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Response of native Hawaiian woody species to lava-ignited wildfires in tropical forests and shrublands

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Abstract Wildfires are rare in the disturbance history of Hawaiian forests but may increase in prevalence due to invasive species and global climate change. We documented survival rates and adaptations facilitating persistence of native woody species following 2002–2003 wildfires in Hawaii Volcanoes National Park, Hawaii. Fires occurred during an El Niño drought and were ignited by lava flows. They burned across an environmental gradient occupied by two drier shrub-dominated communities and three mesic/wet *Metrosideros* forest communities. All the 19 native tree, shrub, and tree fern species demonstrated some capacity of postfire persistence. While greater than 95% of the dominant *Metrosideros* trees were top-killed, more than half survived fires via basal sprouting. *Metrosideros* trees with diameters >20 cm sprouted in lower percentages than smaller trees. At least 17 of 29 native woody species colonized the postfire environment via seedling establishment. Although the native biota possess adaptations facilitating persistence following wildfire, the presence of highly competitive invasive plants and ungulates will likely alter postfire succession.

Keywords Disturbance · *Dodonaea viscosa* · Fire adaptations · Hawaii · *Metrosideros polymorpha* · Sprouting

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Introduction

Wildfires have a dramatic effect on Hawaiian landscapes (D'Antonio et al. 2000). Yet, little is known on the fire history of the Hawaiian Islands and its role in the evolution and development of Hawaiian ecosystems (Vogl 1969; Mueller-Dombois 1981, 2001; Smith and Tunison 1992). Studies of sediment cores collected in bogs and radiocarbon data from charcoal studies indicated that wildfires have occurred in Hawaii prior to European settlement (Mueller-Dombois 1981; Smith and Tunison 1992; Burney et al. 1995). The occurrence of natural ignition sources including lightning and volcanism (Vogl 1969; Tunison and Leialoha 1988) and continuous vegetation cover in many ecosystems (Wagner et al. 1999) further suggests that fire did occur historically and did influence the disturbance history of Hawaiian ecosystems.

Although there is a poor fire record, the response of native woody species to wildland fire provides insights into historical fire patterns because

adaptations evolve within the context of each ecosystem's natural disturbance regime (Kauffman 1990). Species adaptations in ecosystems are linked to their capacity to survive, establish, and reproduce in the disturbance regime of their habitats (White and Pickett 1985). Examples of traits that promote survival of individuals following fire include: thick bark, protected buds from dense leaf bases, and sprouting from either epicormic or subterranean tissues. Adaptations that facilitate establishment of species or populations, but not the individual following fire include: fire-stimulated germination or flowering, seed storage on plants (e.g., serotinous cones), and wind-borne seeds (Kauffman 1990).

Many Hawaiian wet forest species possess characteristics frequently associated with long fire-return intervals (e.g., thin bark, buried seeds requiring heat or other disturbance to germinate, enhanced seedling establishment on downed wood, sprouting). Basal and epicormic sprouting following fire have been observed for *Metrosideros polymorpha,* a dominant Hawaiian tree species (Parman and Wampler 1977; Hughes et al. 1991; Tunison et al. 1995; D'Antonio et al. 2000). Another dominant native tree, *Acacia koa* has the capacity to sprout following disturbance (Tunison et al. 2001) and produces refractory seeds capable of surviving in the soils for decades until disturbance stimulates germination. The tree ferns *Cibotium glaucum* and *Sadleria cyathoides* survive and rapidly produce new fronds, presumably because the meristematic tissues are protected by frond scales (Smith and Tunison 1992).

Wind dispersal and capacity to establish on bare substrate is a common adaptation that facilitates invasion and establishment following disturbance such as fire (Kauffman 1990). *Metrosideros* has long-ranging and abundant wind-dispersed seeds (Drake 1992; Hatfield et al. 1996). Seedling recruitment has been observed following wildfire in *Metrosideros*-dominated wet forests (Tunison et al. 2001). In addition, the seeds of a dominant native shrub species in Hawaiian ecosystems, *Dodonaea viscosa,* were found to break dormancy following exposure to heat (Hodgkinson and Oxley 1990) and have also been found to germinate readily after fire (Hughes et al. 1991; Shaw et al. 1997; D'Antonio et al. 2000).

Although postfire response of many native Hawaiian species suggest that they may be adapted to disturbance, the majority of studies have been limited to the seasonally dry *Metrosideros* woodlands of Hawaii Volcanoes National Park (Hughes et al. 1991; Hughes and Vitousek 1993; Freifelder et al. 1998; Ley and D'Antonio 1998; D'Antonio et al. 2000; D'Antonio et al. 2001; Mack et al. 2001). Nonnative grass invasions during the past century have led to a dramatic increase in fire frequency and size in these dry woodlands (Smith and Tunison 1992). Rapid grass recovery or fine fuel re-accumulation following fire (Hughes et al. 1991) coupled with drier, windier microclimatic conditions (Freifelder et al. 1998) has led to additional fires creating a grass/fire cycle (D'Antonio and Vitousek 1992). Consequently, many previously native-dominated woodlands have been type converted to nonnative-dominated grasslands.

In contrast to the drier Hawaiian woodlands, few recorded fires have occurred and no studies have been conducted in the wetter *Metrosideros* forests with understories dominated by herbaceous species and tree ferns. The effects of fire are expected to differ from those in the dry woodlands because of differences in fuels and microclimatic conditions despite some similarity in species (e.g. *Metrosideros*). Although fires may have been infrequent historically, climate change, nonnative species invasions, and increasing human ignition sources are likely to result in more frequent larger fires in wet Hawaiian forests. Naturally ignited wildfires during particularly strong El Niño (ENSO), mediated droughts in 2002 and 2003 created an opportunity to examine fire effects in relatively intact wet forests as well as adjacent perturbed shrublands.

We hypothesized that native Hawaiian species would persist following fire through individual survival or establish from propagules in the postfire environment because these species evolved in a landscape subjected to a wide array of infrequent disturbance events (fires, volcanism, tropical storms, etc). We measured the response of native Hawaiian woody species and tree ferns for the first two years following the 2003 Luhi and Panauiki lava-ignited wildfires in five community types across an elevation/moisture gradient in Hawaii Volcanoes National Park. The specific objectives of this study were to: (1) examine the postfire survival rates and describe the mechanisms of persistence of native Hawaiian trees, tree ferns, and shrubs partitioned by species and size class; and (2) quantify native woody seedling

establishment across this elevation/moisture gradient for the first two years following fire. Information from this study should provide insights regarding historic fire regimes in this area and native species' response to fire, and will assist managers in evaluating the potential threat of fire to native forest recovery in these unique communities.

Methods

Study site

This study was conducted at Hawaii Volcanoes National Park on the Island of Hawaii (19°20′11″N and 155°7′29″W). Elevation ranged from 350 m in the relatively dry shrub-dominated communities to 825 m in wet forest communities; all communities occurred within 5 km of each other. The study area was located over a very steep precipitation gradient from dry shrublands to wet forest and encompassed four distinct Holdridge life zones: subtropical basal moist forest, subtropical basal wet forest, subtropical lower mountain moist forest, and subtropical lower mountain wet forest (Tosi et al. 2001). Substrate across the gradient consisted of young (400 to 750 yr-old) pahoehoe lava flows with minimal topographic relief (Trusdell et al. 2005). Two basic soil types are present: the Kalapana series and the Makaopuhi series. Both series are very shallow to shallow soils formed in ash deposited over pahoehoe lava with 2–10% slopes, and are classified as Medial, ferrihydritic, isothermic, Lithic Udivitrands (well drained), and Hapludands (poorly drained). The shrub-dominated communities are on the Kalapana dry phase soils, the mesic forest communities are on Kalapana medial course sandy loam, and the wet forest community is on Makaopuhi very paragravelly muck (Jasper 2007).

Metrosideros polymorpha is the dominant forest tree across the elevation gradient, but ranges in percent canopy cover from <1% in the shrublands to >60% in the mesic forests. The study area contained five major plant communities (Ainsworth 2007). The *Dodonaea viscosa/Andropogon virginicus* community (350–450 m) was dominated by native *Dodonaea* in the shrub layer (~9,000 individuals/ha) with the nonnative perennial bunch grass *Andropogon* dominating the understory. A few trees (*Metrosideros*) were scattered across the landscape, but were primarily restricted to lava uplifts where past fires did not kill them. This community is located within the mapped boundaries of past wildfires that occurred in 1972 and 1992 and will be referred to hereafter as the "*Andropogon* shrubland."

The *Dodonaea/Nephrolepis multiflora* shrub-dominated community (450–550 m) is also dominated by *Dodonaea* in the shrub tier (~8,500 individuals/ha) with the nonnative fern *Nephrolepis multiflora* dominating the understory. Similar to the *Andropogon* shrubland, remnant *Metrosideros* trees are scattered throughout this community. This community will be referred to as the "*Nephrolepis* shrubland." While the tree component of these two communities is now sparse due to the recent fires, historic photos indicate that the area was characterized as relatively open *Metrosideros* woodlands with scattered shrubs and a mixed understory prior to the 1972 wildfire (Hawaii Department of Land and Natural Resources 1966).

We sampled the *Metrosideros/Nephrolepis multiflora* forest community (550–640 m) which is dominated by *Metrosideros* in the overstory (~700 individuals/ha) and the nonnative fern *Nephrolepis multiflora* in the understory. This community will be referred to as the "*Nephrolepis* forest." The *Metrosideros/Dicranopteris linearis* forest community (640–750 m) contains *Metrosideros* in the overstory (~850 individuals/ha) and the native, mat forming fern *Dicranopteris* in the understory. This community will be referred to as the "*Dicranopteris* forest." The wettest and highest elevation community sampled was the *Metrosideros/ Cibotium glaucum* forest community (700–850 m). This community has an open canopy overstory of *Metrosideros* (~500 individuals/ha) with a native tree fern *Cibotium glaucum* midstory (~2,800/ha) and the native fern *Dicranopteris* and nonnative grasses in the understory. This community will be referred to as the "*Cibotium* forest."

Fire history

Lava has been an ignition source in this area of the Park at least from 1916 to present (Gassaway et al. 2002). Multiple fires have occurred in the coastal lowlands in the last 30 years including a 1992 fire which burned the *Andropogon and Nephrolepis* shrublands. The Panauiki Fire (January, 2003)

reburned over half (860 ha) of *Andropogon and Nephrolepis* shrublands between 60 and 670 m. In May 2003, the Luhi fire burned over 75% (2,000 ha) of the forested study area (National Park Service 2003). We established replicate plots ($n = 5$) in each of the five vegetation communities in the areas burned in the 2003 wildfires and unburned controls to determine tree and tree fern responses and the postfire seedling establishment.

Field methods

In the burned areas for each of the sampled communities, we established five randomly located 20 × 50 m permanent plots and measured the vegetation response one (2004) and two (2005) years following fire. Sample locations were selected based on composition and structure, elevation, fire history, and proximity to unburned sites. Unburned plots were sampled once—two years (2005) following fire except the *Nephrolepis* forest community which was sampled one year (2004) following fire. We selected unburned plots in each community type based on comparable elevation, and vegetation composition and structure. Flowering plant nomenclature followed that of Wagner et al. (1999), and tree fern nomenclature followed that of Palmer (2003).

We sampled trees, tree ferns, shrubs, and woody seedlings using a nested plot design. Individuals in the burned plots were recorded as sprouts if the live portion was attached to an older burned stem or root. Tree seedlings, defined as individuals less than 1.3 m tall, tree fern juveniles (those with fronds <50 cm long), and shrubs were measured in six subplots (1 × 5 m). Trees <10 cm diameter at breast height (dbh; 1.3 m in height) and tree ferns <10 cm in diameter at the point below past years frond shed were measured in six 2 × 10 m subplots. Trees >10 cm dbh and tree ferns with trunk diameters >10 cm were measured in the entire 20 × 50 m plot. Species with individuals that reached reproductive maturity within the first two years following fire were recorded.

Quantitative measures recorded for all trees, tree ferns, and shrubs included: plant mortality and mode of sprouting (basal if it originated from subterranean plant organs at the base of trees <50 cm above ground, and epicormic if it originated from dormant meristematic tissue in the bole or mainstems) (Kauffman 1990). For trees (>1.3 m tall) diameter at breast height (dbh) and crown mortality were recorded. For tree ferns (with fronds >50 cm long), basal diameter, trunk length, and crown mortality were recorded. From these data, percent crown mortality and individual plant death were calculated for all trees, tree ferns, and shrubs by species, and by diameter size class (<10, 10–20, >20 cm) for the dominant canopy (*Metrosideros*) and subcanopy (*Cibotium*) species. Tree fern survival was also analyzed by length class (<1, 1–2, >2 m).

Analysis

Native Hawaiian woody species and tree ferns were grouped according to Rowe's (1981) plant response classification system which incorporates life history traits of species and characteristics of fire regimes. The five categories include: invaders (high dispersal ability), evaders (long lived propagules stored in the soil), avoiders (shade tolerant and slow invaders following fire), resisters (thick bark or an anomalous arrangement of mertistematic tissues that facilitates fire survival), and endurers (capacity to sprout from dormant surviving meristematic tissues) (Rowe 1981). Species often have multiple or changing adaptations and therefore can fit into more than one category. This universal life-form classification is a useful way to examine species response to fire on a per site basis because categories incorporate the influence of environmental factors (Agee 1993).

The sampling unit used in analysis for all the parameters was the 20 × 50 m plot. Average values were calculated per plot and used in analysis for vegetation parameters that were sampled in subplots (e.g., seedlings, small trees, and tree ferns). *Metrosideros* percentage survival and population structure were analyzed as two factor ANOVA's with tree diameter size class, community, and size class × community as fixed effects. Differences among plant communities were compared using Tukey's multiple comparison tests. Tree count data used to examine population structure were log base 10 transformed (log + 1) to equalize variance. ANOVA and *t*-test analyses were performed at an $\alpha = 0.10$ in order to increase the power ($1 - \beta$).

Differences in *Cibotium* survival among size classes were compared using nonparametric tests (Kruskal–Wallis Rank Test and Wilcoxon Rank Test for pair-wise comparisons). Nonparametric tests were also used to detect differences in native species

seedling density between treatments and years (unburned vs. two year postfire) for each community.

Results

Sprouting response

Wildland fire resulted in greater than 95% crown mortality of the dominant *Metrosideros* trees. There were remarkably few unburned islands within the fire perimeters. Despite the near complete crown mortality, many individuals of the native Hawaiian species survived fire across the elevation gradient via vegetative sprouting. Nineteen tree, shrub, and tree fern species were observed to have survived fire primarily through basal spouting (Table 1). In addition to sprouting from the base or root crown, scattered individuals of three woody species, *Dodonaea*, *Metrosideros,* and *Santalum paniculatum*, were also observed to have sprouted from epicormic tissues. Postfire reproduction of surviving individuals can be rapid as we observed fruiting or spore production of individuals of all tree fern and shrub species within the first two years following fire (Table 1). In addition, two tree species, *Hedyotis terminalis* and *Santalum* were also observed to be fruiting during the second postfire year.

Despite high crown mortality, more than half (57%) of the 911 individual *Metrosideros* trees sampled in the burned communities survived fire through basal sprouting. Survival significantly differed among diameter classes, where trees with larger diameters (>20 cm) were less likely to sprout following fire than those with smaller diameters ($P = 0.05$; Fig. 1). The influence of plant size on survival was most pronounced in the *Dicranopteris* forest community, where >70% of the smaller trees (<10 cm and 10–20 cm dbh) and only 38% of the larger trees (>20 cm dbh) survived fire ($P = 0.02$).

The postfire survival of *Metrosideros* (all sizes combined) differed among communities where survival was 71% in the *Dicranopteris* community, 48% in the *Cibotium* community and 52% in the *Nephrolepis* forest community ($P = 0.07$). However, we found no difference in survival among communities when controlling for differences among size classes by using a two factor ANOVA with size class and community ($P = 0.36$; Fig. 1). Differences in survival among communities were related to differences in *Metrosideros* population structure among communities ($P < 0.01$; Fig. 2). The population structure of the *Dicranopteris* and *Nephrolepis* forest communities was composed of smaller individuals with greater than 75% of *Metrosideros* trees in the smallest size class (<10 cm dbh). In contrast, in the *Cibotium* forest <30% of the trees were in the smallest size class and over 50% in the largest size class (>20 cm dbh).

Tree ferns survived the fires in very high percentages (>86%; N = 1,195 *Cibotium* tree ferns sampled). While existing foliage of tree ferns were killed by fire, the individuals were observed to rapidly refoliate from the apical meristems that were apparently protected from lethal temperatures by the bark, and leaf bases. Tree fern size affected rates of survival where smaller sized individuals (<10 cm diameter) had lower (42%) survival than the larger classes (10–20 cm and >20 cm diameter; Fig. 3). In the largest size class >90% of the individual's possessed live fronds one year postfire ($P < 0.01$). Although there was a difference ($P < 0.10$) in survival between the two larger diameter classes, this difference is probably not ecologically meaningful considering that survival was extremely high (>90%) in both classes. For *Cibotium* individuals >10 cm in diameter, no difference in survival was detected among trunk length classes (<1 m, 1–2 m, >2 m; $P = 0.38$).

Seedling response

There were a total of 29 native woody species and tree ferns that were found on the entire study area, and seedlings or juveniles of 17 were found to occur in the postfire plots (Table 1). Seedlings of 10 species were found only in burned areas while seedlings of three species were found only in unburned sites and seven species were found in both burned and unburned sites. The majority of species found in the burn following fire were present both as seedlings and as sprouts including four tree, six shrub, and two tree fern species. Of the five species present, only as seedlings, two were tree species and three were shrub species. For three shrub species, *Clermontia hawaiiensis*, *Lythrum maritimum*, and *Sida fallax* no individuals (living or dead) were found in the study area suggesting that these species either dispersed into the area from outside or had been present only as

Table 1 Native woody species and tree ferns that survived fire and/or established from seed in the postfire environment

Species	Life form	Individual survival			Postfire
		Apical	Basal	Epicormic	Seedlings
Broussaisia arguta	Shrub		X		
Cheirodendron trigynum	Tree				X
Cibotium glaucum	Tree fern	X*			X
Cibotium menziesii	Tree fern	X*			
Clermontia hawaiiensis	Shrub				X
Coprosma menziesii	Shrub		X*		X
Dodonaea viscosa	Shrub		X*	X*	X*
Hedyotis terminalis	Tree		X*		X
Ilex anomala	Tree		X		X
Leptecophylla tameiameiae	Shrub		X*		X
Lythrum maritimum	Shrub				X
Melicope clusiifolia	Tree		X		X
Melicope radiata	Tree				X
Metrosideros polymorpha	Tree		X	X	X
Myrsine lessertiana	Tree		X		
Myrsine sandwicensis	Tree		X		
Osteomeles anthyllidifolia	Shrub		X*		
Pipturus albidus	Shrub				X*
Psychotria hawaiiensis	Tree		X		
Sadleria cyatheoides	Tree fern	X*			X
Santalum paniculatum	Tree		X*	X*	
Scaevola chamissoniana	Shrub		X*		
Sida fallax	Shrub				X*
Vaccinium calycinum	Shrub		X*		X
Vaccinium reticulatum	Shrub		X*		X
Total		3	16	3	17

Mode of survival was recorded as apical for tree ferns and basal or epicormic sprouting for tree and shrub species. Asterisks denote species with individuals that fruited or flowered within two years following fire

propagules in the soil seed bank. Growth and maturation from seed was rapid for *Dodonaea*, *Pipturus albidus*, and *Sida fallax*. Individuals of these three species were observed to have flowered within the first two postfire (and post germination) years.

There were no differences in shrub species seedling densities when comparing between unburned and burned sites for any community (Table 2) except for the common shrub *Dodonaea*. *Dodonaea* seedlings had dramatically higher densities in burned, compared to unburned sites. For example, in the *Andropogon* shrubland, the second postfire year *Dodonaea* density was 3,333/ha in the unburned and 12,333/ha in burned sites ($P = 0.16$). Similarly in the *Nephrolepis* shrubland, *Dodonaea* seedlings densities were 5,733/ha in the unburned sites, but densities were almost 8-fold greater in burned sites of this community (45,267/ha) two years postfire ($P = 0.01$). In the forest communities, *Dodonaea* was not encountered in the unburned sites (Table 2), but did establish from seed in low densities in the burned sites of the *Nephrolepis* (200/ha; $P = 0.07$), *Dicranopteris* (67/ha; $P = 0.43$), and *Cibotium* (267/ha; $P = 0.18$) forest communities.

The relatively low seedling densities of rare tree and tree fern species did not differ between unburned and burned sites within each community type (Table 2). However, for the canopy dominant species, *Metrosideros*, seedling density did differ between burned and unburned sites within the three forest communities. Only one seedling was found in the unburned plots, but two years following fire many more seedlings were found in the burned plots of the *Nephrolepis* (667/ha; $P = 0.06$) and *Dicranopteris* (267/ha; $P = 0.07$) forests (Fig. 4). Alternatively, in

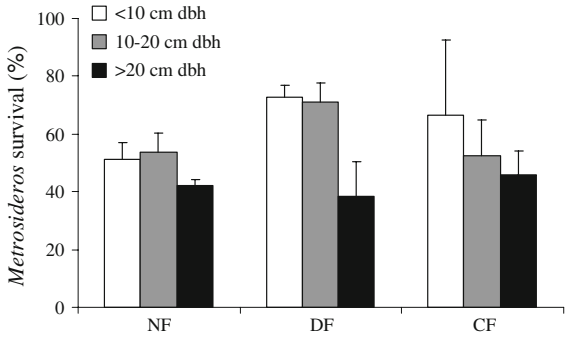

Fig. 1 Postfire survival (%) via sprouting of *Metrosideros polymorpha* individuals in the three sampled forest communities 12 months following fire at Hawaii Volcanoes National Park (NF = *Nephrolepis* forest; DF = *Dicranopteris* forest; and CF = *Cibotium* forest). Survival differed by diameter size class (dbh) across the three forest communities ($P = 0.04$), with the greatest mortality in the largest size class. Survival did not differ among communities when controlling for size class ($P = 0.36$) and no interaction was detected (Size × Community: $P = 0.59$). Data are means +1 SE

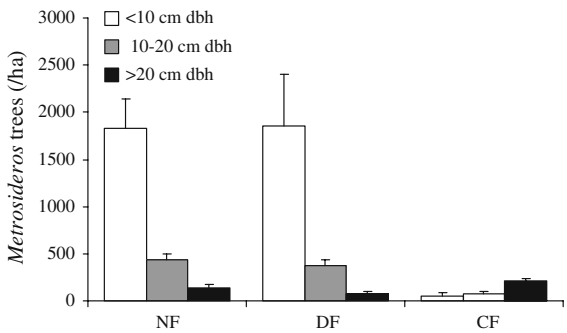

Fig. 2 The population structure of *Metrosideros polymorpha* in the three different forest communities at Hawaii Volcanoes National Park. Structure differed among the three forest communities ($P < 0.01$; NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, CF = *Cibotium* forest). Data are means ±1 SE. A total of 911 trees were measured

the *Cibotium* forest seedling density was high (8,267/ha) in the unburned sites, whereas in the burned sites two years postfire seedling density was significantly lower (733/ha; $P = 0.09$; Fig. 4). Juveniles of the subcanopy dominant tree fern species, *Cibotium glaucum*, were more abundant in the burned *Cibotium* forest two years following fire (3,200/ha) than the unburned forest (400/ha), but this difference was not significant ($P = 0.16$) due to high variation among plots.

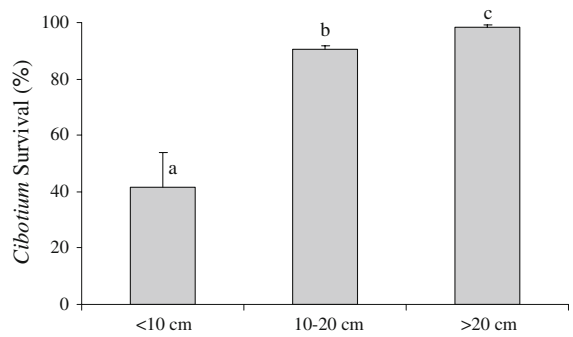

Fig. 3 *Cibotium glaucum* survival by diameter class in the *Cibotium* forest community ($P < 0.01$). The greatest mortality was found to occur in the smallest size class. Data are means +1 SE. Letters indicate significant differences. A total of 1195 tree ferns were measured

Discussion

Previous observations of postfire sprouting have been made for many of the species present in this study (Warshauer 1974; Parman and Wampler 1977; Tunison et al. 1994, 1995; D'Antonio et al. 2000). Yet this study is the first study to quantify survival and mortality rates and how survival differed by species, size class, and plant communities across an elevation gradient. These findings are particularly relevant because context (e.g. community type, elevation, fire characteristics, invasive species, post fire competition, etc) may greatly influence species response to fire (Kauffman 1990; Kauffman and Martin 1990, Sampaio and Kauffman 1993). Given the characteristics of the relatively wet climate and the relatively low incidence of lightning, naturally occurring fires were likely a rare occurrence in native Hawaiian wet forests. However, we observed that native Hawaiian woody plants in this study possessed several adaptations that facilitated fire survival.

The majority of species were characteristic of "endurers" (i.e. they were top-killed, but sprouted after fire; Table 3). Nearly all tree and shrub sprouts originated from the base or root crown where bark tends to be the thickest and where soils provide a great deal of insulation (Agee 1993). Tree ferns were characteristic of "resistors" in that above ground tissues and plant structures survived fire and refoliated within a few months following fire (Table 3). *Cibotium* and *Sadleria* fern species have been observed to recover following wildfires (1969–1973) in the region (Warshauer 1974), but the high

Table 2 Native shrub, tree, and tree fern seedling densities in unburned (U) and burned (B) sites two years following fire for the three forest communities (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, CF = *Cibotium* forest)

Species	NF		DF		CF	
	U	B	U	B	U	B
Shrub species						
Coprosma menziesii	0	0	67 (67)	0	133 (133)	67 (67)
Dodonaea viscosa	0	* 200 (82)	0	67 (67)	0	267 (163)
Labordia hedyosmifolia	0	0	0	0	67 (67)	0
Leptecophylla tameiameiae	67 (67)	0	0	67 (67)	0	0
Pipturus albidus	0	0	0	67 (67)	0	67 (67)
Vaccinium calycinum	0	0	0	0	133 (82)	67 (67)
Vaccinium reticulatum	0	0	0	67 (67)	0	0
Tree species						
Cheirodendron trigynum	0	0	0	0	133 (82)	0
Hedyotis terminalis	0	0	0	67 (67)	0	0
Ilex anomala	0	0	0	67 (67)	0	133 (82)
Melicope clusiifolia	0	0	0	0	400 (245)	1000 (350)
Melicope radiate	0	0	0	0	0	67 (67)
Metrosideros polymorpha	67 (67)	* 667 (236)	0	* 267 (125)	8267 (3165)	* 733 (386)
Myrsine lessertiana	0	0	0	0	267 (125)	* 0
Myrsine sandwicensis	0	0	133 (82)	0	0	0
Tree fern species						
Cibotium glaucum	0	0	0	333 (333)	400 (323)	3200 (1948)
Sadleria cyatheoides	0	0	0	67 (67)	0	0

Mean densities per hectare are reported with standard errors in parentheses. Asterisks denote significant differences ($P < 0.10$) between unburned and burned sites for each community

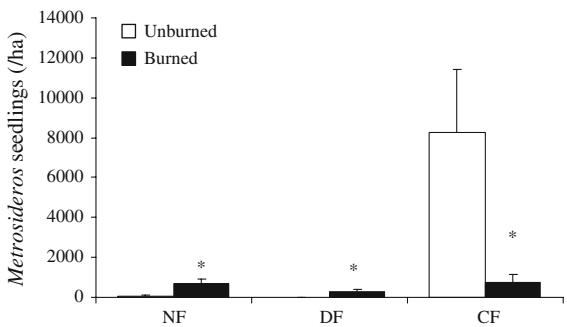

Fig. 4 *Metrosideros polymorpha* seedling density in unburned and burned sites two years following fire in the forest communities (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest and CF = *Cibotium* forest). Means +1 SE are reported and asterisks denote significant differences between treatments for each community

degree of survival (>90%) of these tree ferns has not been previously quantified. In Australia, tree ferns (*Cyanea* spp.) have also been reported to recover rapidly following disturbance including fire (Ough and Murphy 2004). We attribute the high survival of tree ferns to their unique morphology in which the meristematic tissues were protected from lethal temperatures by the thick fibrous bark, live tissues embedded within the main stem, and cover by green frond bases. Survival of species with this suite of morphological traits would be increased with increasing trunk diameter as was observed in this study.

In rare cases, some woody species including *Metrosideros*, *Santalum paniculatum*, and *Dodonaea* were also observed to regenerate from epicormic buds along the stem and in the crown. Vegetative sprouting from trunks of *Metrosideros* individuals has also been observed to occur following tree-fall in unburned wet forests (Drake and Mueller-Dombois 1993). Sprouting from aboveground tissues provides a competitive advantage in terms of rapid recovery of leaf area over individuals sprouting from the base or establishing from seed (Agee 1993). However, in this study,

Table 3 Native woody species and tree fern plant adaptations that facilitate survival following fire in tropical wet forests and shrublands of Hawaii Volcanoes National Park, Hawaii

Adaptation	Trait	Species
Resistors	Protected meristems	Tree ferns (3):
		Cibotium glaucum, Cibotium menziesii, Sadleria cyathoides
Endurers	Sprouters	Trees (8):
		Hedyotis terminalis, Ilex anomala, Melicope clusiifolia, Metrosideros polymorpha, Myrsine lessertiana, Myrsine sandwicense, Psychotria hawaiiensis, Santalum paniculatum
		Shrubs (8):
		Broussaisia arguta, Coprosma menziesii, Dodonaea viscosa, Leptecophylla tameiameiae, Osteomeles anthyllidifolia, Scaevola chamissoniana, Vaccinium calycinum, Vaccinium reticulatum
Invaders	Wind-borne seeds	Tree ferns (2):
		Cibotium glaucum and *Sadleria cyathoides*
		Trees (5):
		Cheirodendron trigynum, Hedyotis terminalis, Ilex anomala, Melicope clusiifolia, Metrosideros polymorpha
		Shrubs (10):
		Clermontia hawaiiensis, Coprosma menziesii, Dodonaea viscosa, Leptecophylla tameiameiae, Lythrum maritimum, Melicope radiate, Pipturus albidus, Sida fallax, Vaccinium calycinum, Vaccinium reticulatum
Evaders	Soil seed bank	Shrubs (2):
		Dodonaea viscosa[a] and *Osteomeles anthyllidifolia*[a]

[a] Hughes and Vitousek 1993

Adaptations follow that of Rowe (1981). Numbers in parentheses are the total number of species where the specific trait was observed

epicormic sprouting was very rare (<1% of individuals), presumably because temperature extremes and durations during the fire reached lethal levels to kill epicormic buds present beneath the thin scaly bark of the *Metrosideros*.

Rapid maturation and reproductive effort following fire is also an adaptation facilitating persistence and establishment following fire (Kauffman 1990). All the eight shrub and the three tree fern species that survived fire vegetatively had individuals that reached sexual maturity (i.e., were observed to be fruiting or produced spores) within two years following fire (Table 1). In addition, two tree species *Hedyotis terminalis* and *Santalum* also had sprouts that reached sexual maturity during the second postfire year. The majority of reproducing *Santalum* originated from previously burned basal or root sprouts, suggesting that flowering for this species was fire enhanced.

Specific characteristics promoting survival in an individual plant will often change with age (Kauffman 1990). Size class distribution of the dominant tree and tree fern species influenced rates of survival. We found that postfire survival rates of *Metrosideros* decreased with increasing size. Tunison et al. (1995) observed that *Metrosideros* survival following fire appeared to be inversely correlated with tree size. Conversely, in the dry *Metrosideros* woodlands D'Antonio et al. (2000) found mortality to be independent of size class. Although increased mortality with age and size has been documented in other tree species such as *Quercus* spp. (Griffin 1980), the loss of sprouting capacity usually signifies a shift in the mode of survival to a general thickening of the bark tissue to protect cambial and meristematic tissues (Kauffman and Martin 1990). In this study, the stem and crown of *Metrosideros* trees were extremely sensitive because of the thin-barked nature of all individuals in all size classes. This heat sensitivity of aboveground tissues of *Metrosideros* was exemplified by the near complete crown mortality and paucity of epicormic sprouting following fire. Based on these findings, predicted increases in fire frequency associated with climate change responses (e.g., warmer temperatures, greater frequency, and severity of El Niño events; IPCC 2007) may limit structural complexity and increase dominance of nonnative species as has already occurred at lower elevations.

In addition to the individual species adaptations to fire, context-specific factors such as pre-fire population, vegetation structure, weather conditions, fire behavior, and fuel consumption may greatly influence individual survival (Agee 1993; D'Antonio et al. 2000). Survival of *Metrosideros* was the greatest in the *Dicranopteris* forest community (71%). Differences in *Metrosideros* population structure between the *Dicranopteris* and *Cibotium* communities partially explain the lower survival in the *Cibotium* community (48%). The *Cibotium* community appears to be a later successional forest with a greater proportion of trees in the largest size class (Fig. 2) which had a lower number of surviving/sprouting individuals. Many explanations as to why the trees are larger in the *Cibotium* community as compared to the *Dicranopteris* community are possible (e.g., older substrate age; less historical disturbance from humans, ungulates, and plants; moister microclimatic conditions; and/or differences in soil ash content).

Total survival of *Metrosideros* in the *Nephrolepis* forest community (52%) was also significantly lower than in the *Dicranopteris* (71%) community ($P = 0.02$), but population structures of these two young forests were similar (Fig. 2). These data suggest that the difference in survival may be related to differences in fire severity (i.e., fuel consumption or fire intensity). In the burned *Dicranopteris* forest community, the quantity of unconsumed residual surface fuels was greater than that of the other two communities suggesting lower fuel consumption. Lower fuel consumption would result in lower heat flux around the base of the trees and could explain the higher survival observed in this community. In the coastal lowlands and seasonal submontane zones of Hawaii Volcanoes National Park, D'Antonio et al. (2000) observed that individual mortality was greater for native Hawaiian woody species in sites where fuel consumption was the highest.

In the burned landscape, about the same number of native Hawaiian plant species were encountered as seedlings (17) as surviving individuals from sprouts (19). Two tree (*Cheirodondron trigynum* and *Melicope radiata*) and four shrub species (*Clermontia hawaiiensis*, *Lythrum maritimum*, *Pipturus albidus*, and *Sida fallax*) were observed to be obligate seeders (i.e., no vegetative survival by sprouting). It is not surprising that many native species can be classified as "invaders" (i.e. those that disperse onto the site following fire) according to Rowe's (1981) classification (Table 3). Mueller-Dombois (1987) also characterized *Metrosideros* as an early successional tree species that colonized new volcanically derived substrates or gaps created by tree falls while remaining dominant in mature wet forest communities.

Species with seeds that can survive fire in the soil seed back or on individual plants are classified as "evaders" (Table 3). Some of the seedlings detected following fire in this study may also have originated from the soil seed bank, but the relative importance of the seed bank is unknown. Hughes and Vitousek (1993) found that some native Hawaiian shrub species retain the capacity to germinate following exposure to high-temperature treatments (120°C for 5 min) including *Osteomeles* and *Dodonaea*.

Seedling establishment following fire differed among species and among communities across the elevation gradient of this study (Table 2). Fewer *Metrosideros* seedlings were found in the burned *Cibotium* forest as compared to those in the unburned *Cibotium* forest (Table 2). Lower *Metrosideros* seedling density in the burned plots is not likely because of limited seed source considering the proximity to unburned forests and the dispersal capabilities of these small wind-blown seeds. The majority of *Metrosideros* seedlings found in the unburned forest had established on moss covered tree fern nurse logs. Although tree fern trunks were abundant in the burned sites, mosses were burned off during the fire, and conditions on the trunks were presumably drier and less favorable for *Metrosideros* establishment.

The short-term changes in *Metrosideros* seedling density following fire in this study do not necessarily indicate differences in the future forest because this site is not likely seed limited as *Metrosideros* is well suited for establishing in canopy gaps (Drake 1992; Hatfield et al. 1996). Drastically lower seedling density in the burned *Cibotium* forest (733/ha) may be inconsequential because the density of 2-year old seedlings was still much greater than the canopy density. In addition, higher light conditions in the burned forest presumably will result in a higher likelihood of reaching the canopy than those seedlings in the unburned forest (Burton and Mueller-Dombois 1984).

In contrast to the *Cibotium* forest, *Metrosideros* seedling recruitment appeared to be enhanced by fire

in the *Nephrolepis* and *Dicranopteris* forests where seedling densities were greater in burned sites than unburned sites (Table 2). Sampling other disturbed sites, Restrepo and Vitousek (2001) found that *Metrosideros* seedling establishment was greater on recent (4 to 17-year old) landslides than undisturbed mesic forests on the Island of Hawaii. Because the *Nephrolepis* and *Dicanopteris* forest communities are younger and lack woody and tree fern nurse logs, the dense herbaceous fern understory in the unburned sites may limit light and space for seedling establishment. Fire temporarily removed understory barriers and allowed for seedling establishment. The fact that, seedling densities remain lower in these communities than the *Cibotium* forest even following fire, supports the idea that seedling establishment across the study area is facilitated by tree fern nurse logs.

The native shrub *Dodonaea viscosa* was the only woody species present in all the five communities following fire. *Dodonaea* colonized the postfire environment through dispersal (i.e. seeds are enclosed in wind-borne bracts) and from the soil seed bank where temperatures during fire scarify the seeds (Hodgkinson and Oxley 1990). Therefore, *Dodonaea* possesses traits characteristic of evaders, invaders, and endurers (Table 3).

In the three forest communities of this study, no *Dodonaea* shrubs were found in the unburned sites and those in the burned sites had established from seed presumably from offsite colonization (i.e. neighboring shrubland communities). In the shrubland communities, however, *Dodonaea* individuals both sprouted and established from seed. This species had higher seedling densities in burned areas than in unburned areas. It is also one of three native woody species to reach sexual maturity from seed within two postfire years. Other fire studies at Hawaii Volcanoes National Park found that *Dodonaea* seedlings were abundant in burned mesic forest and shrublands (Warshauer 1974), submontane sites (Hughes et al. 1991; Hughes and Vitousek 1993; D'Antonio et al. 2000), and coastal lowlands (D'Antonio et al. 2000).

Many of the native Hawaiian woody species and tree ferns in this study area possessed traits that facilitated or ensured the persistence of individuals and/or species following fire. As would be expected the effects of fire differed among species; populations, and vegetation communities. The majority of woody species demonstrated the capacity to sprout, thus conferring these plants with advantages over individuals that rely solely on seeds for establishment in the postfire environment. It is unclear whether these are evolutionary adaptations to fire or causal adaptations of traits derived in response to other disturbances common in the region (volcanism, landslides, hurricanes, etc.). These adaptations may not be sufficient to insure dominance of native species in the future as the presence of invasive plant and nonnative ungulate species coupled with changes in climate may dramatically alter postfire succession and dominance in these ecosystems.

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