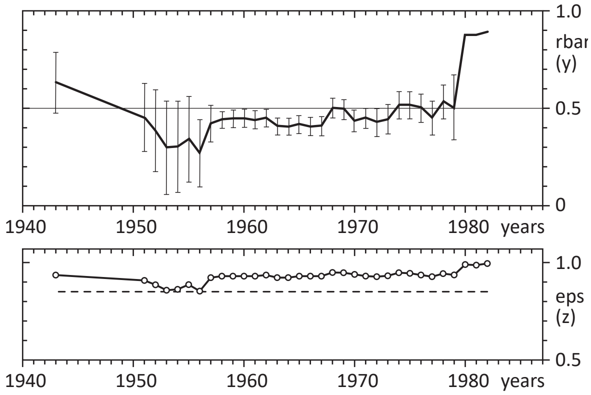

Fig. 5: (Top) Detrended RBar, using a 20-year window and a 19-year overlap, (Bottom) Expressed Population Signal (EPS) values of a 59-year long chronology of 'Akoko *(Euphorbia olowaluana)* from Pōhakuloa Training Area, Hawai'i. This chronology is based on seven 'Akoko cross sections (n=19). RBAR is the running mean correlation among trees in a series. It is considered one of the best measures of the common growth "signal" in a series. Values greater than 0.3 are considered satisfactory, and greater than 0.4 are very good. EPS (expressed population signal) is used as a measure of common variability within a chronology, taking sample depth into account. EPS values greater than 0.85 (red line) are considered satisfactory – this means that the series has strong correlation and there are enough trees for cross-dating to be accurate. (1933–1991).

Tab. 2: General summary statistics from Cofecha of 'Akoko (*Euphorpia olowaluana*) tree-ring chronology crossdated with Cedar (*Cedrus deodara*) tree-ring chronology. Both chronologies are from Mauna Kea, Hawai'i.

Parameter	Dated Cedar Crossdated with 'Akoko
Series intercorrelation	0.639
Average mean sensitiviy	0.507

4 Discussion

Multiple lines of evidence support annual periodicity in 'Akoko, including significant interseries correlations and EPS values in ring width patterns among 'Akoko individuals and with live Deodar Cedar cores. This indicates that 'Akoko and Deodar cedar parallel each other in response to environmental factors and supports the validity of using 'Akoko as a window into climate and past carbon dioxide concentrations (hypothesis 1).

Tree-ring analysis of tree rings from dead 'Akoko cross sections is possible and can result in high interseries correlation. This is the first dendrochronological evidence for annual growth rings in a C_4 plant in general and in 'Akoko in particular. Although this finding should be confirmed by independent methods (e.g., ^{14}C wiggle matching, microscopic wood anatomy or high resolution stable isotope analyses (Pons and Helle 2011) and at other sites or species, it has important implications for future climate change research in Hawai'i. This study has demonstrated that 'Akoko may offer valuable time series data on the responses of C_4 plants to any number of ecological and climate factors. Never before has time series data, with an annual resolution, been extracted from a C_4 plant. Using tree rings, rather than leaves, in C_4 plants allow for comparisons (e.g. between C_3 and C_4 responses) over longer time scales.

4.1 Potential for reconstruction of changes in atmospheric CO_2

The significant relationship between annual 'Akoko $\delta^{13}C$ and atmospheric $\delta^{13}C$ values (Fig. 6) indicates that the wood of C_4 'Akoko contains a valuable archive of time series data relating to historical atmospheric CO_2 concentrations (Buchmann et al. 1996; Feng and Epstein 1995). This supports hypothesis 2. The usefulness of using a C_4 tree for atmospheric CO_2 reconstruction relies on the assumption that C_4 discrimination against ^{13}C during photosynthesis remains constant under differing environmental conditions. However, studies have shown that this discrimination may vary in C_4 plants under varying light and water supplies (Buchmann et al. 1996). Because of this potential variation, it is important to investigate how environmental factors affect 'Akoko tree ring growth.

The Mauna Loa Atmospheric Observatory provides atmospheric CO_2 data beginning in 1958. Because some of our 'Akoko tree individuals date back to before 1958, we can potentially use the isotope data stored within early tree rings to compare with, and supplement the well-known Keeling curve in order to extend the curve back in time. Before this can happen however, a larger sample size of pre- 1958 tree rings must be obtained.

4.2 Comparing C_3 Māmane and C_4 'Akoko intrinsic water-use efficiencies over time

With regards to Hypothesis 3, our findings suggest that, like various other tree species, both Māmane and 'Akoko have increased iWUE under elevated CO_2 conditions (Figs. 7 and 8) (Eamus 1991; Ceulemans and Mousseau 1994). This is, in theory, due to increased atmospheric CO_2 concentration stimulating carbon assimilation and reducing stomatal conductance. This in turn, leads to a decrease in transpirational water-loss (Eamus 1991; Ceulemans and Mousseau 1994).

Interestingly, 'Akoko iWUE seems to have an exponential relationship with rising atmospheric CO_2 levels (Fig. 7). It is not clear why the relationship seems to be non-linear and a significant increase in

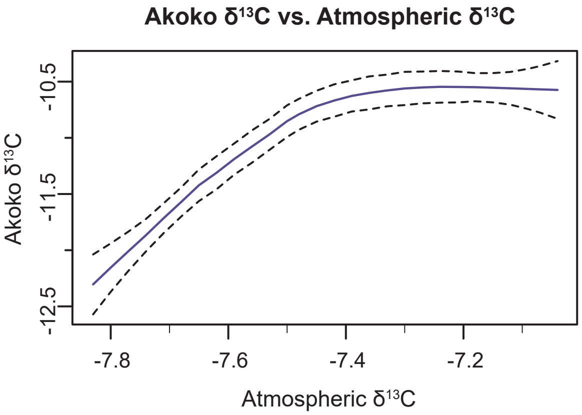

Fig. 6: Generalized multiple regression of 'Akoko $\delta^{13}C$ averages vs. atmospheric $\delta^{13}C$ values. This serves as supporting evidence for annual rings in 'Akoko and also that 'Akoko may be a viable species for atmospheric CO_2 reconstructions. This figure depicts the relationship between these parameters. There is a significant relationship ($p=5.52e-08$, Adjusted $R^2 = 0.673$).

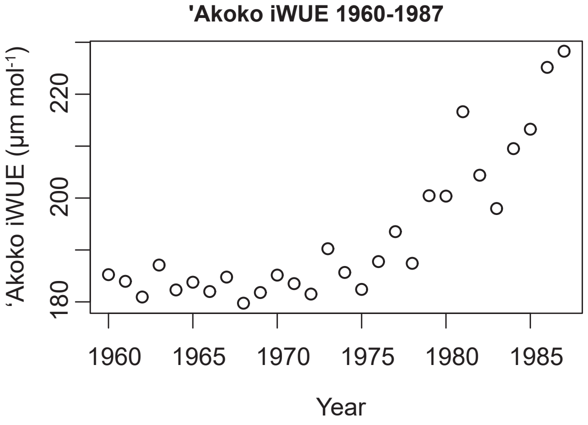

Fig. 7: 'Akoko intrinsic water-use efficiency vs. time (year). Atmospheric $\delta^{13}C$ was only available from 1960 to present. Thus, intrinsic WUE could only be calculated from 1960 onward. Note: relationship seems to be non-linear and a significant increase in iWUE could only be observed post 1975.

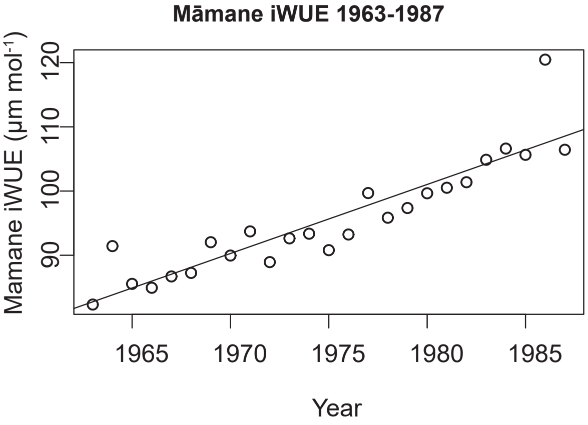

Fig. 8: Māmane intrinsic water-use efficiency vs. time (year). ($y = 1.08x – 2027.56$). Adjusted $R^2 = 0.8134$, p-value = 4.552e-10. Māmane isotope data was only available from 1963 to present. Thus, intrinsic WUE could only be calculated from 1963 onward. Note: distinct linearly increasing trend throughout the observation period.

iWUE can only be observed post 1975. Inspection of the atmospheric $\delta^{13}C$ curve over time, reveals no conspicuous trends occurring after 1975 (when 'Akoko iWUE starts to rise). Further investigation is necessary to determine the cause of this phenomenon. Due to the fact that this is the first demonstration of high-resolution annual time series data of C_4 iWUE, there are no publications to reference in regards to similar findings of a non-linear trend. One possibility is that the sharp increase occurring in 1975 is due to changes occurring in specific site and/or individual plant conditions. A larger sample size of 'Akoko individuals, as well as a more rigorous investigation into the history of this site is required.

5 Conclusion

'Akoko, a woody C_4 plant from the Euphorbiacae family displays annual growth rings that allow for establishing tree-ring chronologies. Hence, the study of this and potentially other woody C_4 species present a unique and valuable opportunity to extract long-term, annual-resolution, time-series data on the response of C_4 plants to changing atmospheric carbon dioxide concentrations. Particularly, annually resolved time series of growth and intrinsic water-use efficiency (from carbon isotopes) data may be very important in assessing the future fate of important annual C_4 crops like maize and millet that evolved under low atmospheric CO_2 conditions millions of years ago and might face some disadvantages compared to C_3 plants under current and future elevated CO_2 partial pressures. Furthermore, tree-ring chronologies of woody C_4 plants potentially allow for reconstructions from arid areas, where chronologies from C_3 trees are not available.

Acknowledgments

Thank you to Susan Cordell (U.S. Forest Service, Institute of Pacific Islands Forestry) for working with us and helping us to gain access to our Pōhakuloa site. Thank you to Sam Brooks (U.S. Forest Service, Institute of Pacific Islands Forestry) for escorting us, sharing knowledge of the Pōhakuloa site and for donating time and skills in the field. Very special thanks to the dendrochronology lab members at the GFZ-German Research Centre for GeoSciences for their positivity and support during TB`s stay in Potsdam, Germany. Another very special thanks to lab members at UH Hilo for their continued support and guidance. Thank you for engaging in "talk story" brainstorming sessions and for graciously offering help and advice whenever needed. Thank you to the student assistants and technicians for their hardwork and diligence in assisting with sample collection and preparation – Robin Rector, Makayla Meyer and Joshua Pang-Ching. Lastly but most definitely not least, thank you to Kainana Francisco who has been an invaluable support partner and consultant throughout this project. Kainana has very generously lended her expertise and donated her free time to helping with everything from methodology and statistics to cultural protocol. 'Akoko samples were collected with the collaboration of the State of Hawai'i Department of Land and Natural Resources and the Pōhakuloa Training Area. This project was funded by the National Science Foundation's Centers for Research Excellence in Science and Technology (CREST) (Award #0833211) and the International Bureau of the German Federal Ministry of Education and Research (grant# 01DM12019).

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