

The impact of an invasive African bunchgrass (*Pennisetum setaceum*) on water availability and productivity of canopy trees within a tropical dry forest in Hawaii

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Summary

1. Tropical dry forests are among the Earth's most threatened ecosystems. On the Island of Hawaii the African bunchgrass *Pennisetum setaceum* (fountain grass) dominates the understorey of the few remaining fragments of native dry forests and is contributing to the degradation of this once diverse ecosystem. In this study, we examined the impacts of *Pennisetum* on water use and productivity of the dominant native canopy tree, *Diospyros sandwicensis*.

2. Over a 3-year period, measurements were made on tree growth rates, and physiological and morphological responses of the most common dry forest native tree, *D. sandwicensis*, growing with an understorey dominated by *Pennisetum*, and on trees growing in plots maintained free of grasses.

3. Analysis of stable oxygen isotope ratios indicated that trees growing in the absence of *Pennisetum* used a higher proportion of water from shallow soil sources. They also sustained higher mid-day water potentials, especially during drier periods.

At the leaf level, no significant differences were found in gas exchange measurements between *Diospyros* trees growing with or without *Pennisetum*. However, trees growing without *Pennisetum* had 30% lower leaf mass per unit area and 40% higher diameter growth than trees growing with *Pennisetum*.

4. These results demonstrate that invasion by *Pennisetum* has a pronounced negative impact on resource acquisition and use by the dominant native tree of this dry forest ecosystem. Although tree death due to these impacts would be much slower than through more immediate processes such as fire and grazing, our findings suggest that long-term conservation of ecosystems threatened by invasions, such those in Hawaiian dry forests, will ultimately require active management of the invading species.

Key-words: tropical dry forest, invasive species, competition, stable oxygen isotopes, water use

Introduction

Coexistence of different plant life-forms is often explained by differences in resource acquisition or niche partitioning (Walter 1971, 1979; Knoop & Walker 1985; Sala, Lauenroth & Golluscio 1997; Dodd, Lauenroth & Welker 1998; Midwood *et al.* 1998; Sankaran, Ratnam & Hanan 2004). Walter's two-layer hypothesis (Walter 1971, 1979), where grasses use shallow water sources and trees utilize deeper sources, functions well as a general framework to explain the coexistence of trees and grasses, particularly where precipitation is highly

seasonal or grasses are dormant part of the year (Walker *et al.* 1981; Walker & Noy-Meir 1982; Schenk & Jackson 2002). Although this concept is likely an over-simplification of the many complex interactions operating above- and below-ground between trees and grasses (Scholes & Archer 1997; Bruno, Stachowicz & Bertness 2003), many empirical studies support this model (Sala *et al.* 1989; Weltzin & McPherson 1997; Dodd *et al.* 1998; Golluscio, Sala & Lauenroth 1998; Van Langevelde *et al.* 2003). However, resource partitioning and species coexistence predicted by this model has not been examined in systems where trees and grasses coexist due to the understorey invasion by alien grasses. The grasses and trees in such situations have evolved in separate habitats, thus the

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mechanisms (e.g. different rooting depths) that allow resource partitioning in naturally evolving tree–grass communities may not exist or facilitate coexistence in this novel community.

While much is known about tree invasions into grasslands and the effects of trees on the composition, spatial distribution and productivity of grasses (see Scholes & Archer 1997), less is known about the impact of grass invasions on the ecophysiological functioning and productivity of native trees. Understanding the mechanisms through which invasive grasses impact ecosystem processes can have important implications for assessing and managing the health, vulnerability and resilience of native ecosystems. Furthermore, the outcome of the tree–grass interaction may be highly dependent on precipitation, seasonality, soil texture and grass cover, among other factors (Knoop & Walker 1985; Sala *et al.* 1989; Stuart-Hill & Tainton 1989; Fernandez-Illescas & Rodriguez-Iturbe 2003; Chesson *et al.* 2004; Brooker 2006; Brown, Scatena & Gurevitch 2006; Kulmatiski, Beard & Stark 2006) highlighting the need to understand the dependency and magnitude of these interactions in light of global change phenomena.

Globally, lowland dry tropical forests are among the most endangered and exploited ecosystems in the world (Murphy & Lugo 1986; Janzen 1988; Lerdau, Whitbeck & Holbrook 1991; Bullock, Mooney & Medina 1995). Alien grasses have invaded many dryland ecosystems throughout the world, often following anthropogenic disturbances (D'Antonio & Vitousek 1992). In tropical dry forests such invasions are often responsible for the conversion of native forests to alien grass dominated rangelands. This conversion can take place rapidly with the introduction of new grass driven fire regimes (Hughes, Vitousek & Tunison 1991; D'Antonio & Vitousek 1992; Brooks *et al.* 2004), but slower conversion can also occur due to competitive impacts of grasses. For example, the dense root system of many invasive grasses can inhibit nutrient and water acquisition by native species, and dense above-ground grass biomass inhibits both germination and growth of natives (Soriana & Sala 1983; Gordon, Menke & Rice 1989; D'Antonio & Vitousek 1992; Cabin *et al.* 2002a,b). Understanding these interactions is crucial to the long-term management of native tropical dry forests and to prevent further degradation and their potential conversion to a non-native ecosystem.

In Hawaii, much like the rest of the world, the once abundant tropical dry forest ecosystems have been heavily invaded over the past century by alien grasses, and these invasions have altered the structure and function of these systems (Smith 1980; D'Antonio *et al.* 1998; Cabin *et al.* 2000; Litton, Sandquist & Cordell 2006). With the introduction of modern ranching in the mid-1800s, large expanses of mesic and dry forests were deforested between 1200 and 2200 m elevation (Cuddihy & Stone 1990); cattle were introduced, and pastures were developed through the introduction of numerous perennial alien grass species. These grasses escaped into adjacent forests and were spread across the landscape by wind, feral mammals and birds. Today the most common of these invaders are alien grasses from Africa (including *Melinis minutiflora*, *Pennisetum setaceum* and *P. clandestinum*), Eurasia (*Anthoxanthum odoratum*) and North America (*Schizachyrium condensatum*

and *Andropogon virginicus*). On the island of Hawaii, one of the most notable of these is *P. setaceum* (fountain grass), which has invaded over 100 000 hectares on the leeward (dry) side of the island. Fountain grass, hereafter *Pennisetum*, is a globally distributed, phenotypically plastic and fire promoting C₄ grass (Williams, Mack & Black 1995). In Hawaii, it has contributed greatly to the transformation of the formerly extensive and diverse forest ecosystems (Cuddihy & Stone 1990; Tunison 1992; Goergen & Daehler 2001) into monospecific grasslands and small fragments of degraded woodlands that often contain scattered native tree overstories with a *Pennisetum*-dominated understorey.

In Hawaii, tropical dry forest fragments can serve as a model system for testing resource partitioning (e.g. as predicted by the Walter model) and the functional consequences of plant interactions after an invasive species of one functional type (i.e. grasses) has invaded an ecosystem dominated by a different functional type (in this case, trees). The objective of this study was to identify the impacts of an alien grass on water use and productivity functions of native trees. Specifically, we hypothesized that *Pennisetum* invasion would limit tree access to important shallow water sources due to its extensive root system in the upper soil horizons where the majority of water resides (Goergen & Daehler 2001). In turn we hypothesized that reduced access to soil resources in the presence of *Pennisetum* would result in measurable differences in tree growth rates, and physiological and morphological responses of the most common dry forest native tree, *Diospyros sandwicensis*. Alternatively, the trees and grasses of this system may be naturally dependent on separate sources of water (as predicted by Walter's two-layer model; Walter 1979), in which case no negative effects would be detected due to resource partitioning and avoidance. Another possibility is that the dominant tree species found in the remaining fragments of Hawaiian dry forests are capable of competing with, and thereby tolerating the presence of the invasive *Pennisetum*, despite relying on similar water sources.

This study will help identify the mechanisms and impacts associated with alien grass invasions in arid forest ecosystems both within Hawaii and globally. Such information is timely due not only to the global demise of these ecosystems, but also to the fact that increased preservation of these systems will require that we understand, and manage for processes related to their long-term decline.

Methods

SITE DESCRIPTION

The field site is located at c. 600 m elevation, (19°46'05" N, 155°56'19" W) within the Kaupulehu dry forest preserve, c. 17 km North of Kailua-Kona, Hawaii County, HI. The 25 ha preserve, identified as one of the best examples of native Hawaiian dry forest remaining on the island of Hawaii, and was fenced in 1997 to exclude alien ungulate browsers.

Average annual rainfall at the preserve from 1999 to 2005 was 514 mm, with a low of 225 mm in 1999 and a high of 1249 mm in 2004. Monthly mean rainfall recorded at a weather station (Onset

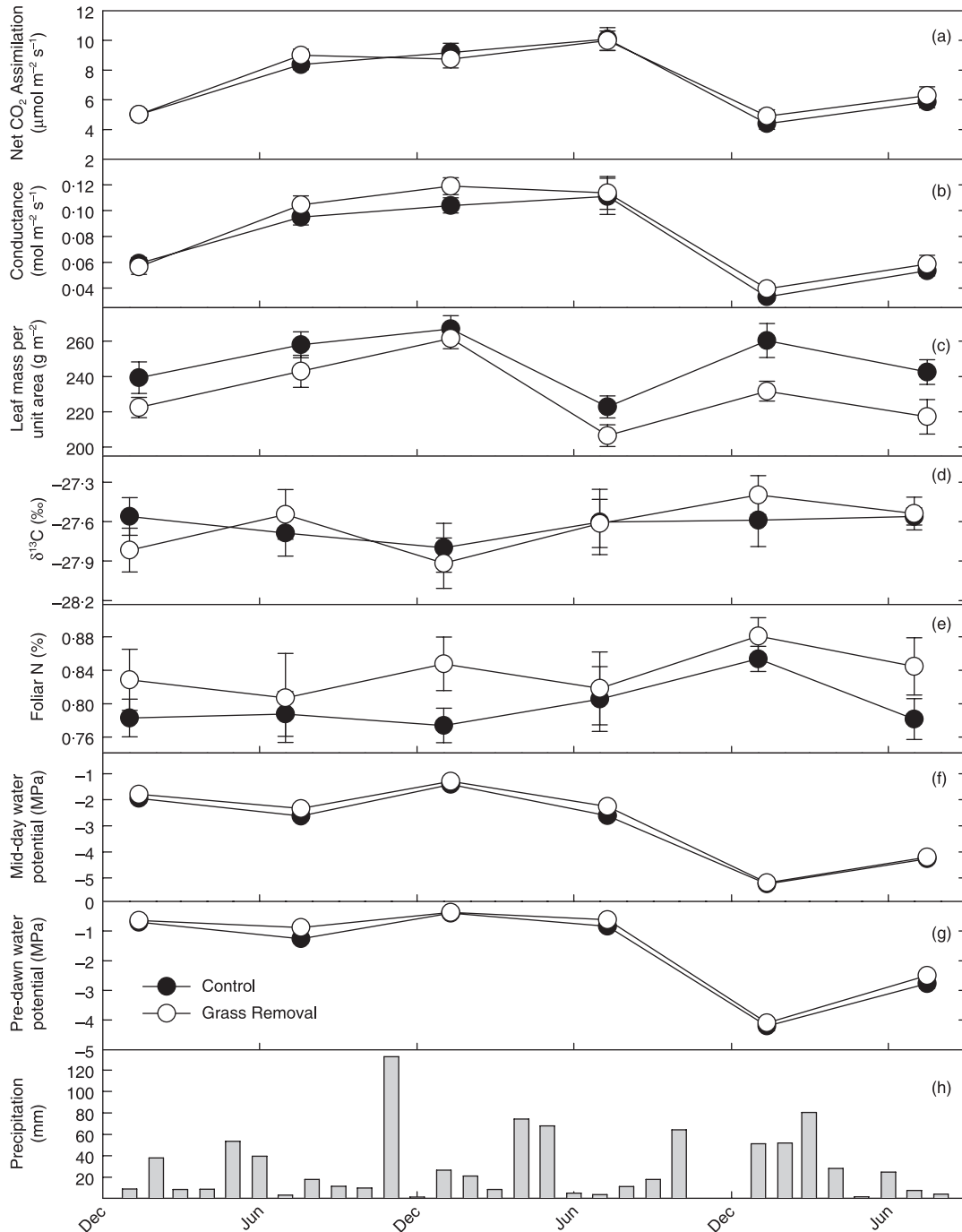


Fig. 1. Physiological and morphological trait values of *Diospyros* trees over a 3-year period (January 2001 to July 2003). Values represent mean \pm SE ($n = 4$). Open circles represent trees in grass-removal plots, and filled circles are those from control plots. Figure 1h represents monthly precipitation totals over the entire sampling period. In (f) and (g) the small but present error bars are subsumed by the symbols.

Computer Corp., Bourne, MA) within the preserve is shown in Fig. 1 (panel h). Typically, winter months receive large rainfall events while summer months are characterized by small infrequent rainfall events generated by local convection. Patterns of seasonal rainfall and temperature are similar to those for longer term records from the area (Giambelluca, Nullet & Schroeder 1986), but average rainfall at the field site from 1999 to 2005 was 20% lower than the long-term average within the region (Giambelluca *et al.* 1986).

The plant community of the preserve is classified as tropical dry forest (Wagner, Herbst & Sohmer 1999), and grows atop an 'a' lava flow estimated to be 1500 to 3000 years old (Moore & Clague 1992). The mixed canopy is dominated by the native tree *Diospyros sandwicensis* A. DC (Ebenaceae) (common name: lama) and co-dominated in places by *Psydrax odorata* A. Gray (Rubiaceae) (common name: alahe'e) which together represent > 90% of the basal area in the study area in this forest (Litton *et al.* 2006). The forest understorey

throughout the preserve has virtually no native species, likely owing to decades of alien ungulate grazing. Instead, the understorey is dominated by the alien invasive bunchgrass, *Pennisetum setaceum* Forssk. (Poaceae) which typically covers > 90% of the forest floor and in places reaches 100% coverage (Cabin *et al.* 2000).

The study site, located within the preserve, consisted of eight 12 × 12 m plots that were randomly assigned to either control or grass-removal groups. In July 2000, all understorey grasses were eliminated from the grass-removal plots by weed-whacking and manual removal of thatch, followed by an herbicide treatment (for procedure, see Cordell, Cabin & Hadway 2002a, Cordell *et al.* 2002b); control plots were left intact. Importantly, stand structural characteristics (species diversity, basal area and stem density) do not differ between treatments (Litton *et al.* 2006).

PLANT MEASUREMENTS AND SAMPLING PROCEDURES

Four *Diospyros* trees were selected in each plot for growth and eco-physiological measurements. All trees were reproductively mature and large enough to tolerate repeated sampling of canopy stems and foliage without significantly reducing the canopy area. Sampling occurred every 6 months, beginning 6 months after grass removal, and lasted from January 2001 to July 2003.

Tree diameter growth rates were determined by measuring trunk growth of fully mature canopy trees at *c.* 1.3 m above-ground level. Custom made spring-loaded metal dendrometer bands were placed around the trees in July 2000 and left undisturbed for 6 months to accommodate a grow-in period. In January 2001, dendrometer bands were marked and the linear distension of the dendrometer band was measured at the end of the study (July 2003). Linear distension values were converted to diameter increment values (mm), and growth rates were reported as percent increase for the 2-year period and as average annual growth rate (change in diameter: mm year⁻¹).

Water potential values were measured using a Scholander-type pressure chamber (PMS, Corvallis, OR). Predawn water potential (Ψ_{PD}), an estimate of maximum daily water status, was measured within 3 h before sunrise. Mid-day water potential measurements (Ψ_{MD}) were sampled between 13:00 and 16:00 h on the same day and used as an indicator of mid-day water stress. For Ψ_{PD} and Ψ_{MD} , at least two replicate canopy stems were measured and averaged for each tree within each plot.

On the same day as water potential measurements, leaf-level gas exchange was also evaluated. Net photosynthesis (area-based) (A_{net}), stomatal conductance (g_s) and internal CO₂ concentration (c_i) were measured between 09:00 and 13:00 h using a portable gas exchange system (LiCor 6400, LiCor Inc., Lincoln, NE). Measurements were made on fully expanded, sun-lit canopy leaves under chamber conditions of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density, ambient relative humidity and air temperature (*c.* 55% and 25 °C, respectively) and a CO₂ concentration of 400 $\mu\text{mol mol}^{-1}$. These measurements were performed on four trees (two leaves averaged per tree) per plot.

Five to ten fresh leaf samples from each tree were also collected on each sample date. The area of these leaves was measured (LI-1300, LiCor Inc.), and the leaves then oven dried at 70 °C to a constant weight. Thereafter, the leaves were weighed to determine dry mass. Leaf area and dry mass were used to calculate leaf mass : area ratio (LMA). This ratio was also used to convert area-based net photosynthesis (A_{net}) to mass-based net photosynthesis (A_{mass}). The dried leaves were later ground to a uniform powder using 40-mesh screen on a Wiley Mill (Thomas Wiley Laboratory Mills, Philadelphia, PA) and a subsample was analyzed for carbon ($\delta^{13}\text{C}$) isotope ratios and mass-based percent nitrogen (% N) at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah.

Stable isotope ratios of oxygen ($\delta^{18}\text{O}$) were used to evaluate differences in soil water between control and grass-removal plots, as well as the differences in water sources used by plants in these plots. Soil samples of 10–15 g were collected at two depths, 5–10 and 10–20 cm, from two randomly placed soil pits dug within each study plot on each sampling date. Soils were sealed in 15 mL glass vials with screw-top lids and Parafilm, and were refrigerated until water was extracted from the samples in the lab (for methods see Dawson 1993). This water was then used to determine the $\delta^{18}\text{O}$ values for water at these depths.

Oxygen isotope values of deeper water had to be estimated instead of directly measured because soil pits in the lava substrate could not be easily excavated below *c.* 30 cm. These deep-water $\delta^{18}\text{O}$ estimates assumed that the $\delta^{18}\text{O}$ value of deeper-soil water (> 80 cm) represents an integration of $\delta^{18}\text{O}$ values from local rainfall weighted for amount (Clark & Fritz 1997). These estimates also include a slight increase of 0.5–1.5‰ from winter to summer (Hsieh 1997). Oxygen isotope data from measurements of precipitation in the Kaupulehu area (D. R. Sandquist, unpublished data) and from rainfall and soil samples taken near Kaupulehu (Hsieh 1997), provided deep-water $\delta^{18}\text{O}$ estimates of –6.0 to –5.0‰ in winter and –5.5 to –4.5‰ in summer.

Plant $\delta^{18}\text{O}$ values were determined for all sample trees in the control and grass-removal plots and for *Pennisetum* within the control plots on all sampling dates, with the exception that no *Pennisetum* samples were taken in July 2003. For trees, three or four fully-suberized stem segments (*c.* 3-cm in length) were collected from every study-tree ($n = 32$) and immediately sealed into 10 mL glass vials with screw-top lids and Parafilm. For *Pennisetum*, four individuals were randomly selected for sampling within each control plot ($n = 16$). Stem samples from *Pennisetum* were cut from the densely packed, non-photosynthetic caudex region and immediately sealed into 10 mL glass vials with screw-top lids and Parafilm. All samples were refrigerated soon after being collected and until water was extracted in the laboratory (Dawson 1993).

Water from soils, *Pennisetum* and tree samples was extracted and isolated for isotope analysis at the Plant Ecophysiology Laboratory at California State University, Fullerton, CA. The $\delta^{18}\text{O}$ values of all water samples were determined on an isotope ratio mass spectrometer at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah (Salt Lake City, UT).

To understand and quantify seasonal precipitation patterns and the relationship between productivity and water use with precipitation, data collected from Kaupulehu between 2001 and 2003 were divided into two categories; total number and amount of monthly events ≤ 5 mm and events ≥ 10 mm.

STATISTICAL ANALYSIS

A repeated measures analysis of variance (ANOVAR) was used to evaluate differences between control and grass-removal plots (treatment factor), among sampling dates (date factor) and the interaction between treatment and date for the following response variables: A_{net} , g_s , LMA, $\delta^{13}\text{C}$, %N, Ψ_{pd} and Ψ_{md} . Measurements made on four trees per plot (two trees for A_{net} and g_s) from each sampling date were averaged so that plot was used as the experimental unit for all ANOVAR analyses ($n = 8$). Assumptions for the application of ANOVAR to plant ecophysiological data followed those of Potvin & Lechowicz (1990). In summary, if Mauchly's criterion *P*-value was > 0.05 (indicating sphericity of data) the uncorrected *F*- and *P*-values based on Pillai's Trace were used. When Mauchly's criterion *P*-value was < 0.05 the Hyund–Feldt (H–F) corrected *F*- and *P*-values were used for date and treatment–date factors if the H–F

epsilon statistic was > 0.7. If H-F epsilon was < 0.7, then data transformation was required. To meet the above assumptions, \log_{10} transformation was required for g_s , Ψ_{pd} and Ψ_{md} , and a square-root transformation was required for LMA.

ANOVAR could not be used for the evaluation of $\delta^{18}\text{O}$ in tree stem water due to the loss of some samples during isotope analysis (i.e. some plots did not have any representative samples within some dates). As such, a standard analysis of variance (ANOVA) was used with plot still serving as the experimental unit (one to four trees averaged per plot), but with only seven plots represented in January 2001, January 2003 and July 2003. ANOVA factors were treatment, date and treatment-date, and the $\delta^{18}\text{O}$ of tree samples conformed to the assumptions of normality and equal variances. In the evaluation of soil-water $\delta^{18}\text{O}$, a third factor, depth, and all additional interactions were included in order to determine if water at 5–10 cm had a significantly different isotope ratio than that at 10–20 cm. The soil-water $\delta^{18}\text{O}$ data also conformed to the assumptions of normality and equal variances.

To identify the proportion of surface water being acquired by trees and grasses of each treatment and on all dates, $\delta^{18}\text{O}$ values were used in a simple two-ended mixing model:

$$\% \text{Surface water} = \frac{\delta^{18}\text{O}_{\text{stem}} - \delta^{18}\text{O}_{\text{deep}}}{\delta^{18}\text{O}_{\text{shallow}} - \delta^{18}\text{O}_{\text{deep}}} \times 100 \quad \text{eqn 1}$$

The upper end member, represented surface water for each date and treatment ($\delta^{18}\text{O}_{\text{shallow}}$), and was taken as the average $\delta^{18}\text{O}$ value of soil water measured from both pits and depths within each treatment on each date. It is assumed that heterogeneity within the surface source is not differentially used between trees and grasses. The lower end member, represented deep soil water ($\delta^{18}\text{O}_{\text{deep}}$), and was based on estimates derived from local rain and soil water measurements (described above). Two estimates of the lower end member value were used for each date in order to better represent the potential range of $\delta^{18}\text{O}$ values for the deep-soil water. These estimates represent the mean summer and mean winter values calculated for $\delta^{18}\text{O}_{\text{deep}}$.

The treatment effect on mean annual growth rate was tested using a Student's *t*-test. Data for this analysis conformed to normality and equal variances among groups. All statistical analyses were performed using JMP statistical analysis software (SAS Institute, Inc., Cary, NC).

Results

PRODUCTIVITY INDICES

Although gas exchange measurements (A_{net} and g_s) showed temporal variation there were no significant differences among treatments at any time (Fig. 1a,b; Table 1). This temporal

variation appeared to correspond with seasonal patterns of precipitation over the 3 years of this study (Fig. 1h). Both A_{net} and g_s were greatest in July 2002 following 2 months of relatively high precipitation (Fig. 1), with their lowest values recorded during January 2003, which followed a 2-month rainless period (Fig. 1).

In contrast to leaf-level gas exchange measurements, leaf morphological and allocation traits showed pronounced differences between treatments (Fig. 1). Leaf mass per unit area (LMA) was significantly different between treatments and over time (Table 1) – it was always greater in control plots (mean = $234.26 \pm 9.65 \text{ g m}^{-2}$) compared to grass-removal plots ($225.46 \pm 8.36 \text{ g m}^{-2}$), and values in both treatments reflected a consistent pattern of higher LMA values in the winter and lower values in the summer (Fig. 1c).

Foliar N values from *Diospyros* leaves of grass-removal plots were higher than those of control plots, especially when collected during relatively wet periods (e.g. November 2001 and January 2003) (Fig. 1e). Mean values were low in both treatments, ranging from 0.77% to 0.88% (Fig. 1e), but differed significantly between treatments (Table 1). Values were variable over time, but no significant differences were found across sampling dates and or for the treatment-date interaction (Table 1).

Carbon isotope ratio values did not significantly vary by treatment or date, and treatment-date interactions were not significant (Table 1). Furthermore, $\delta^{13}\text{C}$ values were very consistent over time, ranging from a low of -27.8‰ to a high of -27.4‰ (Fig. 1d).

Overall, LMA, and foliar N showed trends of higher values in summer and lower values in winter regardless of precipitation. In contrast, measures of gas exchange (A_{net} and g_s) appeared to respond more strongly to variation in precipitation (Fig. 1a–h) regardless of season.

On average, there was a 3.0% (± 0.14) increase in tree diameter at breast height (DBH) in plots where grass was removed. This was significantly greater ($t = -4.12$, $P < 0.05$) than that found for trees of control plots ($1.8\% \pm 0.26$). These values represent an annual growth rate of $0.125 \text{ cm year}^{-1}$ in the grass-removal plots and $0.079 \text{ cm year}^{-1}$ in the control plots.

WATER-USE MEASURES

Pre-dawn (Ψ_{pd}) and mid-day (Ψ_{md}) water potential values of *Diospyros* stems were highly variable across the 3 years of this study, ranging from -0.04 to -4.2 MPa for Ψ_{pd} and -1.3 to

Trait	Treatment	Date	Treatment \times Date
Net CO ₂ Assimilation ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	0.638	0.051	0.996
Log ₁₀ stomatal conductance ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	0.475	0.039	0.994
Sqrt leaf mass per area (g m^{-2})	0.010	< 0.001	0.529
Foliar nitrogen (g m^{-2})	0.049	0.091	0.488
Carbon isotope ratio (‰)	0.988	0.657	0.794
Log ₁₀ water potential – mid-day (MPa)	0.006	0.005	0.552
Log ₁₀ water potential – pre-dawn (MPa)	0.028	0.005	0.449

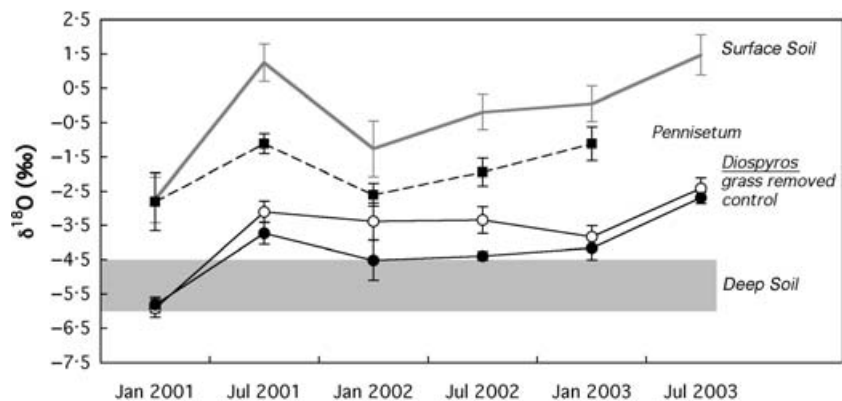
Bold indicates significance at $\alpha = 0.05$.

Table 1. Summary of analysis of variance with repeated measures (ANOVAR) for physiological and morphological traits of *Diospyros sandwicensis* trees compared between grass-removal and control plots (Treatments)

Table 2. Proportion of surface-water used by *Diospyros* trees in the control and grass-removal plots and by *Pennisetum* in control plots only. Estimates are determined from oxygen isotope ratios of plants vs. those of shallow (< 20 cm) and deep (> 100 cm) soil water using a two-source mixing model. A range of values is given for plants within each month based on low and high estimates of oxygen isotope ratios in deep-soil water (see Methods)

	Percent surface-water use (%)					
	January 2001	July 2001	January 2002	July 2002	January 2003	July 2003
<i>Diospyros</i> – control	0–6	13–26	14–34	2–21	17–31	29–39
<i>Diospyros</i> – grass removal	0–2	24–36	39–51	27–41	22–35	36–45
<i>Pennisetum</i>	100	59–65	71–78	59–67	80–83	NA

Fig. 2. Oxygen isotope ratios (mean \pm SE) for plants and soils over the 3-year study period. Stem-water isotope ratios of *Diospyros* trees in control plots (closed circles) were significantly lower overall than for those in grass-removal plots (open circles), with *Pennisetum* isotope ratios (closed squares) consistently greater than both. Surface soil values at < 20 cm (grey line) and deep-soil estimated range values (grey bar) were used in a two-source mixing model to determine the proportion of surface water used by plants within each sample period.



–5.2 MPa for Ψ_{md} (Fig. 1f,g). Both measures of water potential differed significantly among dates and treatments but there were no treatment–date interactions (Table 1). Overall, trees in the grass-removal plots maintained significantly higher mean Ψ_{pd} and Ψ_{md} values (Table 1), with these differences being most apparent during periods with intermediate amounts of precipitation (Fig. 1f,g). Differences between treatments were smaller during the highest and lowest precipitation periods.

The proportion of soil water used by *Diospyros* near the surface (5–10 and 10–20 cm) did not differ between grass-removal and control plots (Table 2), but there was a significant difference among dates – with summer dates having higher average values (–0.22 to +1.63‰) than those of winter sample periods (–3.03 to +0.23‰) (Fig. 2). Soil-water $\delta^{18}\text{O}$ at the 5–10 cm depth was also greater overall than that of the 10–20 cm depth, as would be expected due to greater evaporation from the soil surface (Table 2). This difference was 1.22‰ (\pm 0.25) on average, but there was no depth–date interaction (Table 2), indicating that the difference was relatively consistent throughout the study. These values were therefore combined for use as the ‘shallow’ water source in mixing model analyses (below).

Oxygen isotope ratios of stem water from *Pennisetum* were generally more variable within and among seasons, and were consistently more positive than the $\delta^{18}\text{O}$ values from trees of both control and grass-removal plots (Fig. 2). These higher values indicate greater use of the shallow water sources. Based on the mixing model results, *Pennisetum* utilized 58–100% shallow soil water (5–20 cm) depending on time of year. In

contrast, $\delta^{18}\text{O}$ of *Diospyros* trees reflected use of deep water throughout the year and did not vary greatly except following the wettest (January 2001) and driest (July 2003) periods of the study (Fig. 2). The range of shallow-soil water use for trees of control and grass-removal plots was 0–39% and 0–51%, respectively.

There was a substantial difference in stem-water $\delta^{18}\text{O}$ between trees in the control and those in the grass-removal plots with the latter having higher $\delta^{18}\text{O}$ values throughout most of the study (Fig. 2). These higher $\delta^{18}\text{O}$ values reflect greater use of the shallow water source in plots free of grass competitors.

Dividing the precipitation events into low and high rainfall classes (< 5 and > 10 mm) from 2001 to 2003 illustrates that over 78% of the total rainfall events recorded at the Kaupulehu weather station were < 5 mm (52 events), but these only accounted for 18% of the annual rainfall (Fig. 3). Large rainfall events (> 10 mm) occurred < 10 times a year, on average, yet accounted for 72% of the total annual rainfall (Fig. 3).

Discussion

RESOURCE IMPACTS DUE TO INVASION

Our results indicate that the alien grass *P. setaceum* has a negative impact on below-ground resource acquisition by the dominant tree species in the north Kona dry forest. Ecophysiological indices of productivity were also negatively affected, suggesting that the decline in tree health and population

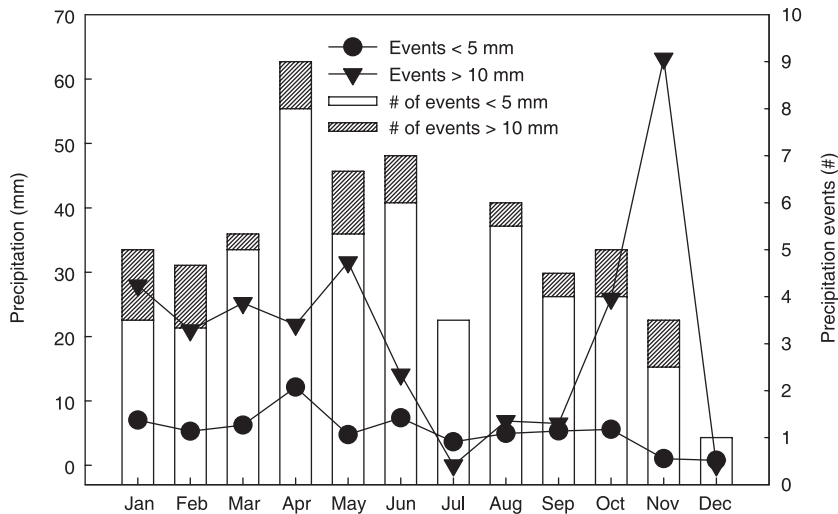


Fig. 3. Precipitation patterns at Kaupulehu dry forest preserve. Symbols represent monthly average values from 2001 to 2003 from two rainfall size classes (circles = rainfall events ≤ 5 mm, and triangles = ≥ 10 mm). Bars represent the average number of precipitation events in the two rainfall size classes that fell between 2001 and 2003. Events < 5 mm accounted for 18% of the mean annual rainfall, and events > 10 mm accounted for 72%.

viability seen in the Hawaiian dry forests (Cabin *et al.* 2000; Litton *et al.* 2006) can be partly if not wholly attributed to *Pennisetum* invasion. These results add to a growing body of evidence that identifies non-native grass invasions as one of the greatest threats to forest diversity and function (D'Antonio *et al.* 1998; Mack, D'Antonio & Ley 2001; Cabin *et al.* 2002a,b; Mack & D'Antonio 2003a,b; Brooks *et al.* 2004).

The invasion of the north Kona dry forest ecosystem by *Pennisetum* significantly changed carbon allocation patterns and water use functions of *Diospyros* (Fig. 1, Table 1), the most dominant tree species of this ecosystem. These changes appear to be partially driven by altered availability and use of shallow soil water (Fig. 2, Table 2), which is likely an important component of tree water budget in this system, particularly during the unpredictable drought periods when water is limiting and evapotranspiration is high.

As indicated by our mixing model results and the high $\delta^{18}\text{O}$ values of *Pennisetum* stems (Fig. 2, Table 2), the dense and shallow root system of this invader appears to be very effective at exploiting shallow water sources in these forests. As such, these plants appear to reduce acquisition of water by native species due to direct competition for water in the upper soil profile or pre-emptive uptake by grasses of water that might otherwise percolate to deeper soil levels. Such impacts on water availability would be especially detrimental during the earliest life stages of native plant development, when developing root systems are in direct competition with mature grass roots.

Although removal experiments are a valuable tool to address inter-specific interactions of native and non-native species (Díaz *et al.* 2003), caution must be exercised when interpreting effects associated with experimental removal of a potential competitor since removal can temporarily alter many site properties such as microbial processes, soil nutrient availability and water availability (Campbell *et al.* 1991; Diaz *et al.* 2003). The differences found in this experiment, however, appeared to be long-lasting (> 3 years) and therefore are

less likely to be simply an ephemeral result of grass removal. Furthermore, the sparse understorey of the grass-removal plots is similar to the natural understorey of pre-invaded and uninvaded Hawaiian dry forests (Litton *et al.* 2006). Regardless of the potential side-effects of grass removal, it is clear that *Pennisetum* is very effective at acquiring and using water from the shallow soil layers of this forest.

This exploitation may have an especially significant impact on water availability to native trees following small rainfall events that penetrate only to shallow depths of the soil profile. As in most arid ecosystems, small pulses of rain in Hawaiian dry forests can play an extremely important role in plant and ecosystem water balance. Rainfall throughout the arid, leeward sides of the Hawaiian Islands is generally derived from two meteorological phenomena: frontal storm systems that are widespread and large, and convective storm cells, which are local and small. The smaller rainstorms are particularly common during the hotter summer months, though not restricted to them (Giambelluca *et al.* 1986). These convective storms can sometimes be intense, but in the north Kona region the amount of precipitation from such storms rarely exceed a few millimetres in any one event, thus the cumulative input by local convective storms only contributes a small proportion to total annual precipitation (i.e. small rainfall events account for almost 80% of the total rainfall events but $< 20\%$ of the total annual precipitation, Fig. 3). Although small rain events in arid ecosystems generally do not contribute substantially to annual primary productivity, such pulses of precipitation, and their intermittent occurrence during drought periods, may be critical for the sustained activity and survival of woody plants (Beatley 1974; Schwinning, Sala & Loik 2004; Potts *et al.* 2006). In the Hawaiian dry forests *Pennisetum* undoubtedly disrupts access to this water source and compromises the ability of native trees to sustain any photosynthetic carbon gain and other activities, including leaf retention, during the unpredictable periods between larger rainfall events.

COEXISTENCE OF ALIEN GRASS AND NATIVE TREES

The arid, aseasonal and often unpredictable climate of Hawaiian dry forests, combined with the presence of frequent small summer rainfall events, predicts that in these ecosystems the opportunistic resource-use strategy of grasses should be favoured over the deeply-rooted woody species that have conservative growth strategies (Soriana & Sala 1983; Melillo *et al.* 1993; Weltzin & McPherson 1997; Stratton & Goldstein 2001). But, these systems also typically experience large winter precipitation events that may favour such woody species. In this type of seasonal environment the coexistence of grasses and woody species has previously been ascribed to phenological asynchrony (i.e. temporal separation of activity), whereas grasses would monopolize rainfall events while trees are dormant (Scholes & Archer 1997). However, at both the phenological (i.e. leaf flush, flower and fruit production) and physiological level, *Pennisetum* and *Diospyros* respond concurrently to large precipitation events (Cordell, unpublished data), and similarly, both exhibit reduced levels of productivity during extended periods of drought (Fig. 1). Therefore, the tree–grass interaction in this system does not appear to follow the coexistence model of balanced competition (Scholes & Archer 1997). Instead, our data indicate that this system is moving towards displacement by grasses through interference and unbalanced competition, with the persistence of native trees likely resulting from high climatic variability in this environment, such as uncharacteristically wet summers (as seen in 2001) and dry winters (e.g. 2003). Such climate variation has been identified as a potential mechanism for preventing extinction or dominance among competitors (see Scholes & Archer 1997).

Regardless of the mechanisms that allow persistence of mature trees in the face of this grass invasion, it is clear that their productivity is decreasing (see also, Stratton & Goldstein 2001; Litton *et al.* 2006). Furthermore, the grass-invaded community likely deters regeneration of these woody species because seedlings and saplings are dependent on the shallow water resources that grasses significantly reduce. Light availability to these young trees is also compromised by the presence of *Pennisetum* (Cabin *et al.* 2000).

Given the paucity of information about past population structure and diversity of Hawaiian dry forests (i.e. prior to invasion) we cannot rule out the possibility that the dominant presence of *Pennisetum* in the understorey has excluded many other species from this system. Indeed, the high species diversity, once common in these forests (Rock 1913), and its accompanying functional diversity (Sandquist & Cordell 2007) are presently in decline (Litton *et al.* 2006) as a result of *Pennisetum* invasion. Thus the apparent coexistence of *Pennisetum* and mature *Diospyros* trees may simply be because this tree species is most tolerant of *Pennisetum*'s presence.

CONSEQUENCES FOR NATIVE TREE FUNCTION

World-wide, there is much evidence demonstrating that alien grasses have strong negative effects of on native-tree population,

but most previous work on this topic has addressed impacts on seedling recruitment or the alteration of disturbance regimes (e.g. fire) (Hughes *et al.* 1991; D'Antonio & Vitousek 1992; Cabin *et al.* 2000). Few studies have addressed alien-grass impacts on native-plant resource use and the physiological functions that lead to these negative consequences (e.g. D'Antonio *et al.* 1998; Mack *et al.* 2001; Litton *et al.* 2006, 2008).

Surprisingly, we found that native trees in grass-removal plots did not have significantly different leaf level carbon-gain characteristics (A_{net} , g_s and $\delta^{13}\text{C}$). Given that tree diameter increase in these plots was almost twice that in control plots over the 3 years of study, we would have expected higher leaf-level carbon gain in the absence of grasses. These trees did, however, have large and consistent differences in investment and allocation functions (LMA, and foliar N). Leaves from trees in the grass-removal plots had significantly lower values of LMA and higher concentrations of mass-based foliar nitrogen than those in the control plots. Lower LMA and higher leaf-N generally translates into a higher carboxylation capacity per unit mass or per unit carbon invested in a leaf (Lambers *et al.* 1998). Additional evidence from concurrent ecosystem-level studies in our plots shows that greater leaf area index (LAI) and litterfall occurs in grass removal plots (Litton *et al.* 2008), further supporting the idea that allocation differences provide the means by which greater above-ground growth was achieved for native trees in the absence of alien grasses. Thus, the negative impact of *Pennisetum* is not through changes in leaf-level photosynthesis, but via alteration of allocation and investment processes, a response similar to that documented for the dominant Hawaiian wet forest tree species, *Metrosideros polymorpha* when provisioned with greater nutrient availability (Cordell *et al.* 2001; Harrington, Fownes & Vitousek 2001). In our case, however, we can link the response to changes in water availability as demonstrated by the significantly greater predawn and mid-day water potentials of *Diospyros* when *Pennisetum* is absent.

These negative consequences are probably even greater than suggested by this study, because our results are limited to a single, albeit dominant tree species. Only one other native tree species, *P. odorata*, appears to persist in the presence of *Pennisetum* in this system (Litton *et al.* 2006; Sandquist & Cordell 2007), suggesting that *Pennisetum* has even more pronounced impacts on the many other dry forest tree species that are in decline or are no longer present in this ecosystem.

We conclude that the coexistence of native dry forest trees and the alien *Pennisetum* is not sustainable in this ecosystem and that in spite of management efforts to eliminate other threats, such as fire and feral ungulate browsing, the death of most dry forest trees will occur as a result of *Pennisetum*'s dominance in the understorey. Furthermore, regeneration of native species is severely hindered by the presence of *Pennisetum* (Litton *et al.* 2008), due presumably to competition for space and resources (Cabin *et al.* 2000, 2001a,b, 2002; Litton *et al.* 2006). As such, the already vulnerable Hawaiian dry forest ecosystem clearly faces the threat of extinction. The results of our study, however, provide a functional understanding of

some of the causes and consequences of alien grass invasion in this semi-arid system, and this information can be used to guide and facilitate management efforts designed to control impacts of alien grasses in general, and the restoration of Hawaii's native dry forest in particular.

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