

Prevalence of Tree Regeneration by Sprouting and Seeding Along a Rainfall Gradient in Hawai'i

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ABSTRACT

Drought stress in tropical dry forests is thought to result in greater asexual regeneration via vegetative sprouting (*e.g.*, basal, root, and branch layering) than occurs in moister tropical forests. We tested this hypothesis by examining the prevalence of tree sprouting and seeding in tropical forests located along a rainfall gradient on the island of Hawai'i. Additionally, we examined the potential for novel disturbance, feral pig *Sus scrofa* rooting and trampling, to alter patterns in tree regeneration mode. We found greater sprouting (in terms of relative density and basal area) in dry forests than in mesic and wet forests, supporting the hypothesis. We also found that feral pig disturbance is negatively correlated with the relative density and basal area of seedlings in wet forests, but is positively correlated with the relative importance of sprouting, and the richness and diversity of sprouting species. Our results suggest rainfall regimes may be an important factor controlling broad-scale patterns in tree regeneration mode, and that exotic ungulates can significantly modify such patterns with potential consequences for the structure and dynamics of tree populations and communities.

Key words: feral pig disturbance; *Sus scrofa*; tropical dry forest; tropical wet forest.

ASEXUAL REGENERATION VIA VEGETATIVE SPROUTING (*e.g.*, basal, root, and branch layering) is common in tropical and temperate forest ecosystems worldwide (Bellingham & Sparrow 2000, Del Tredici 2001, Vesk & Westoby 2004), and the ability to sprout is thought to be an ancestral trait in woody angiosperms (Wells 1969). Sprouting is typically characterized as a disturbance response (Keeley & Zedler 1978, Bellingham *et al.* 1994, Everham & Brokaw 1996, Dietze & Clark 2008), but it can also be locally important in harsh environments, or in other areas affected by spatial or temporal limitations on seeding (Eckert 2002). Beyond these crude generalizations, we have limited knowledge of natural variation in tree regeneration mode across climatic gradients.

The prevalence of sprouting in tropical dry forests is thought to be greater than in moister tropical forests (Vesk & Westoby 2004, Vieira & Scariot 2006). Adaptation to drought is a likely explanation for this trend (Sampaio *et al.* 1993, Bond & Midgley 2001). By maintaining a connection to the parent tree, sprouts obtain essential resources (*e.g.*, water, nutrients, carbohydrates) from a well-developed root system (Harper 1977, Alpert & Mooney 1986). As a result, under drought stress, sprouts have higher survival and growth than seedlings in the earliest ontogenetic stage (Lloret *et al.* 2004).

Tropical dry forests are thought to be the most threatened tropical terrestrial ecosystem (Janzen 1988, Mooney *et al.* 1995); understanding tree regeneration strategies in these forests is crucial for their restoration (Vieira & Scariot 2006). In this study, we test the hypothesis that the incidence of sprouting is greater in tropical dry forests than in higher rainfall forests by examining the prevalence of tree sprouting and seeding along a rainfall gradient on the Island of Hawai'i. Native tropical dry, mesic, and wet forests were

selected where exotic ungulates have been excluded to avoid their confounding impacts on regeneration mode.

Sheep *Ovis aries* and goats *Capra hircus* are common in Hawaiian dry and mesic forests (Spatz & Mueller-Dombois 1973, Scowcroft & Giffin 1983) while feral pigs *Sus scrofa* are more common in wet forests (Diong 1982). Sheep and goats can negatively affect both seed and sprout regeneration (Spatz & Mueller-Dombois 1973, Scowcroft & Giffin 1983); alternatively, trampling on shallow roots may increase sprouting for root-sprouting species (Spatz & Mueller-Dombois 1973). Feral pigs feed heavily on above- and below-ground plant material (Ickes *et al.* 2001). In forests where they are native (*e.g.*, Europe and Asia), rooting by wild pigs reduces the average size and density of seedlings and overall species richness (Ickes *et al.* 2001). Likewise, where they are invasive (*e.g.*, New Zealand, Australia, North America, and Hawai'i), feral pigs negatively affect seedling regeneration by trampling and feeding on native plants (Diong 1982). Additionally, by altering the forest floor, and dispersing the seeds of exotic species, feral pigs can promote invasions by exotic plant species (Spatz & Mueller-Dombois 1973, Stone 1985, Aplet *et al.* 1991). The impact of feral pigs on tree sprouting is unknown. We explore the potential of this novel disturbance to modify patterns in tree regeneration mode by examining the effect of feral pig disturbance on tree regeneration mode in wet forests. Because sprouts are supported by established root systems, and seedlings are not, we expected feral pig disturbance would have a greater negative impact on the density and basal area of seedlings than sprouts. Additionally, feral pig disturbance may stimulate sprouting by damaging the base or roots of trees.

METHODS

STUDY AREA.—The study area includes native dry, mesic, and wet forests on the Island of Hawai'i (site descriptions below). We selected forests where exotic ungulates, including feral pigs, goats, and

Received 13 November 2008; revision accepted 26 March 2009.

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sheep, have been excluded for > 10 yr to minimize their impacts on tree regeneration mode. We believe that contemporary patterns in tree regeneration in these sites are not influenced by the legacy of exotic ungulate disturbance at least a decade ago.

DRY FOREST STUDY SITE.—The Kaupulehu preserve (19°46'05" N, 155°56'19" W) is located on a 1500–3000-yr-old 'a'a lava flow on the western side of Hawai'i at 600 m asl (Moore *et al.* 1987). Annual rainfall is *ca* 500 mm (Giambelluca *et al.* 1986). This 2.3 ha preserve was fenced in 1956 to exclude cattle and feral goats, and is one of the few protected patches of native dry forest on the entire island of Hawai'i (Cabin *et al.* 2000). Exotic species control and restoration efforts are ongoing at the preserve. *Pennisetum setaceum* (fountain grass), *Senecio madagascariensis* (fireweed), and *Lantana camara*, an exotic woody shrub, are actively managed by removal and herbicide treatment. Native trees have also been planted within the preserve. *Lantana camara* and planted native trees (identified in the field by tags) were not included in analyses.

MESIC FOREST STUDY SITE.—Kipuka Ki (19°26'08" N, 155°19'07" W) is a 57.5 ha forest located on a 2000-yr-old deep ash substrate on the southeastern slope of Mauna Loa (Mueller-Dombois & Lamoureux 1967). Elevation range at the site is 1200–1500 m asl, and annual rainfall is *ca* 1500 mm (Bridges & Carey 1973, 1974). Kipuka Ki is part of Hawai'i Volcanoes National Park (HAVO). A systematic and comprehensive program for exotic ungulate removal began at the site in 1980, and by 1988 Kipuka Ki was ungulate-free (Katahira *et al.* 1993).

WET FOREST STUDY SITE.—The Olaa-Koa (hereafter Olaa) rain forest unit (HAVO) (19°28'22" N, 155°15'00" W) encloses 1024 ha on the east flank of Mauna Loa at 1100–1200 m asl. The soil is an inceptisol composed of 1.5 m of ash and cinder on a 4000-yr-old lava base (Lockwood & Lipman 1987). Annual rainfall exceeds 2500 mm, and shows no distinct seasonality (Giambelluca *et al.* 1986). The enclosure was constructed in 1989, and was completely ungulate-free by 1994 (Loh & Tunison 1999).

VEGETATION SAMPLING.—We sampled overstory and understory woody vegetation in 2008 in ten randomly selected 50 × 2 m transect plots in each study site: Kaupulehu, Kipuka ki, and Olaa (ten inside enclosure and ten outside), accumulating a total of 1000 m² per site. All woody plants rooted within each transect > 1 cm diam at breast height (dbh; 1.4 m) were identified and measured for dbh. In addition, we identified and measured (basal diameter) all woody plants rooted within each transect < 1 cm dbh, but > 1 cm diam at basal height. We refer to these understory plants as seedlings. Our understory sampling effort targeted fully established plants, avoiding newly established plants for which mortality is often very high. We determined whether understory plants were seedlings or sprouts (basal, root, or branch sprout) by excavating soil near the base of the plant to reveal the root structure. Sprouts connected to trees located outside transect plots were not counted. For multiple sprouts connected to a single tree (*e.g.*, tree with three basal sprouts), stems were recorded as a single sprout. Because seedlings

(but not sprouts) originating from trees outside plots were sampled, and multiple sprouts from a single tree may reach the canopy, our method for estimating the prevalence of sprouting is conservative. For Kipuka Ki only, where understory tree densities were extremely high, we sampled understory vegetation in 10 × 2 m subplots along transects (at 0–10, 20–30, and 40–50 m). Understory vegetation data (density and dominance) was then normalized to 1000 m² for comparisons with other sites.

DATA ANALYSIS.—To characterize floristic diversity within and between study sites, we calculated importance values (IV) for woody overstory and understory species in each site. Tree ferns were included in the IV analysis only. First, overstory species' density ($D = \text{no. of individuals}/1000 \text{ m}^2$), dominance ($Do = \sum \text{basal area of all individuals}$) and frequency ($F = \text{no. of transects in which the species was present}$) were calculated for each study site. Next, the IV was calculated for each species by summing the relative values (R) of these three parameters: $IV = RD + RDo + RF$. We also calculated the IV for understory species, treating seedlings and sprouts of each species independently.

Statistical estimators of species richness were calculated for trees, seedlings, and sprouts in each study site using EstimateS 8.0 software (Colwell 2007). We calculated the nonparametric Chao 2 incidence-based richness estimator with log-linear 95% CIs and the incidence-based coverage estimator (ICE) (Chao 1987, Colwell & Coddington 1994). These estimators are appropriate for estimating species richness using relatively small samples (ICE), and small grain size (Chao 2) (Brose *et al.* 2003, Hortal *et al.* 2006). For calculations requiring randomization of runs, the default of 50 runs was used without replacement (Colwell 2007).

To evaluate differences in regeneration mode within and between sites, we calculated the relative density and basal area of seedlings and sprouts in each transect (all species combined). Because of low sample sizes for individual species within sites, and few species occurring between sites, we did not analyze intraspecific variation in tree regeneration mode within or between sites. Using transects as replicates, we used nonparametric analysis of variance (Kruskal–Wallis and Dunn's *post hoc*) to compare the relative density and basal area of seedlings and sprouts across forest types. We used nonparametric U tests (Mann–Whitney) to compare the density and basal area of seedlings and sprouts within each forest type; U tests were also used to compare seedlings and sprouts inside and outside the wet forest enclosure, and within each condition, for all species combined. To determine the effect of feral pig disturbance on the diversity of seedlings and sprouts, we used Hutcheson's t (Zar 1999) to compare Shannon's diversity indices for both seedlings and sprouts inside vs. outside the enclosure. Transect data were combined for this analysis. Finally, to evaluate the intensity of our understory sampling effort, we generated species accumulation curves for seedlings and sprouts.

RESULTS

FLORISTIC DIVERSITY.—The dry forest overstory was dominated by *Diospyros sandwicensis* and *Nototrichium sandwicense*; *N. sandwicense*,

Chenopodium oahuense, and *Sida fallax* were all common in the understory (Table S1; Figs. 1A and 2A). In the mesic forest study site, *Sapindus saponaria*, *Pisonia brunoniana*, and *Sophora chrysophylla* were common both as mature trees and as seedlings (Table S1; Figs. 1B and 2B). The exotic *Solanum pseudocapsicum* was also abundant as a seedling. The wet forest was dominated by *Metrosideros polymorpha* and *Cibotium glaucum*, an understory tree fern. *Broussaisia arguta* and *Perrottetia sandwicensis* were common as seedlings and sprouts (Table S1; Figs. 1C and 2C).

Tree and seedling richness was similar in mesic and wet forests; dry forest tree richness was greater, but dry forest seedling richness was reduced (Table S2). The richness of sprouting species in dry and mesic forests was greater than in the wet forest (Table S2). Floristic similarity across sites was minimal (Table S1). Only two species were shared between wet and mesic forests (*Coprosma* sp. and *M. polymorpha*); only one was shared between mesic and dry forest study sites (*S. chrysophylla*).

VARIATION IN TREE REGENERATION MODE WITHIN AND BETWEEN STUDY SITES.—Accumulation curves for understory seedlings and sprouts approach an asymptote in the wet forest study site, and to a lesser extent the dry site, but not in the mesic site (Fig. 3). Comparing

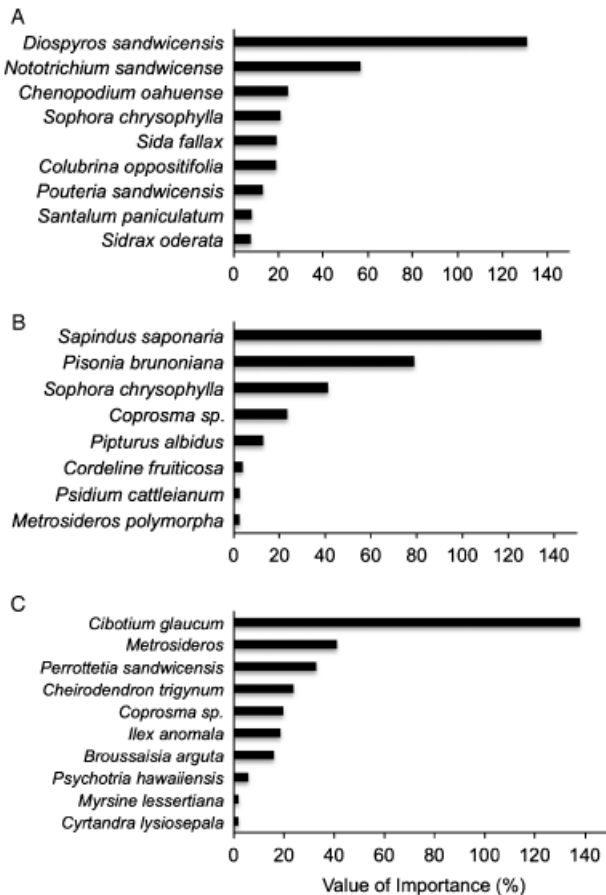


FIGURE 1. Importance values (IV) for overstory species (woody plants > 1 cm dbh) in dry (A), mesic (B), and wet (C) study sites (see text for details).

variation in regeneration mode across study sites, both the relative density and the basal area of sprouts were greater in dry forests than in mesic and wet forests, which did not differ ($P = 0.006$ and 0.021 ; Table 1; Fig. 4). The relative density and basal area of seedlings was greater than sprouts in mesic and wet forests, but did not differ in dry forests (Table 1). Likewise, the overall IV for seedlings was much greater than for sprouts in mesic and wet sites, but approximately equal in the dry site (Fig. 2).

IMPACT OF FIGS.—Inside the wet forest enclosure, the relative density and basal area of seedlings were greater than those of sprouts ($P = 0.002$ and 0.0013 ; Table 2). Only three of the nine understory species present inside the enclosure were observed sprouting, while all nine were regenerating by seed. Outside the enclosure there was

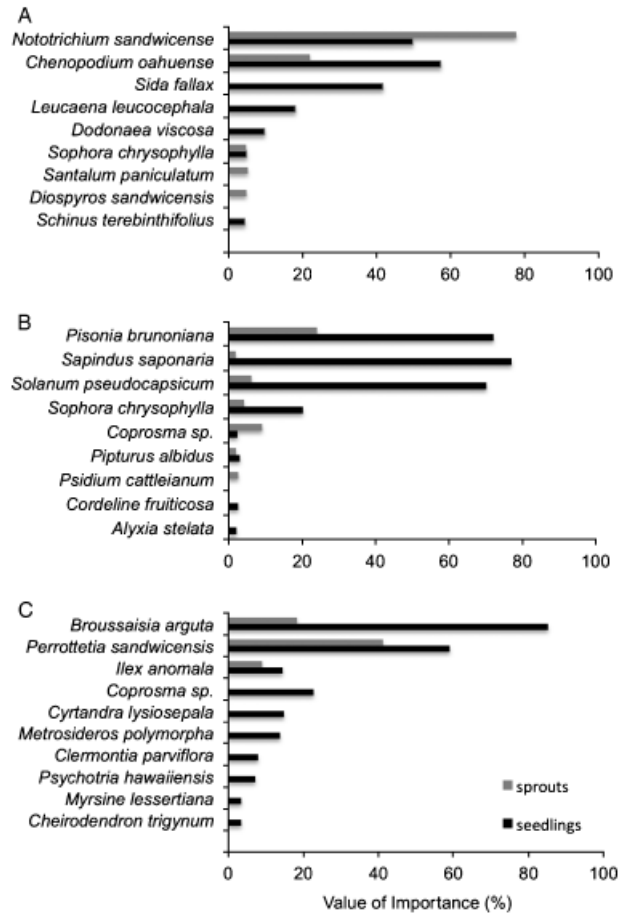


FIGURE 2. Importance values (IV) for understory species (woody plants < 1 cm dbh but > 1 cm basal diam), distinguishing seedlings and sprouts within species, in dry (A), mesic (B), and wet (C) study sites (see text for details). Seedling and sprout IVs in the dry forest study site are similar (seedlings = 185.6, sprouts = 114.4). In contrast, IVs for seedlings are much greater than sprouts in wet (seedlings = 231.6, sprouts = 68.4) and mesic sites (seedlings = 249.8, sprouts = 50.2).

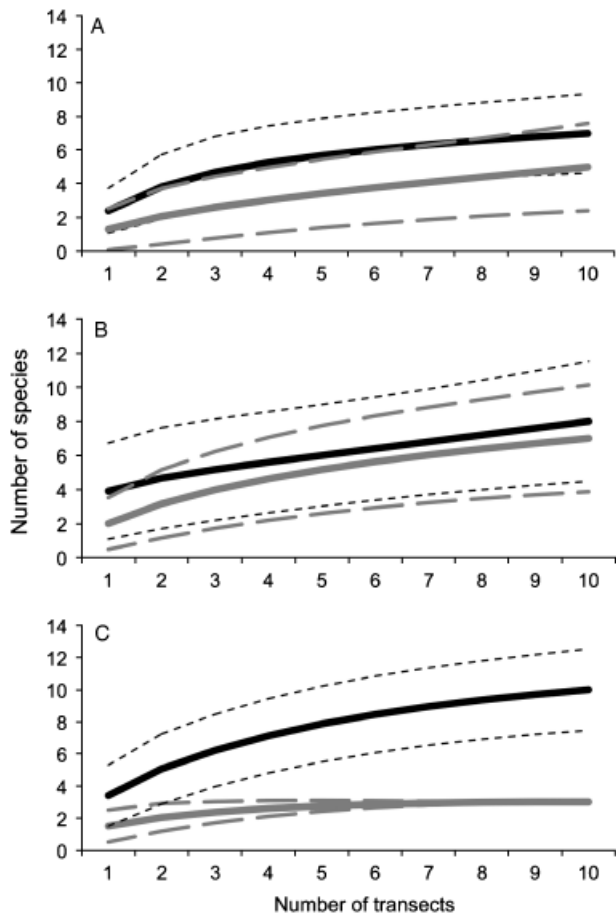


FIGURE 3. Species accumulation curves (with 95% CIs, broken lines) for seedlings (black) and sprouts (gray) in dry (A), mesic (B), and wet (C) study sites.

no significant difference in the relative density or basal area of seedlings and sprouts ($P = 0.34$ and 0.063 ; Table 2).

Comparing regeneration inside vs. outside the enclosure, we found feral pig disturbance had a negative effect on the density and basal area of seedlings ($P = 0.002$ and 0.025 ; Table 2), but not on their diversity ($H_{\text{inside}} = 0.76$ and $H_{\text{outside}} = 0.65$, $t = 1.7$, $P > 0.05$). For all species occurring both inside and outside the enclosure, fewer seedlings were observed outside the enclosure than inside.

Feral pig disturbance did not affect the density and basal area of sprouts ($P = 0.25$ and 0.19 ; Table 2), but did positively affect the diversity of sprouts ($H_{\text{inside}} = 0.40$ and $H_{\text{outside}} = 0.70$, $t = 3.1$, $P < 0.005$). We observed seven of eight total species sprouting outside the enclosure in contrast to only three of nine species sprouting inside the enclosure. Because the density and basal area of seedlings are significantly reduced outside the enclosure, the relative importance of sprouts is greater outside the enclosure than inside the enclosure.

DISCUSSION

Results of this study support the hypothesis that sprouting is more frequent in tropical dry forests than in moister forests. To our

knowledge, this is the first study to examine community-level variation in tree regeneration mode along a rainfall gradient in a tropical forest ecosystem. While we do not test the mechanism(s) responsible for increased sprouting in dry forests, our study design provides support for the notion that increased sprouting in dry forests is likely a result of drought stress. Additionally, results of this study demonstrate that a novel disturbance can significantly alter natural patterns in tree regeneration mode. Feral pig disturbance in the wet forest study site resulted in (1) greater relative importance of sprouting through negative impacts on seedlings and (2) greater richness and diversity of sprouts.

SPROUTING IN TROPICAL FORESTS.—In native Hawaiian forests, moisture availability limits seedling establishment in dry (Stemmermann & Ihsle 1993), but not higher rainfall forests (Denslow *et al.* 2006). Results of our study suggest that increased sprouting in dry forests may be a response to such drought stress. It is also likely that warmer temperatures in the dry site, which is located at 600 m asl compared with the higher (>1000 m asl), cooler mesic and wet study sites, contribute to drought stress and increased sprouting. While sprouting in dry forests can also occur following fire (Kenard *et al.* 2002, Otterstrom *et al.* 2006) and severe wind disturbance (Brokaw & Walker 1991, Van Bloem *et al.* 2005), our dry forest study site has not recently experienced such severe disturbances.

If our assumed mechanism is correct in dry forests, then the lower incidence of sprouting in higher rainfall forests suggests that

TABLE 1. Mean absolute and relative density and basal area for seedlings and sprouts in transect plots located in dry, mesic, and wet forest study sites. Absolute values for density are means of total seedling and sprout counts (all species combined) for all 100 m² transects in each study site. Relative density values are means of total seedling and sprout counts in each transect divided by the total number of overstory individuals in each transect (all statistics done using relative values). P values for analysis of variance (Kruskal–Wallis) comparing seedlings and sprouts between forest types are located below relative values; P values for U tests (Mann–Whitney) comparing seedlings and sprouts within each forest type are adjacent to relative values. Letters (A, B) indicate significant or nonsignificant differences between groups (Dunn's post-hoc test).

	Seedlings		Sprouts		P value
	Absolute	Relative	Absolute	Relative	
Density					
Dry	5.3	1.54	2.4	0.37 ^A	0.06
Mesic	58	0.91	5.7	0.084 ^B	< 0.0001
Wet	8	0.69	2.1	0.16 ^B	0.002
		$P = 0.192$		$P = 0.006$	
Basal Area					
Dry	11.0	0.029	10.2	0.017 ^A	0.085
Mesic	113	0.04	9.34	0.0035 ^B	0.0003
Wet	17.3	0.017	3.54	0.0035 ^B	0.0013
		$P = 0.29$		$P = 0.021$	

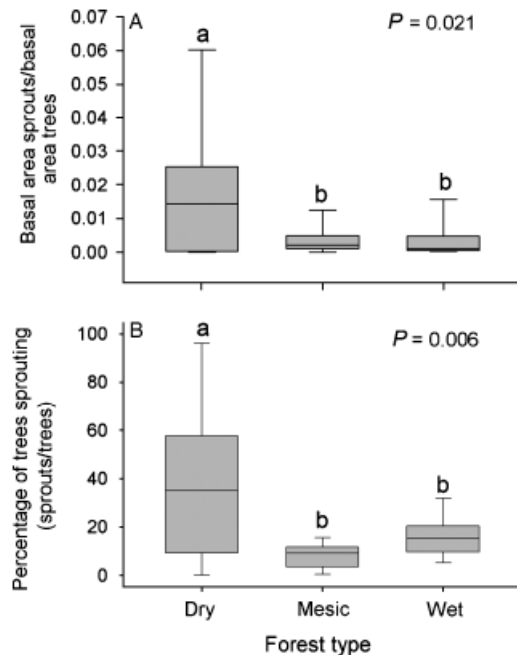


FIGURE 4. Box plots showing 5th, 25th, 75th, and 95th quantiles, and median values for the relative basal area and relative density of sprouts in Hawaiian dry, mesic, and wet forest study sites (P values adjacent to plots). Letters (a, b) indicate significant or nonsignificant differences between groups.

moisture is less frequently limiting to seedling establishment there. However, sprouting does occur in these moist tropical forests. Chronic limbfall and herbivory are important sources of disturbance to understory trees in tropical wet forests (Aide 1987; Clark & Clark 1989, 1991), and many species sprout in response to these disturbances (Putz *et al.* 1983, Putz & Brokaw 1989, Guariguata 1998). Previous research in the Olaa wet forest study site demonstrated that falling fern fronds are a major source of disturbance to tree seedlings (Drake & Pratt 2001). Senescing tree fern fronds were responsible for 60 percent of damage to artificial seedlings (Drake & Pratt 2001). While Drake and Pratt (2001) did not assess the potential for trees to sprout in response to damage, sprouting in response to this type of disturbance is common in other tropical wet forests (Putz *et al.* 1983, Putz & Brokaw 1989, Guariguata 1998), and we observed multiple stemmed juveniles in our transect plots, which indicate the ability to sprout. Falling tree fern fronds may be an important cause of sprouting in our wet forest study site.

SPROUTING AND INVASIVE SPECIES.—Results of our study reveal that a novel disturbance—feral pigs—can significantly modify tree regeneration mode in wet forests. We found reduced relative density and basal area of seedlings outside the enclosure, which we interpret as resulting from pig disturbance given that the basal area and density of tree ferns do not differ inside and outside of the enclosure (P . Busby, unpubl. data). Drake and Pratt (2001) also found greater damage to (artificial) seedlings outside the Olaa enclosure than inside (31% and 20%, respectively). Because seedlings are signifi-

cantly reduced by pig disturbance, the relative importance of sprouting increases in disturbed forests. Our results also indicate that feral pig disturbance is positively correlated with the richness and diversity of sprouting species. Greater sprouting may result from basal or root damage caused by pigs. Together, the positive relationship between feral pig disturbance and relative importance of sprouts, and the richness and diversity of sprouts, suggests that pig disturbance may favor species capable of propagating by sprouts. Obligate seeders, like *Clermontia parviflora*, *Cyrtandra lysiosepala*, and *Psychotria Hawaiiensis*, may decline with feral pig disturbance.

Invasive plant species may also be capable of modifying patterns in tree regeneration mode. On the island of Hawai'i, the invasive tree *Psidium cattleianum* reproduces by both seed and sprouts, and has successfully invaded a wide range of forest ecosystems by replacing native species (Huenneke & Vitousek 1990). A previous study suggested that one reason for the success of *P. cattleianum* may be its greater ability to sprout in response to fern frond damage compared with native tree species (Huenneke & Vitousek 1990). Results of our study provide mixed support for this hypothesis. Only three of nine total native species were observed sprouting inside the wet forest enclosure, suggesting sprouting may not be a universal response among native wet forest species to chronic frond damage. However, outside the enclosure, we observed seven of eight total species sprouting, reflecting a much greater ability to sprout across native species. Given the low occurrence of exotic species in our study sites, we were unable to assess the importance of sprouting for the reproductive biology of exotic species, or for the impact of invasive species on community-level patterns in tree regeneration mode.

TABLE 2. Mean absolute and relative density and basal area for seedlings and sprouts for transects inside and outside the wet forest enclosure. Absolute values are means of total seedling and sprout counts (all species combined) for all 100 m² transects in each study site. Relative values are means of total seedlings and sprouts counts in each transect divided by the total number of overstory individuals in each transect (all statistics done using relative values). P values for U tests comparing seedlings and sprouts inside and outside the enclosure are located below relative values. P values for U tests comparing seedlings and sprouts within each condition are adjacent to relative values.

	Seedlings		Sprouts		P value
	Absolute	Relative	Absolute	Relative	
Density					
Wet inside enclosure	8	0.69	2.1	0.16	0.002
Wet outside enclosure	3.7	0.22	1.9	0.11	0.34
		$P = 0.002$		$P = 0.25$	
Basal area					
Wet inside enclosure	17.3	0.017	3.54	0.0035	0.0013
Wet outside enclosure	2.91	0.0053	0.924	0.0012	0.063
		$P = 0.025$		$P = 0.19$	

CONCLUSION

Despite the recognition that tropical dry forests are the most threatened tropical terrestrial ecosystem (Janzen 1988, Mooney *et al.* 1995), our understanding of the factors influencing tree regeneration in dry forest trees is limited. While both disturbance and resource limitation are known to cause sprouting, we know little about how these factors interact. Given the potential for greater drought stress (Malhi & Wright 2004), and more severe hurricanes (Emanuel 2005, Webster *et al.* 2005) and fires (Goldammer & Price 1998) under future climate scenarios, improving our understanding of tree regeneration mode in tropical forests will be crucial for conservation efforts. We suggest future research efforts aimed at evaluating (1) variation in regeneration mode for native and invasive species across a range of environmental regimes in tropical ecosystems, and (2) differences in the performance of native and invasive seedlings and sprouts in response to biotic and abiotic disturbance. Such studies will be poised to improve our understanding of the importance of sprouting for ecosystem functioning and tropical conservation.

ACKNOWLEDGMENTS

We would like to thank T. Warren, G. Busby, R. Busby, I. Nabers, and M. Stelmach for field help. R. Ostertag, L. Pratt, H. Ferrington, R. Loh, D. Bender, W. Brawner, and Y. Yarber Carter provided advice on study site selection, and logistical support. We also thank two anonymous reviewers for their helpful comments. Permission to sample forests was granted by Hawai'i Volcano National Park and the National Tropical Botanical Garden.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Counts for trees, seedlings, and sprouts (summed across transects) in tropical dry, mesic, and wet (inside and outside enclosure) forest study sites.*

TABLE S2. *Species richness estimators, Incidence-based Coverage Estimator (ICE) and Chao 2, for trees, seedlings, and sprouts in tropical dry, mesic, and wet forest study sites.*

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