Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii

Creighton M. Litton [a,b,*], Darren R. Sandquist [a], Susan Cordell [b]

[a] Department of Biological Science, California State University Fullerton, 800 N State College Blvd, Fullerton, CA 92834, United States
[b] USDA Forest Service, Institute of Pacific Islands Forestry, 60 Nowelo St., Hilo, HI 96720, United States

Abstract

Hawaiian tropical dry forests are a unique and highly endangered ecosystem. Remaining fragments are heavily impacted by invasive plant species, particularly the perennial bunchgrass *Pennisetum setaceum* (Forssk.) Chiov. (fountain grass). Little is known about the impact of invasive species on carbon cycling in terrestrial ecosystems. Biomass estimates are a critical first step in understanding the effects of invasive species on carbon dynamics. Biomass data can be used to quantify carbon pools and fluxes, as well as the impacts of land cover change on carbon sequestration. The objectives of our work were to compare: (1) population structure of the dominant native tree species and (2) carbon pools in aboveground live biomass among three land cover types: *native*—native dominated, largely intact dry forest; *invaded*—intact overstory, but understory heavily invaded by *P. setaceum*; and *converted*—a formerly forested site that has been converted to grassland dominated by *P. setaceum*.

Invasion of Hawaiian tropical dry forest by *P. setaceum* leads to an unsustainable population of native trees characterized by a conspicuous absence of saplings and smaller diameter individuals. Aboveground tree biomass did not differ between native (108.1 Mg ha^{-1}) and invaded (107.0 Mg ha^{-1}) forests due to the preponderance of wood biomass in large *Diospyros sandwicensis* trees at both sites. Grass invaded forest had ~7× more understory biomass than the native forest, but no differences were observed in total aboveground live biomass (tree + understory) between native (108.9 Mg ha^{-1}) and invaded forests (112.1 Mg ha^{-1}). However, total aboveground live biomass was ~93% lower at the converted site (7.8 Mg ha^{-1}), which is the eventual fate of invaded forests with no natural regeneration of native canopy species. Native forests contained significantly more individuals and leaf biomass for the mid-canopy tree *Psydrax odorata*, which increased overall stand leaf area index. This structural difference appears to have prevented *P. setaceum* from invading the native site by reducing understory light levels. These results indicate that large changes in the sequestration of carbon in aboveground biomass have occurred across the landscape following widespread grass invasion and conversion of Hawaiian dry forests to grasslands. These large losses of carbon have important implications for quantifying the effects of invasive species and land cover change on ecosystem carbon storage at landscape and regional scales.
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Keywords: Allometry; Biomass; Hawaii; Invasive species; *Pennisetum setaceum*; Tropical dry forest

1. Introduction

Non-native invasive species (herein, referred to simply as invasive species) are found in virtually all terrestrial ecosystems and are one of the most pervasive elements of global change biology (Vitousek, 1994; Vitousek et al., 1997). These biological invasions can have profound effects on both the structure and function of forest ecosystems (Vitousek et al., 1987; D'Antonio et al., 1998; Ewe and Sternberg, 2002; Ehrenfeld, 2003; Mack and D'Antonio, 2003; Fravolini et al., 2005; Hughes and Denslow, 2005; Vanderhoeven et al., 2005), yet there is little consensus on the mechanisms associated with the establishment and success of invasive species (Mack et al., 2000) or the magnitude and direction of their impacts (Parker et al., 1999; Olden et al., 2004). In particular, very few studies have investigated the impacts of invasive species on terrestrial carbon cycling.

Globally, tropical dry forests once represented the largest proportion of all tropical forest types, yet <33% of the original extent remains (Murphy and Lugo, 1986; Van Bloem

* Corresponding author. Tel.: +1 808 933 8121; fax: +1 808 933 8120.
  E-mail address: clitton@fullerton.edu (C.M. Litton).

et al., 2004). In Hawaii, it is estimated that <10% of the original tropical dry forest is left (Bruegmann, 1996). Remaining fragments of Hawaiian dry forest are found primarily on the island of Hawaii and are typically heavily invaded by the non-native grass *Pennisetum setaceum* (Forssk.) Chiov. (fountain grass), a C_4 perennial bunchgrass from North Africa originally introduced in the early 1900s (first collected on Lanai in 1914; Wagner et al., 1999). This invasive grass has a broad ecological amplitude resulting from high phenotypic plasticity in physiological, growth and reproductive characters (Williams et al., 1995), and it is widely distributed on the dry leeward side of the island of Hawaii from sea level to >2000 m elevation (Wagner et al., 1999).

The spread of invasive species often occurs in concert with changes in local disturbance regimes (D'Antonio and Vitousek, 1992; Mack and D'Antonio, 1998). The success of *P. setaceum* across the Hawaiian landscape can, to a large degree, be explained by increased fire frequency and extent in a region where fire was historically uncommon and native species have few adaptations to fire (Hughes et al., 1991; Freifelder et al., 1998). *P. setaceum* produces large quantities of fine fuels that promote fire which, along with traditional land use practices, non-native ungulates and commercial development, has led to the conversion of much of the original native tropical dry forest on the island to grasslands (Cuddihy and Stone, 1990; D'Antonio and Vitousek, 1992; Mack and D'Antonio, 1998; Blackmore and Vitousek, 2000).

Where fire exclusion has been successful, *P. setaceum* typically forms a dense, often monotypic understory in Hawaiian lowland dry forests. The effects of this invasion on native tree populations are largely unknown. However, prior studies have documented strong, negative impacts of invasive grasses on native woody seedling establishment in Hawaiian forests (Cabin et al., 2002; Denslow et al., 2006). Thus, it is very likely that grass invasion will also adversely impact the long-term structure of native tree populations.

Little is known about the impacts of invasive plant species on carbon cycling, a topic of considerable importance due to rising atmospheric CO_2 concentrations, global climate change, and the unknown role that terrestrial ecosystems will play in mitigating or exacerbating these phenomena. Biomass – the amount of organic matter in living and/or dead plant material – is a critical component of the carbon cycle that provides both short- and long-term carbon sequestration. Understanding the effects of invasive species on carbon pools in live biomass represents a first crucial step towards identifying the potential impacts that biological invasions, and subsequent shifts in land cover, have on carbon cycling.

In this study we investigated the effects of an invasive, perennial bunchgrass on tropical dry forest remnants in Hawaii. The objectives were to compare: (1) population structure of the dominant native tree species and (2) carbon pools in above-ground live biomass (determined from allometric equations developed *in situ*) among three land cover types: *native*—native

dominated, largely intact dry forest; *invaded*—intact overstory, but understory heavily invaded by *P. setaceum*; and *converted*—a formerly forested site that has been converted to open grassland dominated by *P. setaceum*.

2. Methods

2.1. Study site

The study was carried out at the Kaupulehu Dry Forest Preserve (invaded and converted sites; 608 m elevation, 19°46′05″N, 155°56′19″W) and the Palama Nui forest (native site; 238 m elevation, 19°44′37″N, 155°59′53″W), both located on the northwest slope of Hualalai Volcano in the district of North Kona on the island of Hawaii (Fig. 1). Both sites have historically been subject to grazing by non-native ungulates (the Kaupulehu forest was fenced in 1997) and used by traditional Hawaiian communities in the past.

Substrate of the region consists of 'a'a lava with scattered pahoehoe flows 1500–3000 years old (Moore et al., 1987). Soils for both sites are shallow, highly organic, and classified as euic, isothermic, shallow, Lithic Ustifolist (USDA-NRCS, unpublished data). The high organic matter content of these soils indicates that these forests occur on the far upper end of the estimated substrate age range. Vegetation characteristics at both study sites (see below) further suggest that these forests have developed on older substrates (Stemmermann and Ihsle, 1993).

Native vegetation at the forested sites consists of a relatively closed canopy (LAI of 1.4–2.9 m^2 m^{-2}; Table 1) ~7–8 m in height that is dominated by two evergreen trees, *Diospyros sandwicensis* (A. DC) Fosb. and *Psydrax odorata* (Forst. F.) A.C. Sm. & S. Darwin. These two species tend to occupy overstory and mid-canopy positions, respectively, and together account for >91% of the basal area at both forested sites (Table 1). Many of
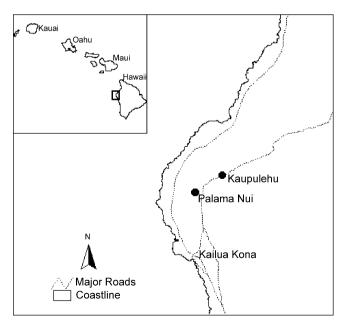

Fig. 1. Study sites (Kaupulehu—invaded and converted; Palama Nui—native) were located on the leeward side of the Island of Hawaii, on the northwest slope of Hualalai volcano.

Table 1
Stand characteristics of tropical dry forest sites sampled on the Island of Hawaii

Stands	BA[a] (cm^2 m^{-2})	% BA in *Diospyros sandwicensis* and *Psydrax odorata*	Total stem density (trees ha^{-1})	% Density in *D. sandwicensis* and *P. odorata*	LAI[b] (m^2 m^{-2} at 1.33 m)
Native	23.5 (2.0)	96.7 (1.1)	12691 (227)	93.6 (2.0)	2.86 (0.24)
Invaded	22.0 (3.5)	91.2 (4.5)	3368 (569)	96.9 (1.5)	1.35 (0.13)
Converted	0	0	0	0	0

Basal area and stand density values are means (± 1 S.E.; $n = 4$) for all individuals >1.33 m height.

[a] Basal area.

[b] Leaf area index was determined with a LAI-2000 (Li-Cor Inc., Lincoln, NE) operating in two unit mode. Eight measurements were taken in each plot and averaged for a single plot value; values presented here are a mean of the four plots at each site.

the trees are multi-stemmed, as is common in tropical dry forests (Van Bloem et al., 2004). The converted site is open grassland dominated almost exclusively by *P. setaceum*.

In addition to the dominant trees, other native woody species at both forest sites include scattered individuals of the shrubs *Sida fallax* Walp., *Dodonea viscosa* Jacq., and *Wikstroemia* sp. Endl. At the invaded site, widely scattered individuals of the canopy trees *Myrsine lanaiensis* Hillebr., *Psychotria hawaiiensis* (a. Gray) Fosb., *Santalum paniculatum* Hook. & Arnott, *Pouteria sandwicensis* (A. Gray) Baehni & Degener, and *Xylosma hawaiiense* Seem. are present. The understory at the invaded site is dominated by an essentially monospecific stand of *P. setaceum*. Small patches of the invasive species *P. setaceum* and individuals of *Grevillea robusta* A. Cunn. Ex R. Br. and *Leucaena leucocephala* (Lam.) de Wit are present at the native site, particularly in canopy openings, and scattered individuals of *Lantana camara* L., *Indigofera suffruticosa* Mill., and *Kalanchoë* sp. Adans. are found at all three sites.

Mean annual rainfall for the study area is 500–750 mm (Giambelluca et al., 1986), with great year-to-year variability in total precipitation. At Kaupulehu, annual rainfall from 1999 to 2005 averaged 514 mm, with a low of 225 mm in 1999 and a high of 1249 mm in 2004. Large rainfall events can occur during any month, but summers tend to be dry and characterized by frequent, small convective storms with more abundant moisture in winter from infrequent but large and widespread low pressure storms. An average of 19% of the total annual precipitation at Kaupulehu falls during the months of June to September. At a nearby weather station (Puu WaaWaa, 709 m elevation, 19°47′42″N, 155°50′43″W), mean daily temperature for the 2004–2005 period was 20.0 °C, with a mean daily maximum of 25.6 °C and a mean daily minimum of 15.1 °C (http://www.wrcc.dri.edu/).

2.2. Tree harvests for allometric regression equations

We harvested *D. sandwicensis* trees from both the Palama Nui ($n = 22$) and Kaupulehu ($n = 6$) study areas, and *P. odorata* trees from Palama Nui ($n = 34$) to develop separate allometric regression equations for predicting biomass of each species. Harvested trees were randomly selected that spanned the range of observed sizes in the study areas (1.8–22.2 cm DBH for *D. sandwicensis* and 0.5–6.1 cm for *P. odorata*). For multi-stemmed trees, each stem was treated as a separate individual.

Trees were cut at ground level and basal diameter, diameter at breast height (DBH), and total height were measured. For each tree, aboveground live biomass was divided into wood (stem plus branches) and twigs plus leaves, and total wet weight for both categories was determined in the field. Three subsamples were taken of both biomass categories for each tree and dried in a forced air oven at 75 °C to a constant weight. Twig plus leaf subsamples were hand sorted to determine the percentage of leaves versus twigs. Percent dry weights and leaf versus twig data were applied to individual field wet weights to determine aboveground live biomass in wood and foliage (kg dry biomass tree^{-1}). Data for *D. sandwicensis* from the two sites were combined to develop allometric regression equations for this species.

2.3. Aboveground live biomass

We established four 144 m^2 plots in each of three sites: native, invaded and converted. For the native and invaded sites, DBH on all trees >1.33 m height was measured in 2005 (for multi-stemmed trees each stem was treated as a separate individual). Aboveground live biomass in trees (wood, foliage and total) was then determined from DBH measurements and the allometric equations developed for the two dominant species. For individuals of other tree species (<5% of all measured trees), we applied the allometric equations developed for *D. sandwicensis* based on similarity in growth form. Understory aboveground live biomass (including seedlings and saplings) in the two forested sites and *P. setaceum* aboveground biomass in the converted site were determined with clip plots during the period of peak biomass (five 1 m^2 quadrats/plot). Live and dead biomass ratios for *P. setaceum* were calculated by sorting a subsample for each clip plot, and aboveground live biomass was determined by multiplying biomass (dry weight) and percent biomass in live tissues.

Size class frequency distributions were constructed for the native and invaded sites for *D. sandwicensis* and *P. odorata* by combining DBH data for individuals >1.33 m height and counts of seedlings (<10 cm height) and saplings (>10 cm and <1.33 m height). At the invaded site, seedling and saplings were counted in a total of thirty 1 m^2 quadrats located at 5 m intervals along three 50 m transects randomly placed in adjacent forest. At the native site, these counts were conducted on a total of 16 randomly located 1 m^2 quadrats from the adjacent forest.

2.4. Statistical analysis

Nonlinear regressions were computed to determine allometric relationships between DBH and biomass (wood, foliage, and total) for both *D. sandwicensis* and *P. odorata* in SPSS 10.0 for Windows (SPSS Inc., Chicago, IL) using untransformed data and a power function:

$$Y = aX^b \tag{1}$$

where Y is the dependent variable (e.g., aboveground live wood biomass; kg dry weight), X the independent variable (e.g., DBH; cm), and a and b are the scaling coefficients derived from the regression fit to the empirical data. All measured independent variables (basal diameter, DBH, and total height) were examined for their utility as predictors of aboveground live biomass categories (wood, foliage, and total). Goodness of fit for all regression equations was determined by examining P-values, the mean square of the error (MSE), the coefficient of determination (R^2), and by plotting the residuals (observed minus predicted values) against DBH.

Tests for among-site differences in mean aboveground live biomass categories and stand structural characteristics were performed using one-way analysis of variance (ANOVA). Posthoc tests for differences between sites were performed with Tukey's honestly significant difference (HSD) method. All statistical tests were performed at $\alpha = 0.05$. While it is possible that differences in site history may account for some of the observed differences among sites, this is unlikely to be the case as: (1) sites were geographically proximate (Fig. 1), (2) stand structural characteristics were similar (Table 1), and (3) sites had similar land use history.

3. Results

3.1. Population structure

Stands in both the native and invaded forests were dominated by two species, *D. sandwicensis* and *P. odorata*, which accounted for >91% of the basal area and stem density (Table 1). There was no woody component present in the converted plots. Total basal area did not differ between forested sites ($P = 0.72$), and was dominated by the overstory tree *D. sandwicensis* which accounted for 86% and 78% of total basal area in native and invaded forests, respectively. Total stem density, however, was ∼4× higher in the native forest ($P < 0.01$). Differences in overall stem density were a result of the mid-canopy tree *P. odorata* ($P < 0.01$) which reached 10,035 trees ha^{-1} in the native site and only 1632 trees ha^{-1} in the invaded site. Stem density did not differ for *D. sandwicensis* between native and invaded sites ($P = 0.64$), which contained 1858 and 1615 trees ha^{-1}, respectively.

Size class frequency distributions also varied between the native and invaded sites for both of the dominant trees (Fig. 2a and b). Both species at each forested site displayed relatively diverse size structures and a generally negative exponential or reverse-*J* pattern typical of uneven-aged forests. However, in the invaded forest both species exhibited a complete lack of
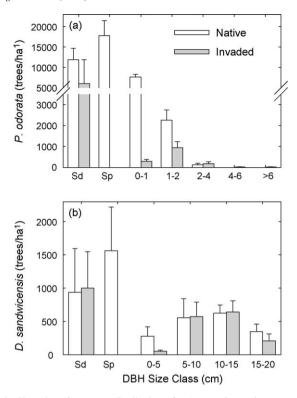

Fig. 2. Size class frequency distributions for (a) *Psydrax odorata* and (b) *Diospyros sandwicensis* in native (open bars) and grass invaded (solid bars) tropical dry forest remnants on the Island of Hawaii. Bars are means (±1 S.E.). Sd: seedlings (<10 cm height) and Sp: saplings (>10 cm and <1.33 m height).

individuals in the sapling category and much lower occurrence of individuals in smaller size classes. The native site contained a diverse array of seedlings, saplings, and individuals in all size classes.
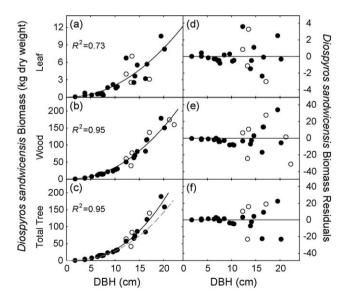

Fig. 3. Allometric relationships for predicting (a) leaf, (b) wood, and (c) total tree biomass from DBH in individuals of *D. sandwicensis*, and biomass residuals (d–f; observed minus predicted values). Equation parameters are given in Table 2. Solid symbols are trees harvested from the native site and open symbols trees from the invaded site. The dashed grey line in (c) is the generalized model for predicting biomass in tropical dry forest trees presented in Brown (1997).
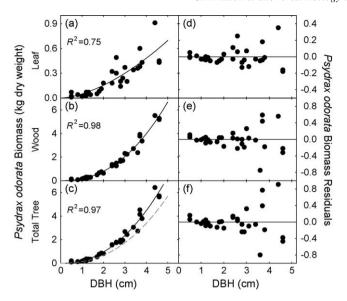
Fig. 4. Allometric relationships for predicting (a) leaf, (b) wood, and (c) total tree biomass from DBH in individuals of *P. odorata*, and biomass residuals (d–f; observed minus predicted values). Equation parameters are given in Table 2. The dashed grey line in (c) is the generalized model for predicting biomass in tropical dry forest trees presented in Brown (1997).

3.2. Allometric regression equations

Diameter at breast height (DBH) was the most effective predictor of aboveground live biomass for both species, although the predictive ability of all measured variables was highly significant (data not shown). The relationship between DBH and individual tree aboveground biomass was highly significant (R^2 values ranging from 0.73 to 0.98; $P < 0.01$) for all biomass categories for both species (Figs. 3a–c and 4a–c and Table 2). Model fits were better for wood and total tree biomass ($R^2 > 0.95$) than for foliage ($R^2 = 0.73–0.75$). Larger diameter trees exhibited greater error variance than smaller trees (Figs. 3d–f and 4d–f). Such heteroscedasticity (i.e., unequal error variance over all observations) is common for biomass data (Parresol, 1993).

Table 2
Regression equations for predicting aboveground live biomass (kg dry weight) from DBH (cm) for *D. sandwicensis* and *P. odorata* individuals >1.33 m height in tropical dry forests of Hawaii

Dependent variable	n	a (S.E.)	b (S.E.)	MSE	R^2
D. sandwicensis					
Leaf biomass	25	0.019 (0.019)	2.034 (0.362)	2.28	0.73
Wood biomass	28	0.251 (0.105)	2.139 (0.144)	178.66	0.95
Total tree biomass	25	0.115 (0.052)	2.450 (0.011)	133.32	0.95
P. odorata					
Leaf biomass	34	0.049 (0.016)	1.648 (0.242)	0.01	0.75
Wood biomass	34	0.161 (0.020)	2.313 (0.091)	0.06	0.98
Total tree biomass	34	0.205 (0.028)	2.221 (0.099)	0.09	0.97

Note: equations for all dependent variables are of the form $Y = aX^b$ where Y is the dependent variable (e.g., leaf biomass, kg dry weight), X the DBH (cm), and a and b are the constants in the equation. S.E. is the asymptotic standard error of the parameter estimate, MSE is the mean square of the error, and R^2 is the coefficient of determination. All models were highly significant ($P < 0.001$).

Table 3
Aboveground live biomass (Mg dry biomass ha^{-1}) in native, invaded and converted tropical dry forest sites in Hawaii

	Native	Invaded	Converted
Trees			
Foliage			
D. sandwicensis	5.3 (0.5) a	4.5 (0.9) a	0 b
P. odorata	1.2 (0.1) a	0.5 (0.1) b	0 c
Other species	0.1 (0.1) a	1.0 (0.5) a	0 a
Total foliage	6.6 (0.5) a	6.0 (1.0) a	0 b
Wood			
D. sandwicensis	93.2 (9.0) a	79.1 (16.0) a	0 b
P. odorata	6.5 (1.1) a	3.7 (0.8) a	0 b
Other species	1.7 (1.5) a	18.3 (8.9) a	0 a
Total wood	101.4 (9.9) a	101.0 (16.7) a	0 b
Total tree biomass	108.1 (10.4) a	107.0 (17.7) a	0 b
Understory			
Pennisetum setaceum	0.2 (0.04) a	5.2 (0.6) b	7.8 (0.7) c
Other	0.6 (0.3) a	0.01 (0.01) a	0 a
Total understory biomass	0.8 (0.3) a	5.2 (0.6) b	7.8 (0.7) c
Total aboveground	108.9 (10.2) a	112.1 (18.0) a	7.8 (0.7) b

Values are means (± 1 S.E.; $n = 4$); means with the same letter within a row do not differ at $\alpha = 0.05$.

3.3. Aboveground live biomass

Total aboveground live biomass (tree + understory) ranged from 7.8 Mg ha^{-1} in the converted site, occupied exclusively by grass, to >108.9 Mg ha^{-1} in the native and grass invaded forests (Table 3). No differences existed in total tree biomass between the native and invaded sites ($P = 0.99$). However, the native site contained more *P. odorata* foliage biomass ($P < 0.01$) and *P. odorata* total tree biomass ($P = 0.04$) than the invaded site. The invaded forest contained ~7× more understory aboveground biomass ($P < 0.01$; Table 3) and ~1.5× more total foliage biomass (tree + understory; $P = 0.04$) than the native forest (Fig. 5). The converted site contained only ~7% of the total aboveground biomass found in the invaded and native forests ($P < 0.01$), but it had higher understory aboveground biomass than either of the forested sites ($P < 0.02$; Table 3) and the same amount of total foliage biomass as the native site ($P = 0.95$; Fig. 5).

4. Discussion

4.1. Population structure

The invasion of Hawaiian tropical dry forests by a perennial bunchgrass has resulted in an unsustainable population for the dominant native species. While native and invaded forests had very similar basal areas (Table 1) and total aboveground biomass (Table 3), stem density data (Table 1) and size class frequency distributions (Fig. 2) indicate that invaded forests are not regenerating. Thus, even if management is successful in assuring the protection of remnant forests from non-native ungulates and fire, our data indicate that the eventual fate of
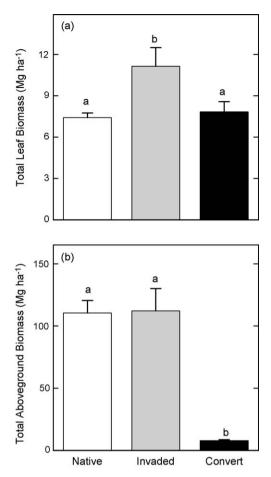
Fig. 5. Total aboveground live biomass in foliage (a; tree + understory) was significantly higher in tropical dry forests invaded by *Pennisetum setaceum*, but did not differ between native and converted stands. Total aboveground live biomass (b; foliage + wood) did not differ between native and invaded stands, but was >14× that found in converted grasslands. Values are means (±1 S.E.; n = 4); means with the same letter do not differ at α = 0.05.

grass invaded forests will be conversion to grasslands as canopy trees die.

The constraint on regeneration does not appear to be at the seedling stage (Fig. 2). In fact, within the grass invaded forest seedlings were able to germinate under the grass canopy, but there were no saplings and few small diameter individuals. Seedlings were of various sizes at the native site, indicating that germination events occurred over multiple years (M. Higashi, unpublished data). In contrast, all of the seedlings at the invaded site were newly germinated (≤1 year) and presumably a result of the high rainfall during 2004 (1249 mm compared to a 7 year average of 514 mm). The high number of seedlings observed in this study in both the native and invaded forests indicates that factors often implicated for lack of stand regeneration in Hawaii (e.g., loss of pollinators and dispersal agents, pathogens, etc.) are not limiting to germination of the dominant native dry forest tree species. Instead, the bottleneck to natural regeneration appears to exist during the subsequent growth and recruitment of seedlings to saplings – a transition period in which plants are competing greatly with *P. setaceum* for limiting resources (Cabin et al., 2002).

Episodic seedling establishment can be expected in dry systems, especially those where year-to-year variation in precipitation is large. Indeed, Cabin et al. (2000) described an establishment pulse that occurred previously in the grass-invaded dry forest of our study area, and these authors proposed that *P. setaceum* may increase native tree seedling survival. However, the complete absence of saplings strongly suggests that while the presence of *P. setaceum* may not inhibit seedling germination, these new seedlings will not become established and survive to become the next cohort of canopy trees.

Floristic diversity was low in our study area compared to other tropical dry forests. Both of our forested stands were dominated by two species, and contained a total of 7 native canopy tree species. Overall, the Kaupulehu area contains 13 native canopy trees but many of these are highly endangered and individuals are widely scattered across the landscape (Cabin et al., 2000). These numbers are well below those reported for other tropical dry forests which commonly contain 50–70 species >2.5 cm DBH (Gentry, 1995). Yet, Hawaiian dry forests are known for their diversity of canopy trees compared to moist and wet forests in the archipelago (Rock, 1974). Tree density numbers in our native site far exceeded the average for neotropical dry forests (3700 trees ha^{-1}; Gentry, 1995). Thus, the comparatively low floristic diversity in Hawaiian tropical dry forests is not a function of containing fewer individuals, but is more likely a result of the unique and isolated evolutionary history of the island's biota.

4.2. Allometric regression equations

Generalized allometric equations exist for predicting biomass in tropical dry forest trees (Brown, 1997), but use of these equations at a particular site can provide biased estimates of as much as 31% (Cairns et al., 2003). Our site- and species-specific regression equations produced biomass estimates that were higher than those obtained with the Brown (1997) general model for tropical dry forests by 10% and 22% for large individuals of *D. sandwicensis* (22 cm DBH) and *P. odorata* (6 cm DBH), respectively (Figs. 3c and 4c). At the stand scale, use of the Brown (1997) equations in our study would have significantly underestimated mean aboveground live biomass by an average of ∼18% (P < 0.01; Paired samples T-test, n = 8). Generalized allometric equations are useful for coarse-scale assessments, but site- and species-specific equations provide more accurate estimates of local and regional carbon pools in biomass.

4.3. Aboveground live biomass

Our aboveground biomass estimates for Hawaiian tropical dry forests (∼110 Mg ha^{-1}) fall well within the range of published values for tropical dry forests globally. Brown (1997) presented data for 11 forests ranging from 28 to 175 Mg ha^{-1} with a mean of 96.3 Mg ha^{-1}. Martínez-Yrízar (1995) presented similar numbers for a different set of forests (n = 14) where aboveground biomass ranged from 23 to 268 Mg ha^{-1} with a mean of 92.9 Mg ha^{-1}.

Published relationships between precipitation and aboveground biomass (Martínez-Yrízar, 1995) predict that the forests in this study area should receive an average of ~940 mm of precipitation annually, well above the 7 year average for our study site (514 mm) and higher than coarse estimates for the region (500–750 mm; Giambelluca et al., 1986). However, much of the 7 year average for our site was associated with a prolonged regional drought where annual precipitation averaged only 318 mm from 1999 to 2003. Thus, it is likely that the long-term average annual precipitation at these sites is ≥750 mm.

The invasion of Hawaiian tropical dry forests by a non-native perennial bunchgrass, and subsequent conversion to grassland, substantially reduced the aboveground carbon sink strength of these systems. The presence of grass in the understory of an intact tree canopy, by itself, did not significantly change carbon pools in aboveground biomass. However, the conversion of these forests to grasslands reduced aboveground live biomass by >90%. Previous studies have documented reductions in aboveground biomass of similar magnitudes when tropical dry forests are converted to grasslands following disturbance (Kauffman et al., 1993, 2003; Jaramillo et al., 2003; Bonino, 2006).

Much of the original tropical dry forest on the island of Hawaii has already been converted to grasslands as a result of historic land use practices, non-native invasions, and concomitant changes in fires regimes. Moreover, our data strongly suggest that even where fire control is successful, the presence of a dense *P. setaceum* understory will lead to the eventual conversion of remaining forest fragments to grasslands without active control of *P. setaceum*. Considering that >90% of the tropical dry forests in Hawaii have been converted (Bruegmann, 1996), a large store of carbon has already been lost from these systems.

In spite of their likely impacts, only a handful of prior studies have examined the effects of invasive plant species on terrestrial carbon cycling and, of these, results have varied. Invasion of perennial sagebrush communities by annual grasses and resulting wildfires reduced integrated daily net carbon exchange in the Intermountain West (Prater et al., 2006). D'Antonio et al. (1998), moreover, found that invasive grasses in seasonally dry, submontane forests of Hawaii reduced native shrub, but not tree, diameter increment. In contrast, invasion of tropical wet forests in Hawaii by nitrogen fixing trees increased growth of individual native trees (Walker and Vitousek, 1991) and stand level basal area (Hughes and Denslow, 2005). However, none of these studies examined the ecosystem-level impact of invasive species on carbon pools in aboveground biomass.

A complete understanding of the effects of invasive species on carbon pools should also take belowground dynamics into account. Globally, root:shoot ratios in tropical dry forests range from 0.09 to 1.01 (Martínez-Yrízar, 1995). Tree belowground biomass would also disappear over time following conversion to grassland. However, many grasses allocate large amounts of carbon belowground that is incorporated into roots and soil organic matter. This does not appear to be the case with *P.*

setaceum which is shallow rooted, has very high decomposition rates and, contributes minimally to soil carbon sequestration (C.M. Litton, unpublished data).

4.4. Conservation implications

Determining how the native forest has remained relatively free of grass invasion is important for the management and conservation of tropical dry forest remnants in Hawaii. Our data indicate that while there is no significant difference in total tree foliage biomass between native and invaded sites, tree canopy LAI is ~2× greater at the native site ($P = 0.01$; Table 1). This can be explained by the significant decrease in stem density and ~60% lower foliage biomass for *P. odorata* at the invaded site. Trees of this species tend to occupy a mid-canopy position and are generally small (<2 cm DBH) and, thus, would have little effect on stand foliage biomass estimates. However, they appear to add an important layer of light intercepting foliage, and *P. setaceum* productivity decreases with decreasing light availability. In our study, *P. setaceum* biomass was significantly lower under tree canopy than in open sites ($P < 0.01$; Table 3), and greenhouse experiments have shown that *P. setaceum* biomass and production are significantly reduced when ambient light is decreased by more than 60% (N. Cervin, unpublished data).

If reduced light levels keep *P. setaceum* from establishing under intact canopy, then grass invasion into the forest most likely occurs in concert with or following a reduction in canopy cover. Disturbance at the invaded site, in the form of non-native ungulates and/or historic land practices, may have removed much of the *P. odorata* prior to invasion. With an increase in understory light levels, *P. setaceum* would have rapidly colonized the site and prevented further regeneration of native trees. Whatever the case, it is clear that once *P. setaceum* becomes established regeneration of native trees ceases in this system.

5. Conclusions

Despite the growing prominence of invasive species in terrestrial ecosystems, our understanding of the impacts of invasion on carbon cycling remains rudimentary. Grass invasion in Hawaiian tropical dry forests substantially reduced the carbon sink strength in aboveground live biomass, but only following conversion to grassland. However, there was a significant change in population structure of dominant trees following invasion that will likely lead to the eventual conversion of remaining forests fragments to grasslands. Taken together with the widespread conversion of Hawaiian tropical dry forests to grasslands, our data indicate that large stores of carbon in aboveground biomass have already been lost from this system. Structurally intact forest canopies, however, appear to decrease understory light levels and limit grass invasion. Restoration of Hawaiian tropical dry forests and the ecosystem services that they provide will require, at a minimum, aggressive management of *P. setaceum*.

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