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Technical Report 167

**Testing native species response to fire – a first step towards building
fire resilient native plant communities at Hawai'i Volcanoes National
Park**

September 2009

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PCSU is a cooperative program between the University of Hawai`i and U.S. National Park Service, Cooperative Ecological Studies Unit.

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Recommended Citation:

Rhonda Loh, Alison Ainsworth, Tim Tunison, and Carla D'Antonio. 2009. Testing Native Species Response to Fire at Hawai`i Volcanoes National Park. Technical Report No.167. Pacific Cooperative Studies Unit, University of Hawai`i, Honolulu, Hawai`i. 30 pg.

Key words:

Fire effects, forest restoration, vegetation, seed additions, fire-tolerant species, alien species

Place key words:

Hawaii, Hawai`i Volcanoes National Park

Editor: Clifford W. Morden, PCSU Deputy Director (e-mail: cmorden@hawaii.edu)

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Abstract

Wildfires, fueled by fire-adapted alien grasses, result in the loss of native tree and shrub species in the dry and seasonally dry communities of Hawai'i Volcanoes National Park. Future wildfires and further loss of native plant diversity is expected given the prevalence of alien grasses in the area. Fire-tolerance, defined in this paper as the ability to survive or colonize after fire, was evaluated in seven controlled burns. Seed germination in response to oven heating was tested in laboratory experiments. Fourteen of 19 native species showed some capacity to survive or colonize after fire. Seedlings of eleven species were able to establish from seeds placed in the field prior to or immediately following controlled burns (*Argemone glauca*, *Bidens hawaiiensis*, *Canavalia hawaiiensis*, *Dodonaea viscosa*, *Myoporum sandwicense*, *Osteomeles anthyllidifolia*, *Santalum paniculatum*, *Scaevola kilaueae*, *Sida fallax*, *Sophora chrysophylla*, *Sesbania tomentosa*). Seven species survived beyond the first year including six that reached reproductive maturity (*Argemone glauca*, *Bidens hawaiiensis*, *Canavalia hawaiiensis*, *Dodonaea viscosa*, *Sida fallax*, *Sophora chrysophylla*). Seeds of ten species tested in oven-heating experiments showed either a positive or neutral germination response to mild heating (90 °C), among these were three species (*Myrsine lanaiensis*, *Rhus sandwicensis*, *Senna gaudichaudii*) not tested in the field. Testing species response to fire is the first step toward building resilient native plant communities in the new fire regime established by alien grasses at HAVO.

1. Introduction

The spread of fire-adapted alien grasses has made native plant communities more susceptible to fire in Hawai'i Volcanoes National Park HAVO (Smith and Tunison 1992). In the seasonally dry 'ōhi'a (*Metrosideros polymorpha*) woodlands (1,500-4,000 ft elevation), fire frequency has increased 3-fold and fire size 60-fold since the invasion and spread of broomsedge (*Andropogon virginicus*), bushy beardgrass (*Schizachyrium condensatum*), molasses grass (*Melinis minutiflora*) and other alien grasses in the 1960's (NPS unpublished data). Over half of the seasonally dry woodlands invaded by grasses have been affected by fire and replaced by alien savannas during the last 25 years (Tunison et al. 1995, 2001). Formerly dominant woody species 'ōhi'a and pūkiawe (*Leptecophylla tameiameia*) suffer high mortalities, and individuals have difficulty re-establishing in competition with fast growing alien grasses after fire (Hughes et al. 1991, Hughes & Vitousek 1993, D'Antonio et al. 1998). In contrast, fire-adapted alien grasses recover vigorously and increase fine fuel loads up to 3-fold greater than in adjacent unburned areas thereby increasing the risk for future wildfires in the area. A grass/fire cycle has established where invading grasses promote fire in environments with little history of fire; fire, in turn, increases the biomass of alien grasses and thus greater fire potential and ultimately greater loss of native vegetation (D'Antonio & Vitousek 1992, Freifelder et al. 1998). Fire risk is exacerbated by the recent dieback of faya tree (*Morella faya*), an introduced species abundant in the area. The resulting dead trees create a woody fuel bed that has the potential to fuel more intense wildfires.

In the coastal lowland (<1,000 ft elevation), the impacts of alien grasses and wildfire on shrublands and grasslands result in the loss of fire-sensitive native woody species such as pūkiawe and 'ākia (*Wikstroemia sandwicensis*) and the increase of fire-stimulated native pili grass (*Heteropogon contortus*) and the indigenous shrub 'a'ali'i (*Dodonaea viscosa*) (Tunison et al. 1994). While the negative impacts of alien grasses and wildfire are less severe in pili grasslands, the net effect is a less diverse assemblage of native plants after fire.

Restoring fire-damaged communities presents a daunting challenge to park managers. Trying to restore formerly dominant but fire-sensitive 'ōhi'a and pūkiawe is impractical given the widespread abundance of alien grasses and the inevitability of future wildfires. Instead, managers are adopting a rehabilitation approach by creating a replacement community of fire-tolerant native plants that can survive and ideally spread in the new grass/fire cycle. The resilience of some native species to survive wildfire and colonize rapidly became apparent from fire effects studies and casual observations of native plant recovery after fire (Table 1). These species were identified by their ability to recover from fire vegetatively or to recruit prolifically from seed after fire (Warshauer 1974, Tunison et al. 1994, 1995, Shaw et al. 1997). Many of these species were once common to 'ōhi'a woodlands and coastal lowland communities but were eliminated by introduced feral goats that roamed the park over the last two centuries (Mueller-Dombois and Spatz 1975). Goats were eliminated from lowland communities in the park in the mid-1970's, but lack of available source material limited natural recovery of many native plants.

This paper summarizes results from field and laboratory experiments conducted between 1993-2001 that evaluated the ability of several native species to resprout and recruit from seed after fire. Seven controlled burns were conducted in which seeds of twelve native species were placed in the field to test seedling recruitment response to fire. Also, seed germination response to oven heating was measured for 18 species to determine the direct effects of elevated temperature on seed germination.

Table 1. Potential fire-tolerant species in Hawai'i Volcanoes National Park.

<u>Scientific name</u>	<u>Common name</u>	<u>Life form</u>
<i>Acacia koa</i>	Koa	tree
<i>Agrostis avenacea</i>	He'upueo	grass
<i>Argemone glauca</i>	Pua kala	herb
<i>Bidens hawaiiensis</i>	Ko'oko'olau	herb/subshrub
<i>Canavalia hawaiiensis</i>	'Āwikiwiki	vine
<i>Dodonaea viscosa</i>	'A'ali'i	shrub
<i>Eragrostis variabilis</i>	'Emoloa	grass
<i>Myoporum sandwicense</i>	Naio	tree
<i>Myrsine lanaiensis</i>	Kōlea	tree
<i>Osteomeles anthyllidifolia</i>	'Ūlei	shrub
<i>Psydraz odorata</i>	Alahe'e	tree
<i>Rhus sandwicensis</i>	Nēnēleau	shrub/small tree
<i>Rumex skottsbergii</i>	Pāwale	shrub
<i>Santalum paniculatum</i>	'Iliahi	tree
<i>Scaevola kilaueae</i>	Huahekili uka	shrub
<i>Senna gaudichaudii</i>	Kolomona	tree
<i>Sesbania tomentosa</i>	'Ōhai	shrub/vine
<i>Sida fallax</i>	'Ilima	shrub
<i>Sophora chrysophylla</i>	Māmane	tree
<i>Tephrosia purpurea</i>	'Auhuhu	shrub
<i>Vaccinium reticulatum</i>	'Ōhelo	shrub
<i>Waltheria indica</i>	'Uhaloa	subshrub
<i>Wikstroemia phillyreifolia</i>	'Ākia	shrub

2. Methods

2.1 Study Area

Study sites are located in the seasonally dry 'ōhi'a woodlands and the coastal lowlands (Figure 1). The climate is warm-tropical with mean annual temperatures of 23-25 °C (Doty and Mueller-Dombois 1966). Average annual rainfall is lower in the coastal lowlands (50-100 cm/year) than in the 'ōhi'a woodlands (75-200 cm/year). Both sites have a pronounced summer dry period. Lava-derived substrates are young (between 200-3000 year old) and soils are poorly developed (Table 2). With the exception of Kīpuka Nēnē, burns were located in kīpuka (vegetation isolated by recent lava flows) to reduce the potential for fire escape and minimize containment costs. All sites had previously burned between 1969 and 1972 from either lava outbreaks or human-caused ignitions. Two sites, Pili Kīpuka II and Muliwai III, are reburns of two 1995 controlled burns.

In the four 'ōhi'a woodland sites (Kīpuka Nēnē, Muliwai Ia&b, II and III), the native vegetation had largely been eliminated and replaced by alien molasses grass, bushy beardgrass and broomsedge. Native 'ōhi'a, 'a'ali'i, 'ūlei (*Osteomeles anthyllidifolia*) and pūkiawe were only sparsely distributed. A small stand of māmane (*Sophora chrysophylla*) was present in Muliwai II.

In the three coastal lowland sites (Kealakomo Waena, Pili Kīpuka I and II), native pili grass co-existed with alien natal redtop (*Melinis repens*), thatching grass (*Hyparrhenia rufa*), and molasses grass. Alien shrubs (*Schinus terebinthifolius*, *Lantana camara*, *Pluchea carolinensis*) were abundant and two native shrubs (*Dodonaea viscosa*, *Tephrosia purpurea*) were present in Kealakomo Waena.

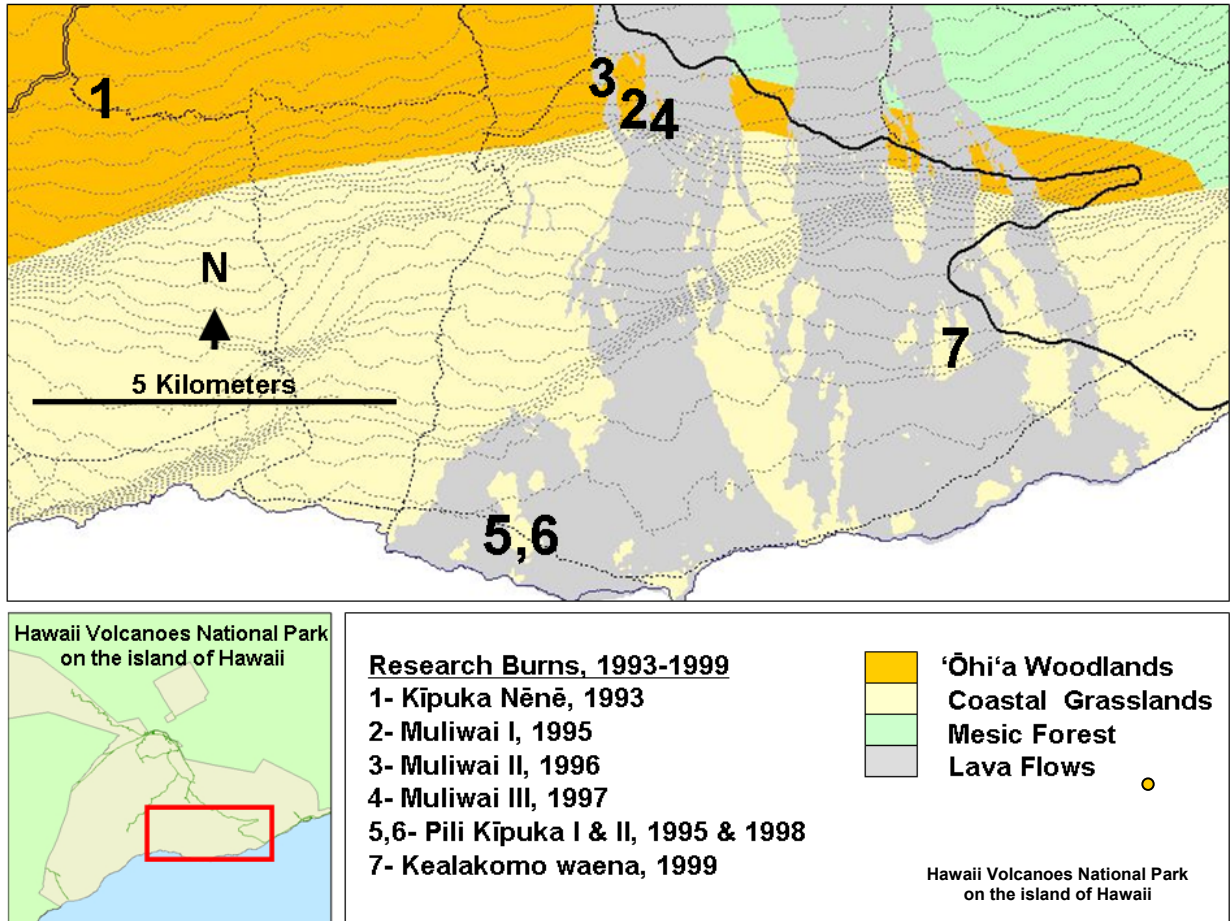


Figure 1. Location of research burns at Hawai'i Volcanoes National Park.

2.2 Controlled Burn Experiments

Between 1993 and 1999 controlled burns were conducted in seven sites (Table 2). Grass fuels were ignited using a gasoline drip torch, and fire was laid down in parallel strip to create a series of small head fires. In six sites that were isolated from adjacent fuels by old lava flows, the fire was allowed to extinguish on its own. In the remaining site (Kīpuka Nēnē) fire was quenched with water at the end of the day. Remaining unburned patches were burned before the day's end. Burn severity of the substrate and vegetation were assessed qualitatively using the burn severity index described in the National Park Service, Western Region Fire Monitoring Handbook (1992): unburned, scorched (litter partially blackened, duff nearly unchanged, wood/leaf structures unchanged), lightly burned (litter charred to partially consumed, wood/leaf structures charred but recognizable, smaller twigs partially to completely consumed), moderately burned (litter mostly or entirely consumed, duff deeply burned, wood/leaf structures unrecognizable, twigs and small stems consumed), heavily burned (litter and duff consumed leaving fine white ash, mineral soil visibly altered often reddish, all plant parts consumed leaving some or no major stems) or not applicable (no fuels in the area).

Table 2. Site characteristics in research burns.

Research Site	Size (ha)	Burn Month/Year	Burn severity		Elevation (m)	Substrate age (years)	Former community	Total annual rainfall the first year following treatment (cm/year)*
			Substrate	Vegetation				
Kīpuka Nēnē	2.0	January 1993	scorch	scorch	880	750-1500	'ōhi'a woodland	167.0
Muliwai I a-bushy beard grass	2.9	June 1995	moderate	moderate	670	200-750	'ōhi'a woodland	213.0
b-molasses grass			heavy	heavy				
Muliwai II	1.2	April 1996	heavy	heavy	670	200-750	'ōhi'a woodland	293.0
Muliwai III	0.8	November 1997	light	light	670	200-750	'ōhi'a woodland	81.5
Pili Kīpuka I	10.1	August 1995	moderate	moderate	15	750-1500	pili grassland	171.3
Pili Kīpuka II	10.1	March 1998	light	light	15	750-1500	pili grassland	122.6
Kealakomo Waena	38.0	August 1999	moderate	moderate	120	1500-3000	alien shrubland/pili grassland	124.9

Scorched = litter partially blackened, duff nearly unchanged, wood/leaf structures unchanged; lightly burned = litter charred to partially consumed, wood/leaf structures charred but recognizable, smaller twigs partially to completely consumed; moderately burned = litter mostly or entirely consumed, duff deeply burned, wood/leaf structures unrecognizable, twigs and small stems consumed; heavily burned = litter and duff consumed leaving fine white ash, mineral soil visibly altered often reddish, all plant parts consumed leaving some or no major stems (NPS 1992).

Table 3. Native species tested in controlled burns and oven heating experiments. X= plots were artificially seeded prior to controlled burns (burn); x= plots were artificially seeded immediately after controlled burns (postburn).

Scientific name	oven heat	Kīpuka Nēnē	Muliwai I	Muliwai II	Muliwai III	Pili Kīpuka I	Pili Kīpuka II	Kealakomo Waena
<i>Argemone glauca</i>	x							Xx
<i>Bidens hawaiiensis</i>	x			x	Xx			
<i>Canavalia hawaiiensis</i>	x					x	Xx	Xx
<i>Dodonaea viscosa</i>	x	Xx	Xx		X	Xx	Xx	Xx
<i>Myoporum sandwicense</i>	x			x	Xx		Xx	Xx
<i>Myrsine lanaiensis</i>	x							
<i>Osteomeles anthyllidifolia</i>	x			x	Xx			Xx
<i>Psydrax odorata</i>	x							
<i>Rhus sandwicensis</i>	x							
<i>Rumex skottsbergii</i>	x							
<i>Santalum paniculatum</i>				x	Xx			
<i>Scaevola kilaueae</i>	x			x	Xx			
<i>Senna gaudichaudii</i>	x							
<i>Sesbania tomentosa</i>	x					x	Xx	
<i>Sida fallax</i>	x				Xx		Xx	Xx
<i>Sophora chrysophylla</i>	x	Xx	Xx		Xx			
<i>Tephrosia purpurea</i>	x							
<i>Waltheria indica</i>	x							

2.3 Seedling Recruitment and Plant Establishment in Seeded Plots

Seeds of twelve native species were tested in seven sites, to evaluate seedling recruitment and establishment in response to fire, postburn, and unburned conditions (Table 3). Species were selected for their potential to establish in a burn based on casual observations, formal studies of native plant recovery from past wildfires, and colonization characteristics of prolific seed production, high germination rates and rapid seedling growth (Table 1). Seeds were collected from the closest sources located within the park. For most species, a minimum of 25 individuals per species served as seed sources. For locally rare species (*Canavalia hawaiiensis*, *Sesbania tomentosa*, *Santalum paniculatum*) 10 to 25 individuals served as seed sources. The choice of species tested in each burn site was based on availability of seed sources and the historic range of the species in the park. For example ‘ōhai (*Sesbania tomentosa*), a coastal form, was tested only at the low elevation sites (Pili I and II Burns); whereas māmane, a species common to seasonally dry ‘ōhi’a woodlands, was tested in sites located above 1,000 ft elevation (Kīpuka Nēnē, Muliwai Ia&b, III).

The research design was similar for each burn, with minor variants for species with limited seed availability (Table 3). The germination response of seeds was tested in 2 x 2 m plots (number of replicates = 2 to 5) randomly distributed in each burn. Seeds were placed prior to (burn treatment), or immediately after (postburn treatment) the burn to look at native seed response to fire and ability to colonize from seed under postburn conditions. An equal number of replicate plots were established in adjacent unburned areas to serve as controls (unburned treatment). Seeds were hand buried 1 to 2 cm below the soil surface. In the Muliwai I burn, treatment plots were pre-stratified according to the dominant grass type: bushy beardgrass (Muliwai Ia) and molasses grass (Muliwai Ib). The number of seeds applied to a plot (50 to 1,500

Table 4. Time intervals research sites were revisited to monitor seedling recruitment.

Research Site	Seedling Recruitment Census Interval								
	3 month	6 month	9 month	1 year	2 year	3 year	4 year	5 year	
Kīpuka Nēnē	x	x		x	x	X	x		
Muliwai I	x	x		x	x			x	
Muliwai II	x	x		x			x		
Muliwai III	x	x	x	x	x	x	x		
Pili Kīpuka I	x	x		x	x				
Pili Kīpuka II		x		x	x	x			
Kealakomo Waena		x		x	x	x			

seeds/plot) varied by species (Table 6). For the Muliwai II and Pili Kīpuka I burns, where the number of seeds for a particular species (*Bidens hawaiiensis*, *Dodonaea viscosa*, *Sida fallax*, *Myoporum sandwicense*, *Osteomeles anthyllidifolia*) was insufficient to test all three conditions, the burn application was omitted in favor of testing postburn seedling recruitment.

For two sites (Pili Kīpuka II and Kealakomo Waena), temperatures experienced by artificial seed banks during the burn were measured using temperature indicator labels (Omega 38 °C to >232 °C) pasted on Pelco mica sheets (5.0 x 7.6cm) placed one to two centimeters below the soil surface in seed plots.

In most cases seedlings were censused at 3 month, 6 month, 12 month, and 1 to 2 year intervals thereafter (Table 4). Seedlings were classified into the following height categories: <10 cm, 10-<50 cm, 50-<100 cm, 100-<150 cm. In later experiments, Muliwai III and Kealakomo Waena Burns, a subsample of individuals ≥ 10 cm height were tagged, monitored and their location mapped to examine individual survivorship across one year. Tagged individuals not found during the second reading were considered dead after a thorough search of the immediate area.

Although seedling recruitment was counted multiple times during the first year (Table 4), only a single census was used to represent first year recruitment to avoid double counting of individuals. After examining all of the first year data, data from the six month interval were chosen as the best representative of first year seedling recruitment for most species across sites. One year seedling recruitment data were used in one site (Pili Kīpuka II) and for four species (*Santalum paniculatum*, *Myoporum sandwicense*, *Osteomeles anthyllidifolia*, *Scaevola kilaueae*) because seedlings did not appear until the first year census. Seedling recruitment (<10 cm height) was analyzed by one-way ANOVA analysis (Minitab ver. 10.0) with treatment (burn, postburn, unburned) as factor. Subsequent plant establishment (>10 cm height) taken at the final census (3 to 5 years) or at reproductive maturity for short-lived species (two years for *Argemone glauca* and *Canavalia hawaiiensis*) was treated independent of first year seedling recruitment and analyzed by one-way ANOVA analysis (Minitab ver. 10.0) with treatment as factor. For both first year seedling recruitment and subsequent plant establishment, a two factor analysis of site and treatment using a General Linear Model for unequal sample sizes (Minitab vers. 10.0) was performed on species that were tested in more than one site. Interactions among treatments and sites could not be analyzed using this approach. All data were log-transformed before analysis and the GLM was weighted by the number of seeds applied to the plots in each site. Tukey paired comparison tests were performed to determine significant treatment responses. Treatments and sites where no individuals established were not included in the analysis but were presented in tables and graphs for illustrative purposes.

An exact Fisher-Freeman-Halton's test (StatXact ver.5) was used to analyze seedling survivorship of tagged individuals (proportion of tagged individuals surviving one year) in Muliwai III and Kealakomo Waena. Total species survivorship was analyzed for Muliwai III. Only *Dodonaea viscosa* seedling survivorship was analyzed in Kealakomo Waena because it was the only species to have individuals >10 cm in height in all three treatments.

2.4 Native Plant Survivorship and Natural Recruitment in Response to Fire

The number of native woody species that naturally occurred in burn sites was too low to adequately look at plant response to fire with the exception of *Sophora chrysophylla* (n = 77) in Muliwai II, and *Dodonaea viscosa* (n = 42) in Kealakomo Waena. Individuals were tagged and height and basal diameter recorded prior to controlled burns. Immediately following the burn, scorch height and percent crown scorch were recorded. Tree survivorship, as evidenced by epicormic and basal sprouts, was recorded at 6 month, 1 year and 2 years following the burn. Natural seedling recruitment beneath tagged individuals of *Dodonaea viscosa* was measured in 2.5m radius plots centered on the main stem of each individual in Kealakomo Waena. Plot radius was much smaller (1 m) for *Sophora chrysophylla* to avoid plots overlapping due to the close proximity of stems in Muliwai II. Seedling census took place prior to and at 6 month, 1 year and 2 years following the burn. The percentage of individuals surviving fire and mean seedling density in plots are reported.

2.5 Seed Germination Response to Laboratory Oven Heating

Seed germination response to laboratory oven heating was conducted for 18 species (Table 3). When ever possible seeds were collected from closest sources located within the park. Seeds of three locally rare species (*Rhus sandwicensis*, *Senna gaudichaudii*, *Myrsine lanaiensis*), were collected from closest known sources outside the Park. Seeds were placed in an oven (Thelco Model 17) and subjected to three temperature treatments: 90; 120; and 140 °C for five minutes. After heat treatment, seeds were placed on 46 cm x 46 cm trays containing 1:1:1 peat moss:perlite:sterilized soil. Untreated seeds were placed on soil trays to serve as controls. Trays were placed in an open nursery located in Volcano, HI (elevation approx. 1,050 m). Emergent seedlings were counted and individuals either marked or discarded at monthly intervals. Monitoring was discontinued 12 months following treatment for most species with the exception of *Myrsine lanaiensis* (10 month) and *Waltheria indica* (6 month). The proportion of seeds germinating in each heat treatment was analyzed using an exact Fisher-Freeman-Halton's test (StatXact ver.5).

3. Results

3.1 Assessment of Fire Damage in Burn Sites

Seven research burns were conducted between 1993 and 1999 (Table 2). Burn severity was moderate to heavy for four sites (Muliwai Ia&b and II, Pili Kīpuka I and Kealakomo Waena) as evidenced by 100% crown scorch among the woody species. Within Muliwai I, burn severity was higher in molasses grass-dominated areas (Muliwai Ib) than in bushy beardgrass-dominated areas (Muliwai Ia). Patches of mineral soil were visibly altered, and the surface soil still hot to the touch one day after firing in Pili Kīpuka I, Muliwai Ia&b, and II. Burn severity was scorched to light for three sites (Kīpuka Nēnē, Muliwai III, Pili Kīpuka II). In Kīpuka Nēnē, the molasses grass was green, and the litter layer moist so that the burn barely penetrated the litter layer. Pili Kīpuka II and Muliwai III were reburns of areas previously burned in 1995, and the litter layer was light (author per obs). In two sites (Pili Kīpuka II and Kealakomo Waena) where measurements were taken, soil temperatures varied considerably within seed plots during the burn (ranging between 38 to >232 °C within a plot).

3.2 Plant Establishment in Seeded Plots

3.2.1 First Year Seedling Recruitment

Seeds of twelve species were tested in seven sites to evaluate seedling recruitment and establishment in response to fire (burn), postburn (postburn), and unburned (unburned) conditions. Germination was evident within the first 6 months following treatment for most species. Rapid germination was displayed (<3 mo) by three species (*Dodonaea viscosa*, *Bidens hawaiiensis*, *Sophora chrysophylla*). For four species (*Myoporum sandwicense*, *Osteomeles anthyllidifolia*, *Scaevola kilaueae*, *Santalum paniculatum*), seedlings were not evident until the first year census. In Pili Kīpuka II, seedlings were not observed until the first year census.

Fire did not reduce seedling recruitment for six species (*Dodonaea viscosa*, *Osteomeles anthyllidifolia*, *Santalum paniculatum*, *Scaevola kilaueae*, *Sida fallax*, *Sophora chrysophylla*) based on first year seedling counts in burned and unburned plots across sites (Table 5a-5k). Prolific seedling recruitment of *Bidens hawaiiensis* occurred among all treatments but was higher in the postburn and unburned than in the burn plots. Seedling recruitment was too low for statistical analysis to be conclusive for the four remaining species tested (*Argemone glauca*, *Canavalia hawaiiensis*, *Myoporum sandwicense*, *Sesbania tomentosa*).

Across sites, seedling recruitment was significantly higher in postburn than in unburned plots for four species (*Canavalia hawaiiensis*, *Dodonaea viscosa*, *Scaevola kilaueae*, *Santalum paniculatum*). Two species (*Bidens hawaiiensis*, *Sida fallax*) showed no significant difference between postburn and unburned plots. One species (*Sophora chrysophylla*) had significantly less seedling recruitment in the postburn than in the unburned plots. Seedling recruitment of four species (*Argemone glauca*, *Myoporum sandwicense*, *Osteomeles anthyllidifolia*, *Sesbania tomentosa*) was too low for statistical analysis to be conclusive.

Species recruitment was highly variable among sites. For example, *Osteomeles anthyllidifolia* seedlings were evident in burn plots in Muliwai III but not in Kealakomo Waena. *Myoporum sandwicense* was tested in 4 sites, but seedlings were only evident in Muliwai II. Seedling recruitment of *Sophora chrysophylla* and *Bidens hawaiiensis* was higher in Muliwai III than in the other sites. Interactions between site and treatment could not be statistically tested but there was evidence, at least for *Dodonaea viscosa*, that interactions were important. *Dodonaea viscosa* responded positively to fire in two sites (Muliwai Ia&b, Kīpuka Nēnē), negatively in one site (Kealakomo Waena) and was unaffected by fire in three sites (Muliwai III, Pili Kīpuka I & II).

Seedling recruitment continued sporadically across the next four years for *Sophora chrysophylla*, *Dodonaea viscosa*, and *Bidens hawaiiensis*. Seeds of *Sophora chrysophylla* have hard protective coats that allow seeds to remain viable for several years. In contrast, viability of seeds stored at room temperature is dramatically reduced across one year for *Dodonaea viscosa* (60% for 3 month old seeds, 7% for 12 month old seeds) and *Bidens hawaiiensis* (92% for 1 month old seeds, 20% for 12 month old seeds) (Loh *unpublished*). So seedlings of these two species that emerged beyond the first year were most likely second generation seedlings derived from seeds deposited by first generation seedlings in the second and third year following the burn.

Table 5a. *Argemone glauca* seedling recruitment and establishment.

<i>Argemone glauca</i>								
Research Site	6 month		ind/plot		postburn		unburned	
	burn	se	mean	se	mean	se	F	P
Kealakomo Waena	0.2	0.2	9.7	3.6	0.0	0.0		

<i>Argemone glauca</i>								
Research Site	2 years		>10cm ind/plot		postburn		unburned	
	burn	se	mean	se	mean	se	F	P
Kealakomo Waena	0.1	0.1	4.4	1.1	0.0	0.0		

Table 5b. *Bidens hawaiiensis* seedling recruitment and establishment. Species response within a site was analyzed by one-way ANOVA with treatment as fixed factor. Species response across sites was analyzed by GLM with treatment and site as fixed factors. Data are log transformed. Tukey multiple comparison tests were performed on significant treatment responses. Means that do not share the same letter are significantly different. Treatments and sites with no individuals are presented for illustrative purposes but were not included in the analysis.

<i>Bidens hawaiiensis</i>										
Research Site	6 month		ind/plot		postburn		unburned		F	P
	burn	se	mean	se	mean	se	mean	se		
Muliwai II			6.3	3.8	0.0	0.0				
Muliwai III	9.0	2.5	38.2	9.1	158.0	29.0	16.85	0.000		
Treatment effects *	9.0b	2.5	28.62a	7.6	98.7a	33.7	5.75	0.012		
Site effects *							29.60	0.000		

Research Site	4 year		>10cm ind/plot		postburn		unburned		F	P
	burn	se	mean	se	mean	se	mean	se		
Muliwai II			4.0	0.6	0.0	0.0				
Muliwai III	2.6	0.7	3.4	1.8	1.2	1.2	1.13	0.356		
Treatment effects *	2.6a	0.7	5.12b	1.4	0.8a	0.8	5.03	0.019		
Site effects *							0.71	0.413		

* Muliwai II numbers adjusted to reflect differences in number of seeds applied to plots

Table 5c. *Canavalia hawaiiensis* seedling recruitment and establishment. Species response within a site was analyzed by one-way ANOVA with treatment as fixed factor. Species response across sites was analyzed by GLM with treatment and site as fixed factors. Data are log transformed. Tukey multiple comparison tests were performed on significant treatment responses. Means that do not share the same letter are significantly different. Treatments and sites with no individuals are presented for illustrative purposes but were not included in the analysis.

<i>Canavalia hawaiiensis</i>								
Research Site	6 month ind/plot						F	P
	burn		postburn		unburned			
	mean	se	mean	se	mean	se		
Pili Kīpuka 1			0.0	0.0	0.0	0.0		
Pili Kīpuka 2	1.0	1.0	2.3	2.3	0.3	0.3	0.21	0.813
Kealakomo Waena	0.0	0.0	1.8	0.4	0.0	0.0		
Treatment effects *	0.3a	0.3	2.0b	0.7	0.2a	0.2	5.74	0.011
Site effects *							0.29	0.596

Research Site	2-3 year >10cm ind/plot						F	P
	burn		postburn		unburned			
	mean		mean		mean			
Pili Kīpuka 1			0.0	0.0	0.0	0.0		
Pili Kīpuka 2	0.0	0.0	1.0	0.6	0.0	0.0		
Kealakomo Waena	0.0	0.0	0.2	0.2	0.0	0.0		
Treatment effects *	0.0	0.0	0.4	0.2	0.0	0.0		
Site effects *								

Table 5d. *Dodonaea viscosa* seedling recruitment and establishment. Species response within a site was analyzed by one-way ANOVA with treatment as fixed factor. Species response across sites was analyzed by GLM with treatment and site as fixed factors. Data are log transformed. Tukey multiple comparison tests were performed on significant treatment responses. Means that do not share the same letter are significantly different. Treatments and sites with no individuals are presented for illustrative purposes but were not included in the analysis.

<i>Dodonaea viscosa</i>								
Research Site	6 month		ind/plot				F	P
	burn		postburn		unburned			
	mean	se	mean	se	mean	se		
Kealakomo Waena	0.15b	0.1	27.5c	4.5	17.0a	4.0	73.27	0.000
Kīpuka Nēnē	4.6b	5.2	2.4ab	2.4	0.5a	0.9	3.75	0.038
Muliwai I (<i>Schizachyrium condensatum</i>)	31.6b	9.8	25.2ab	2.1	6.6a	1.2	9.93	0.003
Muliwai I (<i>Melinis minutiflora</i>)	22.0ab	16.9	37.4b	10.8	1.0a	0.6	9.14	0.004
Muliwai III	42.4	13.1			33.8	13.8	0.00	0.972
Pili Kīpuka I	18.8	14.2	64.0	30.2	16.2	5.5	1.64	0.235
Pili Kīpuka II (12 month)	41.4	18.0	114.6	33.6	31.2	4.0	1.11	0.360
Treatment effects *	19.6a	4.1	102.7b	18.2	36.8a	9.8	22.13	0.000
Site effects *							9.68	0.000
<i>Dodonaea viscosa</i>								
Research Site	3-5 year		>10cm ind/plot				F	P
	burn		postburn		unburned			
	mean	se	mean	se	mean	se		
Kealakomo Waena	0.0	0.0	3.6b	0.7	0a	0.1	13.83	0.000
Kīpuka Nēnē	4.1b	4.5	3.3ab	4.4	0.1a	0.3	8.13	0.002
Muliwai I (<i>Schizachyrium condensatum</i>)	14.2	4.7	11.2	5.3	3.0	1.2	2.17	0.156
Muliwai I (<i>Melinis minutiflora</i>)	9.8ab	4.6	13.8b	3.7	0.4a	0.2	8.21	0.006
Muliwai III	13.0	4.8			4.2	2.1	1.22	0.301
Pili Kīpuka I	0.0	0.0	0.0	0.0	0.0	0.0		
Pili Kīpuka II	0.0	0.0	0.0	0.0	0.0	0.0		
Treatment effects *	5.0b	1.2	18.1c	3.1	1.5a	0.5	21.96	0.000
Site effects *							4.79	0.001

* Kīpuka Nēnē and Kealakomo Waena numbers adjusted to reflect differences in number of seeds applied to plots and sampling methods

Table 5e. *Myoporum sandwicense* seedling recruitment and establishment. Species response within a site was analyzed by one-way ANOVA with treatment as fixed factor. Species response across sites was analyzed by GLM with treatment and site as fixed factors. Data are log transformed. Tukey multiple comparison tests were performed on significant treatment responses. Means that do not share the same letter are significantly different. Treatments and sites with no individuals are presented for illustrative purposes but were not included in the analysis.

<i>Myoporum sandwicense</i>										
Research Site	1year		ind/plot		postburn		unburned		F	P
	burn		mean	se	mean	se	mean	se		
	mean	se	mean	se	mean	se	mean	se		
Kealakomo Waena	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	n	n
Muliwai II			4.0	0.6b	0.3a	0.3	27.75	0.006		
Muliwai III	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
Pili Kīpuka II	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		

Research Site	3-5 year		>10cm ind/plot		postburn		unburned		F	P
	burn		mean	se	mean	se	mean	se		
	mean	se	mean	se	mean	se	mean	se		
Kealakomo Waena	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
Muliwai II			0.0	0.0	0.0	0.0	0.0	0.0		
Muliwai III	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
Pili Kīpuka II	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		

Table 56f. *Osteomeles anthyllidifolia* seedling recruitment and establishment. Species response within a site was analyzed by one-way ANOVA with treatment as fixed factor. Species response across sites was analyzed by GLM with treatment and site as fixed factors. Data are log transformed. Tukey multiple comparison tests were performed on significant treatment responses. Means that do not share the same letter are significantly different. Treatments and sites with no individuals are presented for illustrative purposes but were not included in the analysis.

<i>Osteomeles anthyllidifolia</i>								
Research Site	1year		ind/plot				F	P
	burn		postburn		unburned			
	mean	se	mean	se	mean	se		
Kealakomo Waena	0.0	0.0	0.0	0.0	0.0	0.0		
Muliwai II			19.0	4.0	0.0	0.0		
Muliwai III	1.0	0.4	0.0	0.0	1.2	0.5		
Treatment effects *	1.5	0.7	5.4	3.6	1.3	0.6	0.24	0.793
Site effects *							3.28	0.090

Research Site	3-4 year		>10cm ind/plot				F	P
	burn		postburn		unburned			
	mean	se	mean	se	mean	se		
Kealakomo Waena	0.0	0.0	0.0	0.0	0.0	0.0		
Muliwai II			0.0	0.0	0.0	0.0		
Muliwai III	0.0	0.0	0.0	0.0	0.0	0.0		

* Kealakomo Waena and Muliwai III numbers adjusted to reflect differences in number of seeds applied to plots

Table 5g. *Santalum paniculatum* seedling recruitment and establishment. Species response within a site was analyzed by one-way ANOVA with treatment as fixed factor. Species response across sites was analyzed by GLM with treatment and site as fixed factors. Data are log transformed. Tukey multiple comparison tests were performed on significant treatment responses. Means that do not share the same letter are significantly different. Treatments and sites with no individuals are presented for illustrative purposes but were not included in the analysis.

<i>Santalum paniculatum</i>										
Research Site	1year		ind/plot		postburn		unburned		F	P
	burn		mean	se	mean	se	mean	se		
	mean	se	mean	se	mean	se	mean	se		
Muliwai II			9.5b	2.5	0.5a	0.5	21.80	0.043		
Muliwai III	5.0	4.0	7.0	6.0	0.0	0.0				
Treatment effects *	5.0ab	4.0	8.5b	2.8	0.3a	0.3	6.08	0.036		
Site effects *							0.94	0.369		

Research Site	4 year		>10cm ind/plot		postburn		unburned		F	P
	burn		mean	se	mean	se	mean	se		
	mean	se	mean	se	mean	se	mean	se		
Muliwai II			17.5	7.5	0.0	0.0				
Muliwai III	4.0	3.0	6.0	5.0	0.0	0.0				
Treatment effects *	4.0	3.0	12.3	5.3	0.0	0.0				
Site effects *										

* Muliwai II numbers adjusted to reflect differences in number of seeds applied to plots

Table 5h. *Scaevola kilaueae* seedling recruitment and establishment. Species response within a site was analyzed by one-way ANOVA with treatment as fixed factor. Species response across sites was analyzed by GLM with treatment and site as fixed factors. Data are log transformed. Tukey multiple comparison tests were performed on significant treatment responses. Means that do not share the same letter are significantly different. Treatments and sites with no individuals are presented for illustrative purposes but were not included in the analysis.

<i>Scaevola kilaueae</i>								
Research Site	1 year		ind/plot		postburn		unburned	
	burn mean	se	mean	se	mean	se	F	P
Muliwai II			59.7	14.0	0.0	0.0		
Muliwai III	35.0	15.0	37.5	37.5	1.5	1.5	1.09	0.440
Treatment effects	35.0ab	15.0	50.8b	19.7	0.6a	0.6	6.57	0.021
Site effects							0.28	0.613

Research Site	4 year		>10cm ind/plot		postburn		unburned	
	burn mean	se	mean	se	mean	se	F	P
Muliwai II			0.0		0.0			
Muliwai III			0.0		0.0			

Table 5i. *Sesbania tomentosa* seedling recruitment and establishment. Species response within a site was analyzed by one-way ANOVA with treatment as fixed factor. Species response across sites was analyzed by GLM with treatment and site as fixed factors. Data are log transformed. Tukey multiple comparison tests were performed on significant treatment responses. Means that do not share the same letter are significantly different. Treatments and sites with no individuals are presented for illustrative purposes but were not included in the analysis.

<i>Sesbania tomentosa</i>								
Research Site	6 month		ind/plot		postburn		unburned	
	burn mean	se	mean	se	mean	se	F	P
Pili Kīpuka I			7.0		1.5		24.20	0.039
Pili Kīpuka II	0.0		0.0	0.0	0.0			

Research Site	3-5 year		>10cm ind/plot		postburn		unburned	
	burn mean	se	mean	se	mean	se	F	P
Pili Kīpuka I			0.0		0.0			
Pili Kīpuka II	0.0		0.0		0.0			

Table 5j. *Sida fallax* seedling recruitment and establishment. Species response within a site was analyzed by one-way ANOVA with treatment as fixed factor. Species response across sites was analyzed by GLM with treatment and site as fixed factors. Data are log transformed. Tukey multiple comparison tests were performed on significant treatment responses. Means that do not share the same letter are significantly different. Treatments and sites with no individuals are presented for illustrative purposes but were not included in the analysis.

<i>Sida fallax</i>								
6 month ind/plot								
Research Site	burn mean	se	postburn mean	se	unburned mean	se	F	P
Kealakomo Waena	0.1	0.1	0.4	0.4	0.0	0.0		
Muliwai III	1.5	0.5	1.0	1.0	0.0	0.0		
Pili Kīpuka II (12 month)	1.7	0.9	0.7	0.7	2.3	1.3	0.84	0.478
Treatment effects *	0.6	0.3	0.6	0.4	0.7	0.5	0.16	0.851
Site effects *							6.49	0.004

3-5 year >10cm ind/plot								
Research Site	burn mean	se	postburn mean	se	unburned mean	se	F	P
Kealakomo Waena	0.0	0.0	0.1	0.1	0.0	0.0		
Muliwai III	1.0	0.0	1.0	1.0	0.0	0.0		
Pili Kīpuka II	0.0	0.0	0.0	0.0	0.0	0.0		
Treatment effects *	0.1	0.1	0.2	0.2	0.0	0.0		
Site effects *								

* Kealakomo Waena and Muliwai III numbers adjusted to reflect differences in number of seeds applied to plots

Table 5k. *Sophora chrysophylla* seedling recruitment and establishment. Species response within a site was analyzed by one-way ANOVA with treatment as fixed factor. Species response across sites was analyzed by GLM with treatment and site as fixed factors. Data are log transformed. Tukey multiple comparison tests were performed on significant treatment responses. Means that do not share the same letter are significantly different. Treatments and sites with no individuals are presented for illustrative purposes but were not included in the analysis.

<i>Sophora chrysophylla</i>										
Research Site	6 month		ind/plot		burn		postburn		unburned	
	mean	se	mean	se	mean	se	mean	se	F	P
	Kīpuka Nēnē	1.6	0.9	2.8	1.3	4.8	1.0	2.10	0.165	
Muliwai I (<i>Schizachyrium condensatum</i>)	1.4	1.4	4.6	1.5	4.8	2.0	2.81	0.099		
Muliwai I (<i>Melinis minutiflora</i>)	0.0	0.0	0.4b	0.4	6.8a	1.9	17.12	0.003		
Muliwai III	47.2ab	16.3	9.4b	7.7	54.4a	9.0	4.71	0.031		
Treatment effects *	15.4ab	6.0	9.2b	3.6	26.1a	5.6	9.53	0.000		
Site effects *							13.33	0.000		

Research Site	3-5 year		>10cm ind/plot		burn		postburn		unburned	
	mean	se	mean	se	mean	se	mean	se	F	P
	Kīpuka Nēnē	16.8	4.4	19.5	3.5	17.2	1.6	0.40	0.681	
Muliwai I (<i>Schizachyrium condensatum</i>)	0.4	0.2	0.4	0.2	0.4	0.4	0.03	0.969		
Muliwai I (<i>Melinis minutiflora</i>)	0.2	0.2	5.6	2.7	1.6	0.7	2.40	0.133		
Muliwai III	5.0	3.6	2.8	1.2	13.2	6.0	1.29	0.312		
Treatment effects	5.6	9.1	6.4	8.4	8.1	9.4	1.71	0.191		
Site effects							23.67	0.000		

* Kīpuka Nēnē numbers adjusted to reflect differences in sampling methods

Table 6. Survivorship of tagged individuals naturally occurring in Muliwai III (all species = *Bidens hawaiiensis*, *Dodonaea viscosa*, *S. paniculatum*, *Sophora chrysophylla*) and Kealakomo Waena (*Dodonaea viscosa*).

Research Site	Total number of tagged individuals	Burn (%)	Postburn (%)	Unburned (%)	F	P
Muliwai III	103	75	100	90	12.48	0.001
Kealakomo Waena	182	42	33	0		

3.2.2 Plant Establishment Beyond the Seedling Stage

Establishment of individuals beyond the seedling stage (typically >10 cm height) was generally higher in postburn than in burn and unburned plots. This was statistically significant for two species (*Bidens hawaiiensis*, *Dodonaea viscosa*). Only three species established older individuals in unburned plots (*Bidens hawaiiensis*, *Dodonaea viscosa*, *Sophora chrysophylla*). By contrast, six species established older individuals in burn, and seven did so in postburn plots. Four species (*Myoporum sandwicense*, *Osteomeles anthyllidifolia*, *Scaevola kilaueae*, *Sesbania tomentosa*) failed to establish older individuals in any of the treatments. Establishment of *Canavalia hawaiiensis* and *Sida fallax* may have been higher than measured since some individuals apparently matured, reproduced and died between the first and final census.

Site differences were evident for *Dodonaea viscosa* and *Sophora chrysophylla*. *Dodonaea viscosa* establishment was higher in upper elevation sites than in lower elevation sites. For *Sophora chrysophylla*, establishment was higher in Kīpuka Nēnē than in Muliwai III and Muliwai Ia&b.

Among the seven species that survived beyond the seedling stage, four (*Argemone glauca*, *Bidens hawaiiensis*, *Canavalia hawaiiensis*, *Sida fallax*) had reproducing individuals by the second year; one species (*Dodonaea viscosa*) had reproducing individuals by the third year; and one tree species (*Sophora chrysophylla*) had reproducing individuals by the tenth year following treatment in one or more sites (Loh pers. obs). *Santalum paniculatum*, the remaining tree species, had not reached reproductive maturity at the last monitoring in 2004.

3.2.3 Seedling Survivorship of tagged Individuals

Seedling survival of tagged individuals was higher in the postburn than in burn and unburned plots for the two sites (Muliwai III, Kealakomo Waena) where individuals were monitored (data not shown). Survival of tagged individuals (all species combined = *Bidens hawaiiensis*, *Dodonaea viscosa*, *Sophora chrysophylla*, *Santalum paniculatum*) was greater in postburn plots (100%, n = 20) and unburned plots (90%, n = 30) than in burn plots (75%, n = 53) in Muliwai III (Table 6). *Dodonaea viscosa*, the only species with seedling recruitment in all three treatments in Kealakomo Waena, survived in postburn plots (33% survivorship, n = 131) and burn plots (42%, n = 12), but did not survive in unburned plots (0%, n = 39).

3.3 Native Plant Response to Fire

Among the individuals that naturally occurred in burn sites, seventy-seven percent of tagged *Sophora chrysophylla* individuals survived the Muliwai II Burn. Twenty-one percent of *Dodonaea viscosa* individuals survived the Kealakomo Waena Burn. Individuals had 60-100 % crown scorch and survived by sprouting at the base of burned stems. Only one seedling of *Sophora chrysophylla* (presumably natural recruitment from the soil seed bank) was observed in the vicinity of burned individuals in Muliwai II. Seedling recruitment of *Dodonaea viscosa* was observed around 41% of the burned individuals in Kealakomo Waena.

Table 7. Seed germination response to oven heating.

Species	Total number of seeds	Germination (%)*	Heat response	Room temp (%)	90 C (%)	120 C (%)	140 C (%)	F	P
<i>Argemone glauca</i>	1200	4.4	fair	8.7a	9.0a	0.0b	0.0b	68.49	0.000
<i>Bidens hawaiiensis</i>	600	45.5	poor	77.3a	54.7b	48.0b	2.0c	219.80	0.000
<i>Canavalia hawaiiensis</i>	100	7.0	fair	12.0a	8.0a	4.0a	4.0a	1.64	0.650
<i>Dodonaea viscosa</i>	1860	5.3	fair	8.2a	8.4a	4.5b	0.0c	52.58	0.000
<i>Myoporum sandwicense</i>	600	0.0		1.3	0.0	0.0	0.0	3.517	0.249
<i>Myrsine lanaiensis</i>	600	10.8	good	11.3a	25.3b	6.0a	1.0c	53.33	0.000
<i>Osteomeles anthyllidifolia</i>	1488	7.5	fair	12.6a	14.5a	2.7b	0.0c	102.3	0.000
<i>Psyrax odorata</i>	600	6.5	poor	24.0a	2.0b	0.0b	0.0b	79.41	0.000
<i>Rhus sandwicensis</i>	600	5.2	fair	10.7a	8.0a	2.0b	0.0b	25.58	0.000
<i>Rumex skottsbergii</i>	600	27.1	poor	91.3a	17.3b	0.0c	0.0c	463.40	0.000
<i>Scaevola taccada</i>		0.0		0.0	0.0	0.0	0.0		
<i>Scaevola kilauea</i>	600	0.5		2.0	0.0	0.0	0.0	5.10	0.062
<i>Senna gaudichaudii</i>	300	26.7	fair	26.7a	24.0a	2.7b	0.0b	43.10	0.000
<i>Sesbania tomentosa</i>	200	10.5	fair	20.0a	22.0a	0.0b	0.0b	26.03	0.000
<i>Sida fallax</i>	400	3.2	good	2.0a	11.0b	0.0a	0.0a	20.53	0.000
<i>Sophora chrysophylla</i>	600	4.8	fair	9.3a	9.3a	0.7b	0.0b	29.86	0.000
<i>Tephrosia purpurea</i>	1200	24.5	poor	64.0a	34.0b	0.0c	0.0c	548.30	0.000
<i>Waltheria indica</i>	1200	0.4		1.0	0.7	0.0	0.0	4.48	0.178

Germination measured across ≥ 1 year with the exception of *Myrsine lanaiensis* (10 month) and *Waltheria indica* (6 month).

3.4 Seed Germination Response to Oven Heating

Germination response to mild (90 °C) oven heating was variable among the 18 native plant species tested: eight species showed no significant change in germination response; two species showed a positive response (*Myrsine lanaiensis*, *Sida fallax*); four species showed a negative response (*Bidens hawaiiensis*, *Psyrax odorata*, *Rumex skottsbergii*, *Tephrosia purpurea*) (Table 7). Germination rates were too low to statistically analyze heat effects on four species (*Myoporum sandwicense*, *Scaevola taccada*, *Scaevola kilaueae*, *Waltheria indica*). Despite significant declines in germination, seeds were still able to survive and germinate for nine species following 120 °C heating, and for three species following 140 °C heating.

Discussion

Identification of fire-tolerant native species is a first step towards building native plant communities that are resilient to wildfires. Fire-tolerance, defined here as the ability to survive or colonize after fire, was tested by evaluating plant survivorship and seedling recruitment in controlled burns and germination response to oven heating in laboratory experiments. Fourteen of the 19 native species tested in this study displayed at least one of these characteristics of fire-tolerance (Appendix I).

Testing the response to fire of species naturally occurring in the field is the most direct method for determining species ability to survive wildfire. Unfortunately, very few of the candidate species remained in the affected areas to allow this approach. Of the two species with individuals present in controlled burns, 75% of *Sophora chrysophylla* in Muliwai II and 25% of *Dodonaea viscosa* in Kealakomo Waena were able to survive severe scorching by sprouting from the base of damaged stems. The results were consistent with *Sophora chrysophylla* survivorship (60%) and *Dodonaea viscosa* survivorship (3-50%) reported in natural wildfires of comparable burn severity (Tunison et al. 1994, 1995). *Dodonaea viscosa* establishes primarily by seedling recruitment after wildfire (Hughes and Vitousek 1993; Hughes et al. 1991; Tunison et al. 1994, 1995; Ainsworth 2007). Destruction of the soil seed bank may have contributed to the low recruitment of *Sophora chrysophylla* following the Muliwai II Burn, where much of the organic layer was consumed by fire.

Seed survival is largely dependent on the intensity and duration of the soil heating (Probert 1992). We were unable to measure these two parameters in the field. However, oven heating experiments indicated that at least half of the species we tested were tolerant to mild heating (90 C), and at least a small percentage of seeds of nine species were able to germinate after heating at higher temperatures. The ability of a few seeds to survive elevated temperatures is important to species survival especially when considering that heat distribution is typically patchy in natural wildfires (Slocum et al. 2003). This was also the case in our burns where heat indicators placed in seeded plots (2 x 2 m) exhibited a wide range of temperatures that were unevenly distributed across a small area. So even in a hot burn, it's likely that some seeds will survive in cooler soil pockets if there's sufficient seed in the area. This may explain why *Bidens hawaiiensis* was able to establish vigorously from seeds placed in burn plots despite its sensitivity to mild oven heating.

Variation in burn severity may partially explain the wide range of recruitment response to controlled burns. Nine of twelve species tested showed some capacity for seedlings to recruit from seeds artificially placed in plots before burning. But the response was highly variable. For example, seeds of *Sophora chrysophylla* were able to survive and seedlings recruit under light to moderate severity burn conditions but not under high burn severity conditions. Very few seedlings of *Sida fallax* and no seedlings of *Canavalia hawaiiensis* were able to emerge following burning in Kealakomo Waena (moderate burn), whereas recruitment was much higher for *Sida fallax* in Muliwai III (scorch) and *Canavalia hawaiiensis* in Pili Kipuka II (light).

Ability to colonize rapidly in the postburn environment is an alternate way for species to persist in a fire environment. In previous wildfires, there was very little recolonization by former dominant fire-sensitive species *Metrosideros polymorpha* and *Leptodophylla tameiameia* in dry environments. Few seedlings were observed, growth was slow, and establishment was partially limited by competition with alien grasses (D'Antonio et al. 1998., Hughes and Vitousek 1993, Tunison et al. 1995). In contrast seven of the species tested here were able to establish in the burn and mature in the presence of alien grasses. Six reached reproductive maturity, and the remaining tree species (*Santalum paniculatum*) will likely attain reproductive maturity over the next few years. Unlike their fire-sensitive counterparts, these species grew quickly and established before alien grasses dominated the sites.

Seedlings that survive must be able to endure the exposed conditions that follow burning. Immediately following burning, vegetation is removed and the local environment becomes more xeric (Rhoades et al. 2002). In our experiments, rainfall events required for germination and seedling survival

were episodic and often followed by prolonged dry periods. The timing of burns with relation to rainfall patterns varied widely among sites (Figure 2) and may partially explain differences in seedling recruitment and survival among sites. For example, establishment was poorer in low elevation sites (Kealakomo Waena, Pili Kīpuka I and Pili Kīpuka II) than in high-elevation 'ōhi'a woodland sites that received more rainfall. Rapid revegetation can facilitate seedling survival by ameliorating xeric conditions (Cabin et al. 2002). Grasses returned quickly and combined with litter and unburned grass patches created moist shady pockets that probably contributed to higher seedling survival during drought in Muliwai III (light burn severity) than in Muliwai I and Pili Kīpuka I (higher severity burns) where the litter and organic layer was completely removed and grasses took much longer to re-establish. Herbivory was not addressed in this study but may have been a factor in 'ōhi'a woodland sites where feral pigs (*Sus scrofa*) are commonly observed. Signs of pig disturbance that include uprooted seedlings and soil disturbance were evident in (unrelated) experiments conducted nearby, and pigs may have been a factor that contributed to seedling mortality in the Kīpuka Nēnē site.

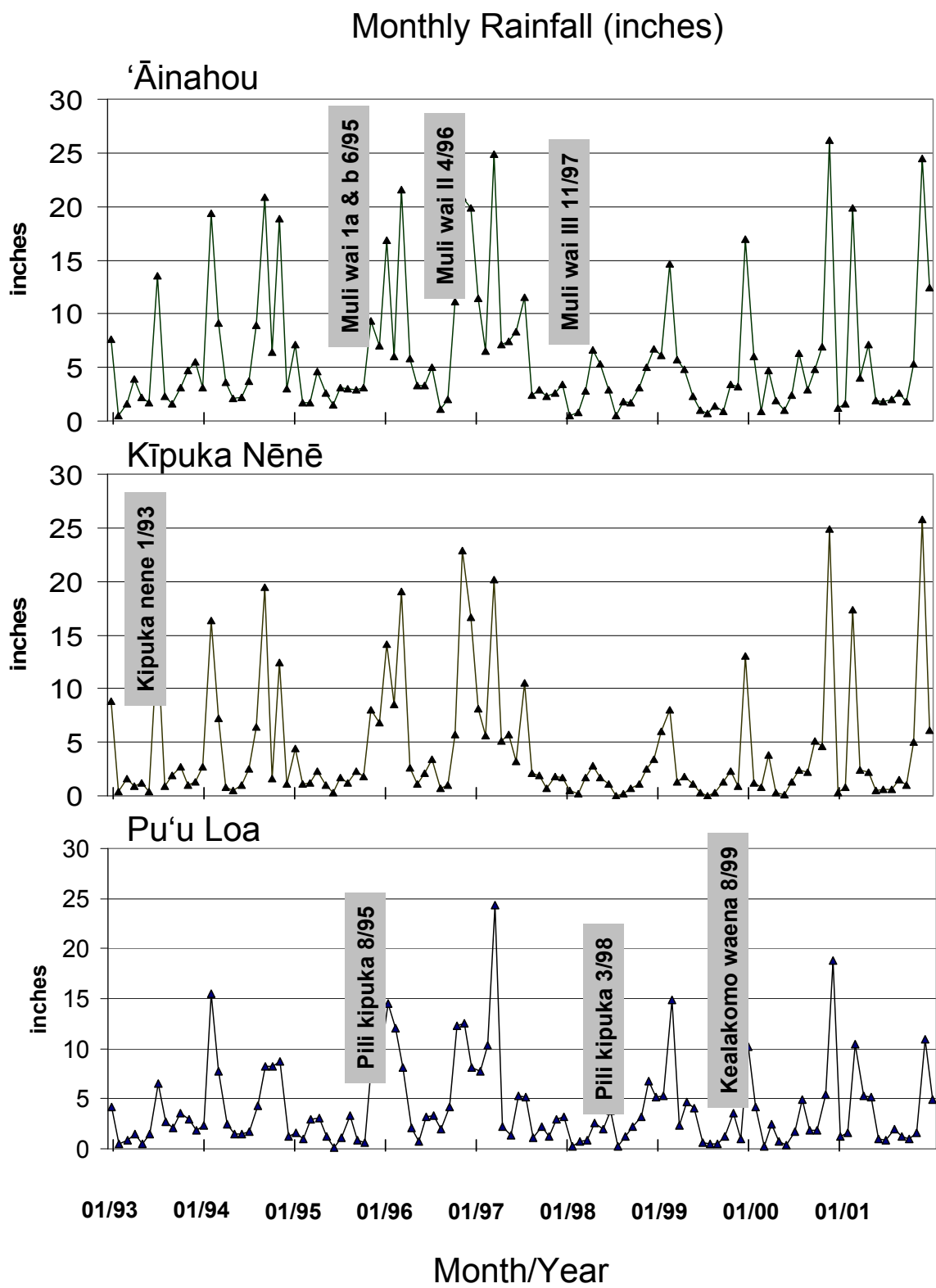


Figure 2. Total monthly rainfall at three sites in Hawai'i Volcanoes National Park, 1993-2001.

Management Considerations

Additional research to identify key conditions required for germination and seedling survival may explain some of the variation in our results among species and sites. Some seeds may require scarification to germinate while others may require a dormancy period (Murdoch & Ellis 1992). Temperature, smoke, release of chemicals, light and rainfall fluctuations also serve as triggers for germination, and seed predation or disease may lower germination rates (Karssen & Hilhorst 1992, Pons 1992, Probert 1992, Pearson et al. 2002, Rokich 2002). None of these factors were addressed in our study. Subsequent survival was also variable among sites and species. Resource availability, environmental conditions, introduced animals and competition with grasses have all been shown to affect native seedling survivorship and need to be further evaluated (Cabin et al. 2002, D'Antonio et al. 1998, Drake & Pratt 2001, Hughes & Vitousek 1993).

Successful establishment of fire-tolerant native species appears to require at least temporary removal of alien grasses that limit native species establishment by competing for resources (Cabin et al. 2000, 2002; D'Antonio et al. 1998; Hughes & Vitousek 1993). In our experiments only three species were able to establish in unburned plots compared to seven species in burn and postburn plots. In burn and postburn treatments, fire temporarily removed grasses and provided a window for native seedlings to establish and grow in their absence. Grasses eventually returned, but some native seedlings were able to survive, grow to overtop the grass layer, and attain reproductive maturity. Based on these initial experiments, larger scale (> 100 ha) efforts by managers to establish fire-tolerant native species by seeding and planting are currently being implemented in three recent wildfires (Loh et al. 2007, McDaniel et al. 2008). But alternative methods to fire are needed for areas where the risk of escaped fire is unacceptable. The park is currently testing chemical and mechanical treatments to temporarily remove grasses and assist establishment of native species by planting or seeding into sites.

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Appendix A. Species Tested in Controlled Burns and Oven Heating Experiments.

Argemone glauca, Pua kala (Papaveraceae)

Status: Uncommon in the Park

Endemic to Hawai'i, this perennial herb occurs in coastal dry forest and subalpine forest on the leeward sides of all the main islands (Wagner et al. 1999). In Hawai'i Volcanoes, scattered individuals are most often found in dry disturbed or open areas between 1,000 and 5,500 ft elevation. Seeds tolerated mild heating (90 °C). In Kealakomo Waena, the one burn where this species was tested, germination was observed in the burn and postburn but not in the unburned treatment suggesting that this species prefers disturbed areas. This species is a good candidate for seeding into burn areas if sufficient seed can be found.

Bidens hawaiiensis, Ko'oko'olau (Asteraceae)

Status: Rare in the Park, State Species of Concern, formerly a category 2 candidate endangered species.

Endemic to Hawai'i, this perennial herb occurs in three disjunct areas of Kohala, Puna and Kīlauea (Wagner et al. 1999). In Hawai'i Volcanoes, two populations occur in dry 'ōhi'a woodlands between 3,000 ft and 3,500 ft elevation in the park. The species was once reported near Kīpuka Puauulu and in lowland Puna just outside the Park boundary. Germination rates dropped from 77% (room temperature) to 55% (90 °C) and 48% (120 °C) with oven heating. However, overall germination rates remained relatively high compared to other species. In the field, this species readily established from seed broadcast into postburn and unburn plots. Individuals grew quickly, matured to produce plentiful seed, despite alien grasses, within the first two years of establishment. The federally listed endangered Nēnē were observed eating young shoots, however this did not appear to kill plants, which resprouted from the base. This species is a good candidate for seeding into burn areas.

Canavalia hawaiiensis, 'Āwikiwiki (Fabaceae)

Status: Rare in the Park

Endemic to Hawai'i, this perennial vine occurs in dry to mesic forest on the islands of Lāna'i, Maui and Hawai'i (Wagner et al. 1999). In the park, populations occur in Kūkala'ula and in dry to mesic forest below Nāpau Crater. Seeds tolerated mild to moderate heating (90-140 °C). Germination occurred in burn, postburn and unburned treatments. However, individuals survived beyond seedling stage only in the postburn treatments. This species successfully established mature individuals from seedlings planted in the Kupukupu Burn (McDaniel *in press*). Most individuals occur in remote areas and seeds are difficult to obtain in the park. This species is a good candidate for seeding or planting into burn areas if sufficient seed can be found.

Dodonaea viscosa, 'A'ali'i (Sapindaceae)

Status: Common in the Park

An indigenous shrub, this species is widespread from the coast to subalpine, but occurs primarily in open, mesic to dry sites in the park. Seeds tolerated mild heating (4-8%) to 120 °C. Seedlings established best in postburn treatments, but germination was high in all treatments relative to other species tested. Subsequent, seedlings survival was highest in postburn, moderate in burn, and low in unburned treatments. Based on fire effects studies conducted in the park's coastal lowlands and submontane 'ōhi'a woodlands, this species responds vigorously to fire (Tunison et al. 1994, 1995). This species is a good candidate for establishing into burn areas.

Myoporum sandwicense, Naio (Myoporaceae)

Status: Uncommon in the Park

This indigenous tree occurs on Cook Islands and in Hawai'i (Wagner et al. 1999). In Hawai'i, plants are occasional to common in dry to wet forest and from coastal strand to subalpine forest. Past grazing by cattle and goats has reduced this species to scattered individuals in dry communities from lowland to subalpine in the Park. Germination rates were extremely low in oven heat trials and in the field. Seedlings did not survive beyond the first year in the one controlled burn where germination was observed. From casual observations in the field, this species colonizes readily after wildfire. This species requires further evaluation to determine if disease is affecting seed viability at HAVO. Based on

fire effects studies outside the park, this species is a good candidate for establishing by planting into burn areas.

Myrsine lanaiensis, Kōlea (Myrsinaceae)

Status: Rare in the Park

A tree native to leeward dry forest on most of the main Hawaiian Islands (Wagner et al. 1999), individuals occurred infrequently in dry forest between 1,500 and 2,500 ft elevation in HAVO (Fosberg 1966). Individuals are currently limited to 'Āinahou in the Park. Germination was increased from 11% to 25% with mild heating (90 °C). Germination was observed in only one of the four controlled burns this species was tested. No seedlings survived beyond the first year. This species requires further evaluation.

Osteomeles anthyllidifolia, 'Ūlei (Rosaceae)

Status: Common in parts of the Park

This indigenous shrub occurs in a wide variety of habitats in dry shrubland, and dry to mesic forest, and persists in disturbed habitats on most of the main islands (Wagner et al. 1999). In the park, shrubs occur in dry to mesic montane and lowland shrublands and woodlands. Seeds tolerated mild heating to 90 °C, but germination fell significantly at higher temperatures. In the field, germination was sporadic and no seedlings survived beyond the first year in any of the treatments. In fire effects studies, this species does not survive very well in severe burns (Tunison et al. 1994, 1995). However, individuals were observed to resprout under less severe burn conditions. Further evaluation in the field to determine germination and seedling requirements are recommended. Based on its ability to resprout, this species is a good candidate for planting into burn areas.

Psyrax odorata, Alahe'e (Rubiaceae)

Status: Uncommon in the Park

A small tree indigenous to Hawai'i, this species occurs in dry to mesic shrubland and forest on most of the main islands (Wagner et al. 1999). Lava flows have covered much of the area this species formerly occupied in the Park. This species is the most common understory tree in dryland forest kīpuka remaining in the Park. Seeds have low tolerance to even mild oven heating (90 °C). This species was not tested in controlled burns. However, based on one fire effect study conducted in the 1990's (Tunison et al. 1994), individuals are capable of resprouting under low burn severity conditions. Further evaluation is required to determine the ability of seedlings to colonize burn areas.

Rhus sandwicensis, Nēnēleau (Anacardiaceae)

Status: Rare in the Park

A small tree endemic to Hawai'i, individuals typically occur in relatively wet to dry, disturbed areas on most of the main islands (Wagner et al. 1999). In the park, this species is known from a handful of sightings in Nāulu and East Rift forests. Seeds tolerated mild heating (90 °C) with no significant reduction in germination rates. This species was not tested in controlled burns and further evaluation is required to determine its ability to colonize burn areas.

Rumex skottsbergii, Pāwale (Polygonaceae)

Status: Uncommon in the Park

This endemic shrub typically occurs in low elevation, open lava fields on the Island of Hawai'i. Germination was significantly reduced from 91% to 17% by mild oven heating to 90 °C. This species was not tested in the field and further evaluation is required to determine the ability of seedlings to colonize burn areas.

Santalum paniculatum var. paniculatum, 'Iliahi (Santalaceae)

Status: Uncommon in the Park

Endemic to Hawai'i, this species of 'Iliahi is restricted to Hawai'i Island (Wagner et al. 1999). A partially parasitic small tree or shrub that occurs in dry woodland from lowland to the subalpine zone, the species is locally common in only a few sites in the park (Abbott and Pratt 1996). Seeds are frequently predated by rats and are difficult to obtain without localized trapping or baiting around trees. Seeds were not oven heat tested. Germination and seedling survival was higher in postburn and burn than in unburned treatments. Successful establishment from seeds or plantings has been documented in the Broomsedge

(Loh et al. 2007) and Kupukupu Burn (McDaniel et al. 2008) and in herbicide treated grass plots (Ainsworth pers.comm.). This species is a good candidate for seeding or planting into burn areas if sufficient seed can be found.

Scaevola kilaueae, Huahekili uka (Goodeniaceae)

Status: Rare in the Park, State Species of Concern, formerly a category 2 candidate endangered species
This endemic shrub occurs on old lava flows and ash substrate, in 'ōhi'a forest and shrubland in Ocean View Estates, Ka'u District, and vicinity of Kīlauea on Hawai'i Island (Wagner et al. 1999). In the park, this species occurs in dry 'ōhi'a shrublands and woodlands between 3,000 and 3,500 ft elevation in the park, and was historically observed on Mauna Loa (Pratt pers. comm.). Germination was 2% at room temperature and no germination occurred for seeds heated at higher temperatures. In two controlled burns, germination was much higher in the burn and postburn than in the unburned treatments. However, no seedlings survived beyond the seedling stage. Additional testing is needed to determine conditions needed for seedlings to survive and attain maturity.

Senna gaudichaudii, Kolomona (Fabaceae)

Status: Rare in the Park

Indigenous to Hawai'i, this shrub occurs primarily in talus slopes, lava flows, or rocky sites in coastal shrubland, dry forest, and lower portions of mesic forest on all of the main islands except Ni'ihau and Kaho'olawe (Wagner et al. 1999). In the park, kolomona was formerly present as an uncommon shrub in the Kamoamo area, but individuals perished when lava flows inundated the area. This species was last documented in the mid-1990's as a single individual growing in dryland forest in Kealakomo (Abbott and Pratt 1996). Seeds tolerated mild heating (90 °C) but germination dropped considerably at 120 °C heating. This species was not tested in controlled burns. Based on performance of other legumes, this species is likely to germinate in burn, postburn and unburned conditions, but more testing is needed to determine conditions needed for seedlings to survive and attain maturity.

Sesbania tomentosa, 'Ohai (Fabaceae)

Status: Rare in the Park, Federally listed endangered species

Endemic to Hawai'i, this sprawling or decumbent shrub formerly occurred in dry habitats on all of the main islands (Wagner et al. 1999). In the Park, individuals occur in dry lowland communities between 50 and 3,000 ft elevation. Seeds tolerated mild heating (90 °C) but germination dropped considerably at 120 °C heating. Because of the difficulty in obtaining seed due to its rareness, only the coastal variety of this species was tested. Germination but not survivorship was observed in one of the two burns this species was tested. Both sites provided only marginal habitat for this species and additional testing of the upland variety is recommended.

Sida fallax, 'Ilima (Malvaceae)

Status: Uncommon in the Park

This indigenous shrub is typically found in dry to mesic low elevation shrubland and forest on all the main islands (Wagner et al. 1999). In the park, a prostrate form is found in coastal strand and upright individuals in upland areas. For these experiments the inland variety was used. Germination was stimulated (2% to 11%) by mild oven heating to 90 °C. In the field, low germination occurred in burn, postburn and unburned treatments, but individuals survived to reproductive maturity only in the burn and postburn plots. This species is a good candidate for establishing by seed or planting into burn areas.

Sophora chrysophylla, Māmane (Fabaceae)

Status: Uncommon in the Park

Endemic to Hawai'i, plants are typically found in dry to mesic shrubland and forest on most of the main islands (Wagner et al. 1999). Past grazing by cattle and goats has reduced this species to scattered individuals throughout the lowland to subalpine zones of the Park. Seeds tolerated mild oven heating at 90 C with no significant reduction in germination rates. In the field, germination and seedling survivorship occurred in burn, postburn and unburned treatments. Reproductive individuals were observed six years after treatment. In the Muliwai II Burn, tagged individuals survived the controlled burn primarily by resprouting at the base. Individuals were successfully established by seeding and planting in the

Broomsedge Burn (Loh et al. 2007) and in the Kupukupu and Kīpuka Pepeiao Burns (Mcdaniel et al. 2008). This species is a good candidate for establishing by seeding or planting into burn areas.

Tephrosia purpurea, 'Auhuhu (Fabaceae)

Status: Uncommon in the Park

Considered a Polynesian introduction, this small shrub is native from Africa to southern Asia and tropical Australia (Wagner et al. 1999). This species occurs as scattered individuals in the coastal lowlands of Hawai'i Volcanoes. Germination rates dropped from 64% to 34% with mild oven heating at 90 °C. However, overall germination rates remained relatively high compared to other species. This species was not tested in controlled burns. Based on casual field observations and performance of other legumes, this species is likely to germinate in burn, postburn and unburned conditions, but more testing is needed to determine conditions needed for seedlings to survive and attain maturity.

Waltheria indica, 'Uhaloa (Sterculiaceae)

Status: Common in the Park

This indigenous shrub occurs in dry, often disturbed sites below 4,000 ft elevation on all the main islands (Wagner et al. 1999). In the park, this species is most abundant in dry lowland communities below 2,500 ft elevation. Germination was too low (<1%) to determine any significant response to oven heating. Based on fire studies conducted in the park's coastal lowlands and submontane 'ōhi'a woodlands, this species responds vigorously to fire (Tunison et al. 1994, 1995). Because of its widespread abundance, no further measures to establish this species in burn areas are recommended.