FIRE AND INVASIVE PLANTS IN HAWAIʻI VOLCANOES NATIONAL PARK

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ABSTRACT

Hawaiʻi has been invaded and colonized by many nonnative plants, including fire-promoting tropical and subtropical grasses that have invaded many dry and mesic environments in the leeward areas of the islands. Since the invasion of fire-enhancing grasses during the 1960s and early 1970s at Hawaiʻi Volcanoes National Park, fire frequency has increased 3-fold and fire size over 60-fold. The most severely impacted ecosystem is seasonally dry ʻohiʻa (*Metrosideros polymorpha*)-dominated woodland, invaded by alien broomsedge (*Andropogon virginicus*) and beardgrass (*Schizachyrium condensatum*). With little prior history of fire, recent wildfires have converted native woodland into alien grass savanna, often dominated by dense mats of molasses grass (*Melinis minutiflora*), yet another alien, fire-promoting species. The invasion of alien grasses into native woodland, post-fire thinning of the tree canopy, and increased fine fuel biomass have established a grass/fire cycle that degrades biodiversity. Broomsedge and beardgrass also invaded portions of the coastal scrub, and other fire-promoting grasses invaded the coastal grasslands after the control of feral goats (*Capra hircus*) populations during the early 1970s. Fire impacts are not as deleterious in the coastal ecosystems because of the presence and persistence of 2 or 3 fire-tolerant shrub and native grass species. Fire-promoting alien grasses have not widely invaded montane rain forest and montane mesic environments. Consequently, fires have been less frequent and widespread and have not had nearly as much impact on native biota in these environments.

Park fire and resource management programs now emphasize rehabilitation in the seasonally dry woodlands and coastal lowlands where fire has been the most widespread and/or had the greatest impact on native ecosystems. The rehabilitation goal in the seasonally dry woodlands is to establish fire-tolerant native trees and shrubs which can persist or spread in alien savannas that have been created by wildfire. The goal in the coastal lowlands is to enhance fire-stimulated native grasslands and find native shrub species that can persist in a prescribed fire-maintained ecosystem. A number of fire-tolerant species have been identified, and the current focus is to develop techniques for introducing these species. Methods to establish fire-tolerant native species are being tested. The most successful technique to date is to broadcast or sow seeds in areas where alien grasses are temporarily removed by prescribed burning. The most important fire research priorities in Hawaiʻi are to assess the impact of alien grass invasions and fire in affected communities throughout the state and to support rehabilitation efforts for fire-damaged ecosystems.

keywords: fire, grass–fire cycle, invasive plants, Hawaiʻi, Hawaiʻi Volcanoes National Park, *Melinis minutiflora, Metrosideros polymorpha,* molasses grass, ʻohiʻa, rehabilitation.

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INTRODUCTION

Island ecosystems are notoriously susceptible to biological invasions (Elton 1958). The Hawaiian Islands in particular have been successfully invaded and colonized by many introduced species (Loope and Mueller-Dombois 1989, Stone et al. 1992). For example, >90 alien plant species in Hawaiʻi form extensive monotypic stands or vegetation layers in native ecosystems (Smith 1985, Stone et al. 1992). Introduced species now dominate many areas of the state, especially in areas below 1,000 m in elevation.

Two reasons are often cited to explain the success of invasive species in remote islands. One is that introduced organisms are underrepresented biota taking advantage of opportunities presented by a disharmonic flora and fauna in which many groups of organisms may be underrepresented (Loope and Mueller-Dombois 1989). For example, social insects, such as ants, and terrestrial mammals may be successful invaders because these groups are absent in the native fauna of Hawaiʻi.

The other reason for the success of invasive species in islands is disturbance to which native species are not adapted (Loope and Mueller-Dombois 1989). Often this disturbance is caused by introduced species, for example, feral pigs (*Sus scrofa*). One way that alien plants modify native ecosystems is by altering disturbance regimes (Smith 1985, D'Antonio and Vitousek 1992). Among the most important invasive species altering disturbance regimes are fire-promoting tropical and subtropical grasses. These species usually colonize after land clearing or invade intact forests and woodlands where continuous fine fuels were not previously present (Mueller-Dombois 1981, Mueller-Dombois and Goldammer 1990). In Hawai‘i, fire-promoting C_4 grasses from Africa and the Americas have recently colonized many dry or seasonally dry habitats, typically in the leeward or rain shadow areas of the islands that are sheltered from the nearly daily trade winds rains. In some cases these grasses have invaded forest, woodland, or scrub which creates a much more continuous bed of fine fuels between existing native woody plants in communities in which fire may have been an unusual occurrence (Mueller-Dombois 1981). In Hawai‘i Volcanoes National Park (HAVO), these invasions have resulted in larger and more frequent fires and the conversion of forest and woodland to fire-prone alien savannas or grasslands. This has been documented in the seasonally dry woodlands of the park (Hughes et al. 1991, D'Antonio and Vitousek 1992, Smith and Tunison 1992, Tunison et al. 1995, D'Antonio et al. 2000). The role of alien grass invasions and the impact of fire in coastal, rain forest, and montane mesic environments at HAVO vary from those observed in the seasonally dry woodlands. However, alien plant species are typically important in succession after fire, at least during early successional stages (Smith and Tunison 1992).

Changes in fire regimes and succession after fire have been studied in depth in Hawai‘i only at Hawai‘i Volcanoes National Park (Hughes et al. 1991, Tunison et al. 1994, Tunison et al. 1995, D'Antonio et al. 2000). The impact of fire on Hawaiian ecosystems has been studied in nearly 40 sites in 4 ecosystems at HAVO. The most detailed studies were conducted in the seasonally dry woodlands, the park ecosystem in which fire has been the most prevalent and has had the greatest impact.

In this paper we describe the effects of alien grass invasions at HAVO on fire frequency and size and on plant succession. In addition, we outline efforts of the park staff to restore or rehabilitate fire-degraded ecosystems, as well as the research needed to successfully implement rehabilitation. We emphasize the seasonally dry woodland ecosystem where the impacts of fire are best understood and where fire has been most destructive to native biota. We also briefly describe the role of invasive species, fire history, succession, and rehabilitation in the coastal, rain forest, and montane mesic environments of the park.

FIRE HISTORY AND CHANGES IN FIRE REGIME

Assessing the impact of alien species invasions on fire regimes before recent decades is limited by the lack of precise tools available to determine fire history in Hawaii. Dendrological analysis is not applicable in Hawai‘i because of its tropical climate and lack of annual ring formation in trees. Dated charcoal fragments found in sediment cores in Hawaiian bogs indicate that natural fire occurred in some Hawaiian ecosystems. Although it is not possible currently to develop a detailed fire history from these cores, general patterns of fire history can be inferred. Pollen records from these cores indicate a climate alternating between wet and dry periods throughout the last 40,000 years (Burney et al. 1995, Hotchkiss 1998). Higher concentrations of charcoal were found in strata dominated by ‘ohi‘a, and grass pollen and less charcoal was found in strata dominated by pollen from wet forest species. A marked increase of charcoal in sediments indicate an increase in fire since European contact 200 years ago (S.C. Hotchkiss, University of Wisconsin, unpublished data).

Fire history of the park before 1924 is understood partially for at least 1 ecosystem. The coastal lowlands were burned deliberately starting with Polynesian occupation nearly 1 millenium ago. Anthropogenic burning by prehistoric Polynesians is thought to be responsible for the deforestation of the coastal lowlands of Hawai‘i (Kirch 1982). Polynesians burned to clear vegetation for swidden agriculture and to stimulate the growth and abundance of pili grass (used as thatching material) and other desirable plants. A detailed analysis of historic accounts in the Hilo area of Hawai‘i Island indicate that there was a broad belt of cleared land up to 440 m in elevation (McEldowney 1979). Although a similar historical analysis has not been done specifically for HAVO, Polynesian burning practices certainly modified the coastal lowlands of HAVO and may also have affected lower portions of the seasonally dry woodlands upland of the coastal zone. Agricultural mounds and other archaeological features are found in this elevational zone of the park, although they are more abundant or noticeable on younger lava flows with open vegetation. In any case, anthropogenic burning would have had little effect on the evolution of plants in Hawai‘i because Polynesians arrived in the islands <2,000 years ago.

Detailed park records dating back to 1924 document the recent history of fire in HAVO. Fire frequency and size at HAVO increased dramatically starting during the late 1960s. During 1924–1963, there were 35 fires recorded or 0.9 fires per year on average (Table 1). These fires burned 87 total ha or an average of 2.5 ha per fire. Most of these small, infrequent fires were concentrated in visitor use areas along the rim of Kilauea Caldera, in pastures leased to cattle ranchers on the slopes of Mauna Loa, and in the vicinity of Civilian Conservation Corps camps or work projects. During 1964–1995, there were 97 fires or slightly more than 3 fires per year. These fires burned approximately 13,950 total ha or an average of 144 ha per fire.

The approximately 3-fold increase in fire frequency and nearly 60-fold increase in fire size followed the introduction and spread of alien fire-promoting grasses starting during the 1960s. Two tall bunchgrasses, beardgrass from tropical America and broomsedge from the southeastern United States, invaded and spread very rapidly in many HAVO plant communities below 1,300 m in elevation, particularly affecting sea-

Table 1. Fire history at Hawai'i Volcanoes National Park, 1924–1995.

Years	Human-caused *n*	Human-caused Area (acres)	Lava-caused *n*	Lava-caused Area (acres)	Other causes *n*	Other causes Area (acres)	Total fires (*n*)
1924–1931	8	38	0	0	0	0	8
1932–1939	6	124	0	0	0	0	6
1940–1947	11	2	0	0	0	0	11
1948–1955	4	50	0	0	0	0	4
1956–1963	3	1	3	198	0	0	6
1964–1971[a]	3	1,686	4	2,716	1	215	8
1972–1979[b]	15	2,211	5	5,063	1	1	21
1980–1987	29	3,327	5	1,184	5	10,942	39
1988–1995	8	4,407	16	2,325	5	395	29

[a] First fire in broomsedge/beardgrass fuels during 1969.
[b] Goats controlled in park lowlands during 1972.

sonally dry woodland, but also the coastal scrub and grasslands and disturbed gaps in rain forest. Beardgrass and broomsedge were not found in a systematic botanical survey of the park lowlands during 1959 (Stone 1959). By 1966, these grasses were characterized as the dominant species of many vegetation types in the park (Mueller-Dombois and Fosberg 1974). They now form approximately 30% of the understory biomass and 65–80% of the understory cover in seasonally dry woodland (D'Antonio and Vitousek 1992, D'Antonio et al. 1998). The invasions of broomsedge and beardgrass may have been facilitated by high densities of feral goats that suppressed potentially competitive native woody vegetation (R.K. Loh, J.T. Tunison, and J.A.K. Leialoha, unpublished data).

Fire-promoting grasses also spread rapidly in the coastal grasslands following the control of feral goats during the early 1970s. The coastal grasslands and scrub were an anthropogenic landscape created by Hawaiian agricultural practices over the last 700 years (Kirch 1982), cattle grazing, and 200 years of feral goat browsing and grazing activities (Williams 1990). Grasslands prior to goat control were dominated by short-statured annual grasses (i.e., alien lovegrass [*Eragrostis tenella*]) or mat-forming stoloniferous grasses (i.e., alien Bermuda grass [*Cynodon dactylon*]; Mueller-Dombois and Spatz 1975). An effective goat control program was begun during 1970. Within 2 years following the exclusion of goats, the short-statured grasses were largely replaced by tall, introduced, fire-promoting, perennial grasses including thatching grass (*Hyparrhenia rufa*), molasses grass, Natal redtop (*Melinis repens*), broomsedge, and beardgrass, as well as by the perennial native pili grass (*Heteropogon contortus*; Mueller-Dombois 1980). Thatching grass continued to expand in the coastal grasslands during the 1980s and 1990s (R.K. Loh, unpublished data).

In the seasonally dry woodland, park vegetation maps and fire records indicate that broomsedge and beard grass invaded an ecosystem with little previous history of fire. Prior to invasion, seasonally dry woodland was apparently dominated by an open to closed cover of native shrubs and a discontinuous groundcover of lichens, bryophytes, and sedges (Mueller-Dombois and Fosberg 1974, Cuddihy and Stone 1990). Native grasses may not been an important component of this ecosystem to provide fine fuels to carry fire. The only native grass present in the seasonally dry woodland, a native lovegrass (*Eragrostis variabilis*), is rarely encountered.

The invasion and spread of fire-promoting grasses in seasonally dry woodland and coastal ecosystems coincided with an era of renewed volcanic activity that started during the late 1960s and continues to the present. Visitation in the park has also increased since the 1960s. It is not possible to strictly separate the increased potential for ignitions by humans and lava flows from the impact of invading fire-promoting grasses. However, most of the fire activity occurred in the 2 ecosystems of the park invaded by pyrophytic grasses during the 1960s and 1970s: the dry 'ohi'a woodland and the coastal grasslands–scrub. The first fire to occur in the park in the newly arrived broomsedge and beardgrass fuels was recorded during 1969 (G. Smathers, University of North Carolina, personal communication). From 1965 to 1995, 81% of the area burned, and 90% of the fires in the park were in the seasonally dry woodland and coastal grasslands–scrub (R.K. Loh, J.T. Tunison, and J.A.K. Leialoha, unpublished data). Prior to 1965 just 5 small fires burned in the seasonally dry woodland; only 1 fire was recorded for the coastal grasslands–scrub (R.K. Loh, J.T. Tunison, and J.A.K. Leialoha, unpublished data). As an ignition source, lava flows may contribute to increased fire size because of the difficulty of controlling fires ignited along the edges of a moving lava flow.

IMPACT OF FIRE ON VEGETATION

We studied the impacts of fire primarily in the seasonally dry woodlands. Succession after fire was also studied in the coastal lowland, rain forest, and montane mesic ecosystems. Sites were largely selected in areas where wildfires occurred from 1985 to 1990. Two well-documented fires from the 1970s were also studied. Sites were generally first monitored within 6 months of the fire and every 6–24 months thereafter. The majority of burns were sampled for 5–6 years and 2 burns were sampled 12 years post-fire.

Sampling sites were selected in the burns along fire control lines in areas where vegetation was relatively homogeneous, fire intensity was known, and topography was relatively similar. Untreated controls were established across fire control lines from the burned area sampled to compare succession in burned areas with equivalent unburned areas. The cover and density of vegetation in untreated controls was considered to represent the successional pattern of the site without the influence of fire.

Point-intercept methods, using a 1.25 m tall point-frame with 5 sharpened rods were used to evaluate changes in plant cover along 40-m long transects. We sampled 200 points per transect. Dead vegetation intercepted by the point-frame was recorded as live if it was still attached to a living plant. Transects were laid out in a stratified or random-stratified fashion. In stratified-random sampling, azimuths of each transect were located at random, and the transects were located at fixed distances from one another. In random-systematic sampling, an arbitrary starting point was selected and then a random azimuth chosen for the first transect. All other transect azimuths and distances to the next transects were then fixed. Transects were rejected if they fell over prominent pahoehoe tumuli, lava tube openings, or other rock outcrops. These features are associated with lower cover of alien vegetation.

Tree and shrub densities, including seedling recruitment, were determined in 4 height classes in 5 2- × 2-m plots along transects at randomly determined distances. We tagged individual burned trees and shrubs in the vicinity of the transects immediately after a burn and monitored for 1–2 years to determine resprouting or mortality.

The impact of fire was determined by evaluating the response of individual species and total native and alien cover by life-form. Cover and density values of species in burned and unburned areas were compared with *t*-tests after data were arcsine transformed to improve normality.

Seasonally Dry Woodland

The seasonally dry woodland, or dry ‘ohi‘a woodland, is located in the leeward zone of the park from approximately 300 to 1,200 m in elevation. In the seasonally dry woodland, precipitation averages 100–150 cm per year, with most rain falling between November and April during most years. Soils, derived from volcanic ash, are generally thin and patchy over young pahoehoe flows <1,000 years old. Prior to fire, the woodlands are dominated by open stands of ‘ohi‘a with an understory of native shrubs, the most common of which are pukiawe (*Styphelia tameiameiae*), ‘a‘ali‘i (*Dodonaea viscosa*), ‘ulei (*Osteomeles anthyllidifolia*), and ‘akia (*Wikstroemia phillyreifolia*). Alien grasses form a nearly continuous matrix between the open shrubs. Typically, beardgrass is the dominant grass in unburned seasonally dry woodland, with molasses grass and broomsedge as minor components. Molasses grass was present in the park during the early 20th century, but was largely confined to roadsides, probably due to feral goat browsing. It spread into seasonally dry woodland during the 1970s and 1980s, apparently after goats were controlled (R.K. Loh, J.T. Tunison, and J.A.K. Leialoha, unpublished data). Molasses grass seed is ubiquitous in the soil in the unburned woodland. The current dominance of beardgrass in the unburned woodland is due to the fact that it became established on site prior to the spread of molasses grass.

We studied plant succession after fire in 14 sites in the seasonally dry woodlands, with reported sampling periods after fire ranging from 4 to 17 years (Hughes et al. 1991, Tunison et al. 1995). Fire greatly reduced native woody vegetation in the seasonally dry woodland, especially ‘ohi‘a and pukiawe, the dominant species. On average, 55% of the ‘ohi‘a were killed by fire. Some surviving trees were protected partially from fire on pahoehoe tumuli with little alien grass fuel. More typically, aerial portions of the trees were killed and surviving individuals recovered by crown or epicormic sprouts (Parman and Wampler 1976, Tunison et al. 1995). ‘Ohi‘a mortality was positively related to fire severity, with height of char on the bole the best predictor of mortality. On average, 60% of ‘ohi‘a in high severity sites and 29% in low intensity sites were killed. ‘Ohi‘a is a very slow growing species. Crown sprouts, by far the most common method of recovery, were only 3–5 meters tall after 17 years. ‘Ohi‘a seedlings did not become established. In fact, ‘ohi‘a seedlings were not found in any recently burned seasonally dry woodlands (Tunison et al. 1995). The loss of mature ‘ohi‘a and failure of ‘ohi‘a to recruit from seed resulted in the conversion of open canopied woodlands to savannas characterized by scattered to very scattered trees (Hughes et al. 1991, Freifelder et al. 1998).

Three of the 4 native shrub species common in the seasonally dry woodland before fire were sharply reduced in cover and density following fire, and showed little sign of recovery, even 17 years after fire (Hughes et al. 1991, Tunison et al. 1995). The aerial portions of all 4 shrubs were readily killed by fire, although resprouting occasionally occurred under low-intensity fire conditions (Tunison et al. 1995). Native shrub cover as a whole was reduced nearly 2 orders of magnitude. Pukiawe, the dominant shrub before fire, was nearly absent in most burned areas; it declined 10-fold in cover and 3-fold in density after fire. Although some seedlings were observed, no seedlings of pukiawe recruited successfully to larger size classes in any burned site (D’Antonio et al. 2000). Although mature plants of the common shrub ‘a‘ali‘i were killed by fire, this native shrub species generally recovered to pre-fire abundance. Recruitment from seed was substantial (Hughes et al. 1991); recruitment into larger size classes occurred through dense grass cover, and densities of large plants were similar in older burns to densities in unburned areas (D’Antonio et al. 2000). Although sample sizes were very small, the small native tree mamane (*Sophora chrysophylla*) resprouted nearly invariably from the root crown, even after severe fires (Tunison et al. 1995).

Alien grass cover increased on average by 33% after fire (Tunison et al. 1995, D’Antonio et al. 2000). Alien grass biomass increased 2–3-fold after fire, increasing fuel loadings. Molasses grass cover increases the most in burned sites where it was present prior to fire. Fire disrupts the priority effect of beardgrass, and molasses grass effectively out-competes beardgrass in burned sites for both light and nutrients.

The rapid reestablishment and long-term persistence of alien grasses inhibit shrub colonization and growth (Hughes and Vitousek 1993). This was particularly common in sites where molasses grass was present (D’Antonio et al. 2000); native shrub cover was lowest in these sites. The vigorous response of this mat-forming species creates a formidable environment for native species regeneration. Low light levels under alien grasses in burned areas, rather than lack of soil moisture or nutrients, were responsible for the lack of recruitment of native shrubs (Hughes and Vitousek 1993). The native shrub ʻaʻaliʻi persists in burned areas because of its rapid germination and growth.

Grass–Fire Cycle

The main fire-promoting grasses of the park that invaded and/or spread during the 1960s and 1970s—broomsedge, beardgrass, thatching grass, and molasses grass—have characteristics that facilitate fire spread and rapid recovery after fire. Broomsedge, beardgrass, and thatching grass are tall perennial bunchgrasses. Molasses grass is a rhizomatous, mat-forming grass. All maintain high dead : live biomass ratios throughout most of the year, except during heavy rainy periods. Consequently, these grasses provide a high standing biomass of dead material and a continuous fuel bed of dry, fine fuels. Broomsedge and molasses grass have higher surface-to-area volume, loadings, and fuel depth estimates than the corresponding parameter of standard grass models (Fujioka and Fujii 1980). Molasses grass fuels in HAVO have been measured as high as 25,370 kg/ha (R.K. Loh, J.T. Tunison, and J.A.K. Leialoha, unpublished data). In addition, molasses grass leaves are coated with a resinous material and may have a high heat content. All 4 grasses appear to have high moistures of extinction and can carry fire at high relative humidity, even as high as 80–90% (J.T. Tunison, unpublished data). All grow with increased vigor after fire and recover by resprouting or seedling recruitment (Hughes et al. 1991, Tunison et al. 1995). Fountain grass (*Pennisetum setaceum*) is another tall perennial, pyrophytic bunchgrass that has invaded dry forest or shrublands and even relatively bare lava flows and created fire problems in other areas of Hawaiʻi Island (Takeuchi 1991, Shaw et al. 1997). This species is now effectively controlled in HAVO and does not currently affect the fire regime of the park (Tunison et al. 1994).

The invasion of broomsedge and beardgrass into the seasonally dry woodland has established an alien grass–fire cycle (Hughes et al. 1991, D'Antonio and Vitousek 1992, Freifelder et al. 1998), a process facilitated by the fire-promoting and post-fire colonizing characteristics of these grasses. Grass invasion of seasonally dry woodlands promotes fire in a previously fire-independent ecosystem and alters the disturbance regime of this ecosystem. After fire, grasses out-compete native woody plants and increase in cover and fuel loading (Hughes et al. 1991, D'Antonio et al. 2000). Burned sites are then predisposed to more severe fires compared with adjacent unburned woodlands because of increased fuel loadings and, more importantly, because wind speeds are substantially greater in the more open post-fire savannas (Freifelder 1998). Contrary to expectations, temperatures are higher and relative humidities are lower in the unburned woodland than in the burned, adjacent savanna. The open canopied woodlands (40% tree cover [Hughes et al. 1991]) apparently serve as a windbreak but do not shade the understory sufficiently to reduce near-ground temperatures as much as tall, dense mats of molasses grass do in burned areas.

Changes in Nitrogen

Nitrogen changes after fire have been studied in the seasonally dry woodland. The most detailed studies compared 4 related sites: an unburned woodland site, a 17-year-old burn, a recent burn, and a twice-burned site. Soil pool sizes of available N were significantly increased (Hughes and Vitousek 1993) in all burned sites compared with the unburned woodland. Pool sizes were greatest in the recently burned site, but were lower in the twice-burned and old burned sites, indicating a decline over time after fire and with successive fires. However, rates of N fixation were greater in the unburned woodland (Ley and D'Antonio 1998) than in the burned sites. N fixation occurs asymbiotically on leaf litter and wood debris. These substrates are absent from the burned sites, except for unconsumed wood debris. The decrease in N fixation in burned sites indicates that ecosystem-level rates of N accretion are reduced by fire and that N lost during volatilization due to fire is not replenished over the long term by N fixation.

Coastal Lowlands

The impact of fire varied between the 2 major vegetation types in the coastal lowland environment, near-native shrublands in the east and largely alien grasslands in the central and eastern parts of the coastal lowlands below 300 m in elevation (Tunison et al. 1994). In the near-native shrublands, a matrix of broomsedge and beardgrass filled in the gaps in open shrubland and carried the wildfires that have occurred there. Even though the fire-intolerant native shrub ʻakia was nearly eliminated by fire and cover of native plant species was reduced, other native shrubs, including ʻaʻaliʻi and ʻuhaloa (*Waltheria americana*) recovered rapidly from seed, and the native shrub ʻulei recovered by resprouting. There was a net increase in native plant cover because of a positive response of native pili grass to fire. In the central coastal lowlands, fire had little long-term effect on the composition of alien grasslands because the recovery to pre-fire composition and abundance was rapid. Fire also enhanced the cover of native pili grass in pili–Natal redtop communities.

Fire in the coastal lowlands was not as damaging to native ecosystems as it was in the seasonally dry woodland, even though alien, fire-promoting grasses had invaded this ecosystem (D'Antonio et al. 2000). Part of this favorable response can be attributed to the presence of shrub species that recovered by resprouting or became established from seed. However, the favorable response is also partly due to the persistence of native pili grass that survived cattle, feral goats, and the spread of tropical and subtropical alien grasses after goat control. Pili is a fire-stimulated species and has a history of responding to fire in the lowlands. It was apparently an important historical component of

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the coastal lowlands, and Polynesians used fire in the coastal areas to stimulate pili.

Rain Forest

Wildfire is uncommon in rain forest and no fires have been recorded in the park in tree fern (*Cibotium* spp.)-dominated rain forest (R.K. Loh, J.T. Tunison, and J.A.K. Leialoha, unpublished data). However, fires can occur in uluhe (*Dicranopteris linearis*)-dominated rain forest after several weeks of drought. This community is characterized by open-canopied stands of ‘ohi‘a, along with other native tree species, and an understory dominated by uluhe, a climbing fern 1–5 meters in height, which forms dense, continuous, tangled mats between trees. The understory also contains scattered tree ferns and native shrubs, sedges, grasses, and other ferns.

In uluhe rain forest, alien broomsedge, foxtail (*Setaria geniculata*), and Himalayan raspberry (*Rubus ellipticus*) invade and dominate the post-fire community during the first 2 years (R.K. Loh and J.T. Tunison, unpublished data). Early successional native plants also invade immediately after fire. These species include sedge ‘uki (*Machaerina* spp.), the grass ‘ohe (*Isachne distichophylla*), and the shrub naupaka (*Scaevola chamissoniana*). In sites without aggressive alien plants before fire, uluhe recovers and dominates the understory of the rain forest within 11 years. Tree ferns, shrubs, and ‘ohi‘a resprout in varying degrees. ‘Ohi‘a successfully establishes from seed. In sites with aggressive alien plants, recovery of native vegetation may be disrupted by the rapid spread via resprouting and growth of alien plants. In 2 2-year-old burns, kahili ginger (*Hedychium gardnerianum*) and bamboo (*Phyllostachys nigra*) have responded quickly following fire by resprouting and now dominate early successional sites.

The rapid, post-fire recovery of native vegetation in intact rain forest contrasts with the poor recovery in seasonally dry woodland. We can speculate about possible reasons. Rain forest with dense canopy cover was not invaded by fire-promoting grasses before fire. In addition, much of the heat generated by fire in uluhe may have been high in the canopy and thus did not affect the seed bank or fern rhizomes. Although broomsedge invaded following the burn, it did not create dense mats that inhibit seedling establishment as does molasses grass in the seasonally dry woodland. Instead, uluhe regenerates vegetatively and suppressed alien grasses which initially dominated the post-fire environment. Although uluhe clearly suppresses other native plants, many native species are able to germinate, grow, and reproduce under uluhe or in gaps in the uluhe mat. A favorable plant environment and consistent rainfall in rain forest sites may account for the fact that the only burn observed in the park with ‘ohi‘a seedling recruitment was in the rain forest.

Montane Mesic Forest

Fires are also uncommon also in the Hawaiian montane mesic environment (R.K. Loh, J.T. Tunison, and J.A.K. Leialoha, unpublished data). Only 1 fire has occurred there during the last 25 years. Fire-prone communities in this environment include stands of koa (*Acacia koa*) forest, native shrublands that have significant admixture of native and alien grasses, and occasional small grasslands dominated by native or alien grass. Fire may have been an important component of the montane mesic ecosystem (Mueller-Dombois 1981). This is inferred from the fact that native shrubs and grasses form a nearly continuous fine fuel bed, and many native species recover rapidly from fire. Fire appears to change the composition of these communities very little (R.K. Loh and J.T. Tunison, unpublished data). There is little change in species composition of koa forest. Koa resprouts readily from root suckers to reestablish the forest overstory within a decade. Understory species, largely dominated by the alien meadow ricegrass (*Ehrharta stipoides*), rapidly recovers vegetatively, are little changed. Shrublands and grasslands change only subtly in composition after fire, with a shift in cover from less fire-tolerant pukiawe to the more fire-tolerant ‘a‘ali‘i and no net increase in alien species cover, including alien grasses.

These observations about fire in montane mesic forest are based on succession following a single fire during 1975. New alien species have become established in the park and vicinity since that fire and others have increased in abundance. These changes may affect succession after future fires.

POST-FIRE REHABILITATION

Efforts to rehabilitate post-fire sites have focused exclusively on the seasonally dry woodland and coastal grasslands where fire has been the most prevalent and has had the greatest impact on native Hawaiian ecosystems. The testing of rehabilitation methodologies began during 1993 in small experimental plots to identify and introduce fire-tolerant native plants.

Seasonally Dry Woodland

Approximately 66% of the seasonally dry woodland of HAVO has burned during the last 25 years. Fire-damaged dry ‘ohi‘a woodlands present a formidable ecological restoration challenge. Fire thins out the tree canopy, reduces native shrub cover and diversity, and increases the cover and biomass of grasses. In many sites molasses grass becomes the dominant plant species after fire.

In the seasonally dry woodland, a rehabilitation approach to ecological restoration has been pursued, rather than efforts to restore the original pre-fire community. It is futile to attempt to restore ‘ohi‘a and pukiawe, the dominant species of the unburned community. Little regeneration could be expected from sown seeds or even outplantings, given the rapid recovery of grasses, especially molasses grass (Hughes and Vitousek 1993). Even if successfully reestablished, ‘ohi‘a and pukiawe would be largely removed by the next inevitable and probably more intense wildfire. A rehabilitation approach uses elements of the

Table 2. Potential species for rehabilitation of burned sites in Hawai'i Volcanoes National Park.

Site type	Common name (Hawaiian)	Scientific name
Seasonal woodland	ʻAʻaliʻi	*Dodonaea viscosa*
	ʻEmoloa	*Eragrostis variabilis*
	Heupueo	*Agrostis avenacea*
	ʻIliahi	*Santalum paniculatum*
	Kupaoa	*Dubautia ciliolata*
	Koʻokoʻolau	*Bidens hawaiiensis*
	Kolea	*Myrsine lanaiensis*
	Mamane	*Sophora chrysophylla*
	Naio	*Myoporum sandwicense*
	Neleau	*Rhus sandwicensis*
	Naupaka kīlauea	*Scaevola kilaueae*
	ʻOhelo	*Vaccinium reticulatum*
	Pawale	*Rumex skottsbergii*
	Pua kala	*Argemone glauca*
	ʻUlei	*Osteomeles anthyllidifolia*
Coastal	ʻAwikiwiki	*Canavalia hawaiiensis*
	Pili	*Heteropogon contortus*
	Konakona	*Panicum nephelophilum*
	Kaioio	*Panicum pellitum*
	ʻIlima	*Sida fallax*
	ʻOhai	*Sesbania tomentosa*

former system to create a near-native replacement community of fire-tolerant native plant species that can persist in a community dominated by alien grasses. These species could also survive and ideally spread after inevitable wildfires. We hope that, over time, the fire-tolerant components of this community may become increasingly important. Eventually they may suppress grasses, reduce fire potential, and permit the recovery of fire-intolerant species found in the original seasonally dry woodland.

Fire-tolerant species are identified by their ability to recover from fire by crown or root sprouts or to recruit prolifically from seed after fire. In the context of burned seasonally dry woodlands, sprouts and seedlings must be able to recruit through the rapidly growing alien grass sward. A number of fire-tolerant species occur in the seasonally dry woodland, but many are currently uncommon, possibly because of the history of intense browsing by feral goats. For example, a high percentage of mamane plants resprout vigorously after wildfire (Tunison et al. 1995). A few relictual individuals of mamane occurred in lava tube skylights and other sites inaccessible to goats. Mamane plantings made during the 1950s along a road in HAVO proliferated after wildfires during 1970 and 1987. ʻAʻaliʻi resprouts only after very low-intensity fire. However, recruitment from seed after fire is often abundant and germination of ʻaʻaliʻi seeds can be stimulated by heat (Hodgkinson and Oxley 1990).

During 1993, park resource managers began testing the suitability of native species for use in rehabilitation projects in seasonally dry woodland. Fifteen target species with apparently some tolerance of fire have been identified (Table 2). The suitability of most of these species has been studied in laboratory and field tests. Germination was measured after laboratory heat treatments simulating tolerance of seed banks to fire. Field tests utilized small-scale prescribed burning. Seeds were sown in small plots prior to the burns and after the burns. Both low-intensity and high-intensity fires were tested. Germination and growth through the recovering grass sward was evaluated and compared with germination and growth in sown unburned control areas.

The following species have been tested and appear to be suitable species for rehabilitating seasonally dry woodland sites: mamane, ʻaʻaliʻi, pua kala or Hawaiian poppy (*Argemone glauca*), koʻokoʻolau (*Bidens hawaiiensis*), and sandalwood (*Santalum paniculatum*; R.K. Loh, J.T. Tunison, and J.A.K. Leialoha, unpublished data). Mamane and ʻaʻaliʻi are highly effective and large amounts of seed have been collected and stored for future post-fire rehabilitation needs. Testing the suitability of other candidate species depends largely on seed availability.

Current research emphasizes the development of methods for reintroduction of fire-tolerant native plants to burned areas. Efforts have emphasized prescribed burning because this technique removes the dense grass sward that inhibits the establishment of native woody species in the seasonally dry woodland. Prescribed burning also simulates the effects of wildfire and tests the ability of rehabilitation species to survive and establish after wildfire. The effectiveness of prescribed burns depends largely upon unpredictable post-burn rains (R.K. Loh, J.T. Tunison, and J.A.K. Leialoha, unpublished data). Both seasonally dry woodland and coastal environments have unpredictable precipitation regimes. Drought period following the burns appears to be the most important factor constraining germination, growth, and survival. Although some target rehabilitation species, such as mamane, do better after low-intensity burns, most target rehabilitation species can germinate, grow, and survive following high-intensity fire, as long as the burn is followed by favorable rains.

Other planned methods of reintroduction to be tested include the use of herbicides or mechanical scalping for temporary control of grasses, followed by the outplanting of fire-tolerant species. In some areas, the fuel beds are too extensive and remote, or the risk from an escaped fire is too great for use of prescribed burning. Current research also emphasizes rehabilitation of model communities of approximately 10–50 ha to test landscape-scale rehabilitation strategies. These utilize small, discontinuous nodes of intensive seeding or outplanting in favorable sites. These landscape-level strategies are being tested within the boundaries of a 400-ha wildfire that occurred during July, 2000 in seasonally dry woodland. Outplantings and seeds are being placed in <1,000 nodes located in locally deep pockets of soil. We intend to create 2 associations, one dominated by mamane and the other by koa. Individuals of the sown or outplanted species are predicted to mature, spread to adjacent sites, create a seed bank, and proliferate following future fires.

Coastal Grasslands

Rehabilitation in the coastal environment of the park emphasizes enhancement of the fire-tolerant native pili grass by prescribed burning. Because of extensive lava flows from Puu Oo over the last 17 years, remnant native shrublands persist only in the eastern coastal lowlands. Most of this area has been burned by lava-ignited fires and now is dominated by the fire-tolerant native shrub ‘a‘ali‘i and pili grass (Tunison et al. 1994) and does not require rehabilitation. The grasslands that characterize the central and western lowlands are dominated by alien grasses, primarily thatching grass and Natal redtop, mixed with native pili grass. Native pili is found in both grassland communities. Studies of fire effects in the coastal grasslands indicate that pili grass increases in cover relative to Natal redtop after wildfire (Tunison et al. 1994).

Prescribed burns have been conducted to assess the most effective means of stimulating pili grass in competition with Natal redtop or thatching grass. As expected from fire effects studies (Tunison et al. 1994), pili grass cover increased strongly against Natal redtop after 2 fires (R.K. Loh, J.T. Tunison, and J.A.K. Leialoha, unpublished data). Current research efforts focus on the timing and intensity of burns to maintain pili grass cover as well as to identify native shrubs which can germinate, survive, and mature under this burning regime. Current research also emphasizes the timing and intensity of burns or other treatments to provide pili a competitive advantage in grasslands where thatching grass is present. In prescribed burns conducted to date, cover of thatching grass has persisted or increased in in competition with pili grass.

RESEARCH NEEDS

The impacts of alien grasses on fire regimes and fuels and the impacts of fire on Hawaiian ecosystems needs to be addressed throughout Hawai‘i. Almost all fire ecology studies, to date, have been conducted at Hawai‘i Volcanoes National Park. Only 2 studies have been conducted elsewhere in the state. A descriptive report of fire effects in a dry lowland forest in Kona on Hawai‘i Island was prepared for the Hawai‘i Division of Forestry and Wildlife (Takeuchi 1991). A long-term study of a 1994 fire at Pohakuloa Training Area on Hawai‘i Island is underway (Shaw et al. 1997). Both studies found that wildfire carried by alien fountain grass fuels was highly damaging to native woody species. The suite of alien grasses promoting fire at HAVO and the invaded seasonally dry woodland dominated by ‘ohi‘a on young lava flows is largely unique in Hawai‘i. Different suites of invasive grass species and invaded plant communities are present in other parts of the state.

There is an urgent need in the state for fire management agencies to become more effective in protecting fire-vulnerable ecosystems. Fire ecology studies at HAVO have had this effect on fire management in the park. Studies at Hawai‘i Volcanoes were stimulated initially by the need to assess fire effects and to revise a Fire Management Plan that permitted prescribed natural fire from lava flow ignitions in some areas of the park. Fire effects studies at HAVO were valuable in refocusing fire management policy on aggressive, total suppression of all fires and an emphasis on fire prevention. The number of human-caused fires has declined considerably since stringent fire prevention measures were undertaken starting during the late 1980s (Table 1). Fire effects studies were also valuable in identifying fire-tolerant species and the potential for a rehabilitation strategy.

Rehabilitation of burned areas should become a major focus of fire ecology research in Hawai‘i. The importance of intact native overstory or restored native overstory on invasive fuels should be determined to evaluate the role of restoration or rehabilitation in reducing fire hazard. In a 400-ha burn at HAVO during 2000, backing and flanking fires did not carry through stands of koa, with a dense understory of pukiawe and ‘a‘ali‘i or through mesic forest stands with a well developed subcanopy of mesic forest trees (R.K. Loh, unpublished data). Dense cover in the understory appears to suppress alien grass cover. As part of the rehabilitation following the burn, resource managers are outplanting and sowing seeds to create dense woody plant understory and overstory canopies that will suppress grass establishment. Efforts at establishing native fire-resistant stands of vegetation are focusing on an urban interface of the park and on the margins of a species-rich, unique mesic forest stand.

More fire-tolerant native plant species can be identified and tested for rehabilitation. An intensified, replicated, and more manipulative research effort may result in separating the factors that limit successful rehabilitation efforts, including timing, fire intensity, and soil moisture, and may lead to effective post-seeding strategies. The ability of a rehabilitated plant community, established by sowing or mature outplanting, needs to be evaluated for its tolerance of wildfire. This can be tested by determining how a fire-tolerant species regenerates after prescribed burning and developing a seed bank. Strategies for landscape-level rehabilitation need to be tested. Rehabilitation research should also focus on understanding how alien species that recover well after fire inhibit native plant recovery, e.g., determining why molasses grass is such an effective competitor. Understanding the factors that make alien species effective competitors may provide tools for rehabilitation.

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