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Experimental restoration trials in Nakula Natural Area Reserve in preparation for reintroduction of Kiwikiu (*Pseudonestor xanthophrys*)

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ABSTRACT

The native montane mesic forest in the Kahikinui region of Maui, Hawai‘i USA has been degraded by non-native ungulates for over a century. This has resulted in large areas of non-native grassland and savanna with small intact native forest patches, mainly in steep gulches. The Nakula Natural Area Reserve (NAR), on the southwestern slope of Haleakalā volcano, was selected as the site of the reintroduction of Kiwikiu (*Pseudonestor xanthophrys*), a critically endangered songbird currently found only in a small range on the northern slope of the volcano. This area was selected for the reintroduction because it is located within a mesic koa (*Acacia koa*) forest representing some of the best potential habitat outside of the current Kiwikiu range. Historic accounts noted the Kiwikiu’s affinity for koa as a foraging substrate, although little koa forest remains on Maui. Intensive forest restoration has created new habitat and enhanced the existing habitat in Nakula to the point where the reserve may now be capable of supporting a small population of Kiwikiu and other native birds. As a precursor to reintroduction efforts, we designed experimental trials to inform managers of the most efficient and effective techniques to restore the forest in Nakula NAR and surrounding region. Trial plots were established in open grass-dominated areas within a fenced, ungulate-free portion of the reserve to investigate natural regeneration, outplanting, and seed broadcast as restoration techniques under a number of conditions. Treatments to suppress and/or remove non-native grass were implemented as these grasses likely reduce germination of native seedlings and potentially influence outplanting success. Some plots were treated with herbicide and the dead grass biomass was removed to expose bare topsoil in a subset of these plots. Additional plots were established under mature koa trees to investigate natural recruitment and the success of these same restoration techniques in this microhabitat. In two years, natural regeneration was largely limited to ‘a‘ali‘i (*Dodonea viscosa*) and koa, and was enhanced by the application of herbicide followed by the removal of the grass biomass. Outplanting survivorship was high in most species, exceeding 80% after two years in five of seven species. Treatment application had little effect on survivorship, but the growth rates in four of the seven species planted was greatest in plots where herbicide was applied prior to planting. Seed broadcast was not found to be an effective treatment of producing seedlings. Based on our results, we recommend non-native grass biomass removal combined

with outplanting as the primary method of forest restoration in Nakula NAR and the surrounding region.

INTRODUCTION

Historical Background

Since the first human contact, many of Hawaiʻi's ecosystems have been altered and have shifted from primarily forested habitats to agricultural and rangeland (Kirch 1982, Gon et al. 2006). Early Hawaiians significantly reduced low elevation forests for agriculture and human habitation (Kirch 1982). Later, European explorers and settlers introduced several ungulate species including goats (*Capra hircus*), pigs (*Sus scrufa*), and cattle (*Bos taurus*) (Rickman 1785, Vancouver 1798, Cox 1992). Hawaiʻi had no native large terrestrial mammals and the feral populations of these introduced animals were extremely detrimental to the native ecosystems that evolved in isolation from mammalian herbivores.

The dire state of the native Hawaiian forests was evident by the late 19th and early 20th centuries prompting early conservation efforts by the Hawaiian royalty and others (Raymond 1906, Cox 1992, Woodcock 2003). However, during this time people intentionally and unintentionally introduced a host of non-native plant and animal species that would further alter or supplant native forests (Cox 1992, Conry 2010). The legacy of disturbance and introductions is evident today, where native vegetation occurs on less than half of the land area of the State (Gon et al. 2006, Conry 2010). Native forests persisted on high elevation mountain slopes away from human habitation. However, even when not completely converted, these native forests still experience constant invasion and settlement of non-native species, including incursions by ungulates.

Some early efforts were made to control ungulates including the reversal of a kapu (i.e. forbidden by royalty) on killing cows in 1830 and direct trapping and hunting to reduce cattle numbers. However, in much of Hawaiʻi the rapid loss of native forest continued largely unabated until the early- to mid-20th century when some of the first conservation measures were put in place to specifically control and reduce ungulate populations in native habitats. In 1901, J. H. Raymond (1906), a forester with the Department of Agriculture and Forestry for the territorial government, commented on the destruction of the Kahikinui forests on Maui by feral cattle and erected the first barbwire fences across much of the slope to begin controlling the cows. Raymond was able to reduce the number of cows in the area and saw regrowth of native trees in areas where cattle were excluded. What he described over a century ago are essentially the same measures being implemented across the State to protect the remaining forests – it is clear that the forests can only truly begin to recover once ungulates have been removed or at least severely limited. Whether this forest habitat can return to a condition similar to what it was prior to ungulate disturbance or even a functional ecosystem is unknown. The future of this forest following ungulate removal depends on a variety of factors including how removed the current condition is from historic conditions and the level of management applied to control continuing threats, such as weeds.

On Maui, the vast majority of remaining native forest is montane wet forest on windward (north- and east-facing slopes) East Maui and the upper elevations of West Maui (Gon et al. 2006, LANDFIRE 2008). These forests are dominated by a canopy of ʻōhiʻa (*Metrosideros polymorpha*) and represent the majority of native forest bird habitat on the island today. The upper elevation leeward (south- and west-facing slopes) forests of Maui are montane mesic forest dominated by koa (*Acacia koa*), ʻōhiʻa, and a variety of other tree species. The warm and comparatively dry conditions made the leeward slopes of Haleakalā attractive as agricultural and, later, grazing lands (Kirch 2014). As a result, less than 10% of native mesic forest exists on leeward Maui today (LANDFIRE 2008) and much of it is still threatened by feral ungulates. The largest tract of remaining montane mesic forest on Maui is in the Kahikinui and Nuʻu regions and extends ~ 12 km from the Kaupō Gap in the east to an area on Department of Hawaiian Home Lands (DHHL) property in the west (Figure 1). Due in large part to the remoteness of the area and a steep elevational moisture gradient, most of this remaining native vegetation exists above 1200 m in elevation (Loope and Giambelluca 1998). Commercial grazing of cattle and sheep has historically been limited to areas below this elevation.

The majority of the remaining, leeward montane mesic forest is managed by DHHL, the State of Hawaiʻi Department of Land and Natural Resources (DLNR), Haleakalā National Park (NP) and Haleakalā Ranch (Figure 1). This habitat exists in a degraded state, with intact native forest patches persisting in a mixture of savanna, open grassland, and even bare soil and rock where the topsoil has eroded away due to ungulate trails and heavy grazing. In many tropical area around the world "savanna" habitat, a matrix of woodland and grassland consisting of widely scattered shrubs and trees, are maintained by disturbance by large mammals. In some areas of Nakula, primarily flat areas, ungulates appear to have removed nearly all native woody plants leaving an open grassland of mostly non-native grass species. In other areas, the ungulate damage was less severe and limited enough to maintain a savanna-like habitat. The animals severely limted germination by consuming most tree seedlings leaving large adult trees and grasses underneath. In deep gulches where plants were more difficult to reach, ungulate damage to the environment was very limited leaving intact patches of dense forest. The quality of these forest patches varies throughout the region due in large part to topography and the degree to which ungulates could access plants.

The conditions of this forest prior to Polynesian or European contact are largely unknown. The pre-human Kahikinui forest may have been closed canopy similar to extant forests like those in Kaupō or Manawainui, or the forest may have been naturally more open and unlike any existing native forests on Maui. Soil analysis indicates that the area largely contains andisols rather than mollisols, which suggests the area was not historically dominated by grassland (HDOH 2012). In 2011, approximately 10% of Nakula Natural Area Reserve (NAR) below 2100 m in elevation, the approximate tree line on the windward slopes, had tree canopy cover (Burnett 2015), predominately native trees. The remaining forest on leeward Haleakalā is disjunct from other forest habitats (Figure 1). The forest on DHHL is separated from Kula Forest Reserve (FR), which is primarily a non-native forest, across a gap of approximately 4 km of grassland and native shrubland. The forest on the eastern edge of the leeward forest band is separated from other native forest in the Kaupō Gap by nearly 8 km of talus and native shrubland. Although connected by native shrubland, the lack of contiguous forest likely limits the immigration of native birds into the leeward forests.

The current ranges of the six extant native Hawaiian finches (i.e., Hawaiian "honeycreepers") on Maui are largely influenced by the distribution of appropriate habitat and extent of invasive avian diseases. The two endangered species, Kiwikiu (Maui Parrotbill, *Pseudonestor xanthophrys*) and ʻĀkohekohe (*Palmeria dolei*), are restricted to the last remaining large, contiguous native forest on windward East Maui (Simon et al. 1997, Berlin and Vangelder 1999). The other four honeycreeper species, ʻApapane (*Himatione sanginea*), Hawaiʻi ʻAmakihi (*Chlorodrepanis virens*), ʻIʻiwi (*Drepanis coccinea*), and Maui ʻAlauahio (*Paroreomyza montana*), are found in their highest densities in this same native forest but also persist in forests with varying densities of non-native tree species (Motyka 2016, Judge et al. 2018). In addition to being habitat restricted, most of these species are limited to high elevation (> 1500 m) forests where avian malaria (*Plasmodium relictum*) and avian pox (*Avipox*) (Warner 1968, LaPointe 2007) and their non-native mosquito (*Culex quinquefasciatus*) vectors are limited by cool temperatures (van Riper et al. 1986, 2002, Atkinson and LaPointe 2009). Two species, ʻApapane and Hawaiʻi ʻAmakihi, are exhibiting disease resistance and are recolonizing low-elevation portions of their former ranges (Foster et al. 2007, Hobbelen et al. 2012). Unless the other species show similar signs of disease resistance, their ranges will remain restricted to the upper elevation forests of Haleakalā until the application of emerging technologies to control these diseases on the large scale. Fortunately, much of the upper elevation forests of windward Haleakalā are fenced and afforded the highest levels of protection offered by The Nature Conservancy (TNC), the State of Hawaiʻi and the US National Park Service. A host of non-native passerines are sympatric with the native finches throughout their ranges. Three non-native passerines, Japanese White-eye (*Zosterops japonicus*), Red-billed Leiothrix (*Leiothrix lutea*), and Japanese Bush Warbler (*Horornis diphone*), are particularly well established and common within the forests inhabited by the native honeycreepers.

Despite the lack of ungulates and the high quality habitat in these windward forests, the long-term persistence of the native forest bird species is still threatened by non-native mammalian predators (i.e., cats, mongooses, and rats) and disease. In addition, fungal pathogens in the genus *Ceratocystis* threaten the long-term health and integrity of the ʻōhiʻa-dominated communities that comprise the majority of windward forest bird habitat (Barnes et al. 2018). Fortunately, these fungal pathogens have not yet been found on Maui but there is a high risk that these diseases will reach the island. Frequent heavy rains may also make high elevation wet forests suboptimal for species like Kiwikiu, which often experience nest failures following these weather events (Becker et al. 2010, Mounce et al. 2013, Simon et al. 2000). Additionally, climate change is predicted to warm Hawaiʻi's climate, increasing the frequency and intensity of damaging storms and allowing diseases and disease vectors to move up in elevation, further eroding suitable habitat for the birds (Atkinson and LaPointe 2009, Fortini et al. 2015). The need for more high-elevation habitat for native forest birds has prompted large-scale forest restoration efforts particularly along the southern slope of Haleakalā. Whether these birds can be protected from extinction may depend on maximizing suitable habitat in all available high-elevation areas such as those in Kahikinui.

The Kahikinui region was once a diverse ecological area and still contains many rare and endangered taxa. Several rare plant species are found in the area, many of which are endemic to the Kahikinui (DOFAW 2015). Subfossil evidence indicates that the region once supported a wide variety of bird species including Kiwikiu and ʻĀkohekohe (James and Olson 1991). ʻIʻiwi are abundant in the windward native forests and the leeward non-native forest in Kula Forest Reserve (FR). However, this species has not been documented in the Kahikinui region in the past 30 years although sub-fossils indicate they were once found in the region (James and Olson 1991). Whether Maui ʻAlauahio still exist in Kahikinui is equivocal and the lack of observations in the past 30 years suggests the species is no longer present. Nearby populations of ʻIʻiwi and Maui ʻAlauahio in Kula FR allow the possibility that these species may recolonize Kahikinui as habitat conditions improve.

Management History

For over a century, surveyors, foresters, and land managers commented on the need to curb the destruction of the Kahikinui forest by feral ungulates (e.g., Raymond 1906, DOFAW 2015). Efforts to control and contain large cattle herds began in 1901 (Raymond 1906) but had little lasting effect. In 1928, the Hawaiʻi Territorial Government Division of Agriculture and Forestry created Kahikinui FR totaling 6480 ha and much of the reserve above 1200 m was fenced to exclude feral cattle and protect the remaining leeward forest (Figure 1). In 1983, the State of Hawaiʻi DLNR Division of Forestry and Wildlife (DOFAW) added new fences along the lower edge of Kahikinui FR and made a concerted effort to drive the feral cattle out of the area (Scott et al. 1986). It is unclear how successful these exclusion efforts were, but animals either recolonized or remained in the area and cattle were still present in large numbers in the early 2000s. In 1984, Kahikinui FR was reduced in size when the State of Hawaiʻi placed 3540 ha of the original FR under the management of DHHL.

Although the destructive capacity of goats in this region began to receive heightened attention in the 1980s, their populations were largely unchecked throughout the 20th century and reached exceptionally high densities in the 2000s (Medeiros et al. 1986, Scott et al. 1986). The fences originally erected to control cattle did not exclude goats or pigs. In 1980 while doing forest bird surveys, Scott et al. (1986) noted large herds of goats in the reserve, resulting in a denuded landscape, and these authors again emphasized the need for habitat protection. During the 1980s and 1990s, Kahikinui FR was largely managed as a hunting unit to maintain pressure on feral ungulates, however, the remoteness of the site limited the number of hunters. In 1994, the DHHL rescinded a public access agreement with DLNR that provided the only available route for public hunters to access the reserve and effectively stopped all hunting pressure on ungulates (DOFAW 2015). It was not until 2007 when DOFAW completed an ungulate-proof fence (capable of excluding cattle, goats, pigs, and possibly deer) enclosing ~1100 ha of Kahikinui FR (mostly above 1500 m in elevation) followed by removal efforts that effective ungulate reduction could begin.

The State of Hawaiʻi established the Nakula NAR on the leeward slope of Haleakalā Volcano in 2011 (DOFAW 2010, State of Hawaiʻi 2011). The Natural Area Reserve System was created to protect and preserve native ecosystems and is managed by DOFAW Native Ecosystem Protection and Management (NEPM). The newly created 614 ha reserve, formerly a portion of Kahikinui FR, was designed to protect some of the best remaining montane mesic forest on Maui. Nakula is situated in the center of leeward Haleakalā, between DHHL property to the west and Kahikinui FR to the east (Figure 1). To protect the Nakula NAR forest from further damage, the first goal for NEPM was to install ungulate-proof fencing and remove all feral ungulates. The western and southern boundaries had been fenced in 2005-2007 when the NAR was still part of Kahikinui FR. The first fully enclosed and ungulate-free section of Nakula NAR was completed in November 2012 following the construction of an interior fence section. This 170 ha parcel, dubbed the Wailaulau unit (1050 m – 1925 m in elevation), contained the majority of the intact forest patches in the reserve (Figure 1). However, as is the case throughout much of the reserve, the majority of the habitat within this unit is best classified as remnant forest, savanna, and open grassland (Figure 2). To reverse the decline in native plant species in the reserve NEPM and Maui Forest Bird Recovery Project (MFBRP) began large-scale outplanting efforts in the fall of 2013, shortly after the eradication of ungulates from the unit, and these efforts continue through the present. As of October 2018, MFBRP had planted > 63,000 seedlings in the Wailaulau unit.

In the same time, NEPM planted more than 100,000 seedlings in the Wailaulau and West Pahihi units.

To the east of Nakula, the DOFAW Forestry Section also conducted large-scale outplantings in Kahikinui FR, planting > 50,000 seedlings in the fenced area above 1500 m as of January 2018. National Park Service staff are planning restoration work in the Nuʻu Unit of Haleakalā NP, to the east of Kahikinui FR (Figure 1). Farther to the east, Leeward Haleakala Watershed Restoration Partnership (LHWRP) is conducting restoration efforts on private ranchland in Nuʻu. On the other side of Nakula to the west, LHWRP is in the process of fencing a large section of DHHL property and ungulates are being removed from this area. The LHWRP and NEPM have also implemented control and removal efforts of invasive plant species. Of particular concern are Tree poppy (*Bocconia frutescens*), Silk Oak (*Grevillea robusta*), and Australian Tree Fern (*Cyathea cooperii*), all of which are listed as target weeds in the Nakula NAR Management Plan (DOFAW 2015). Together these efforts will help restore the native forests across the southern slope of Haleakalā.

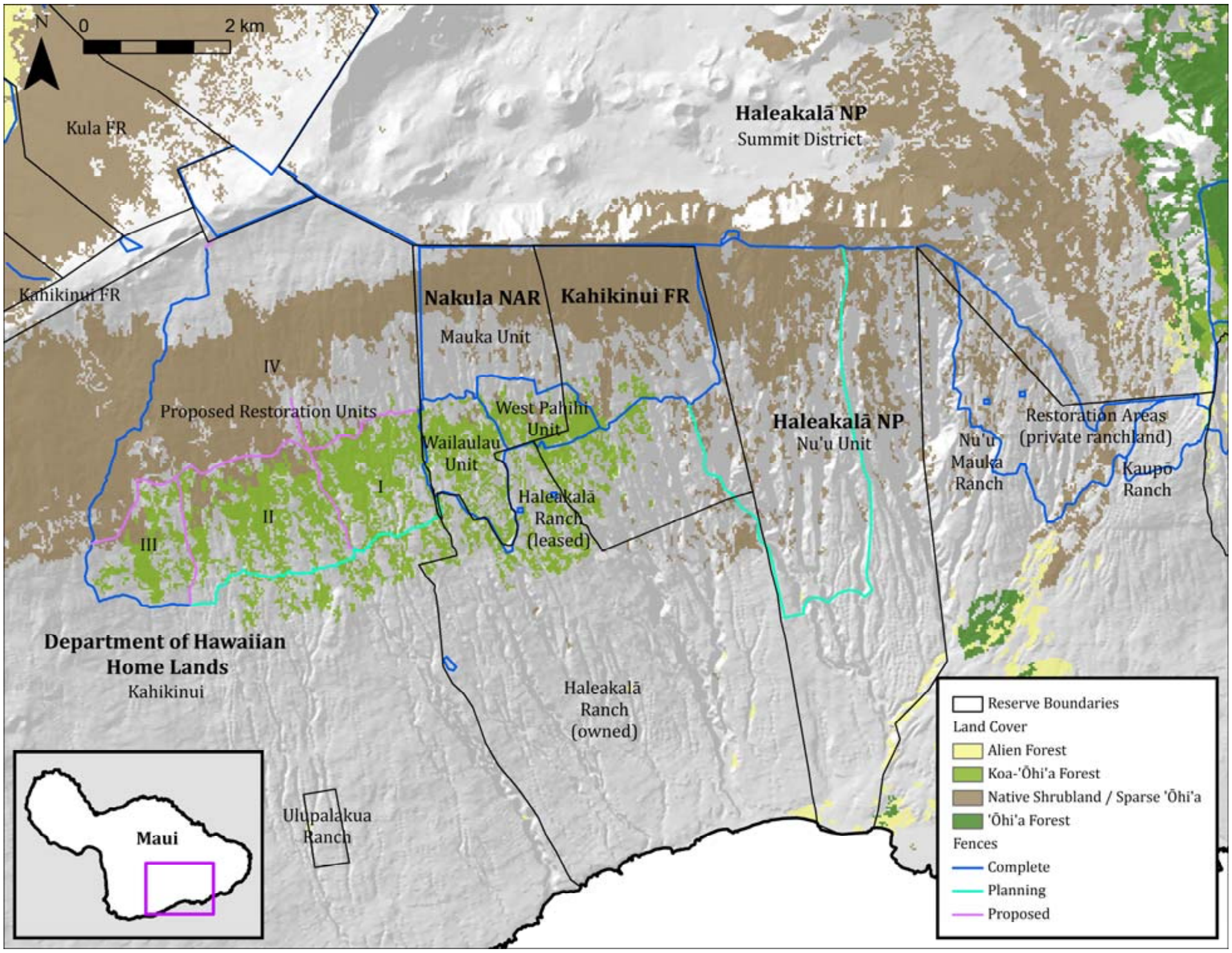

Figure 1. Land management units on leeward Haleakalā Volcano in east Maui showing the extent of native and alien forest types and native shrubland (USGS GAP 2011 [based on 2001 imagery]) and current and future fenced restoration areas (as of Feb. 2018).

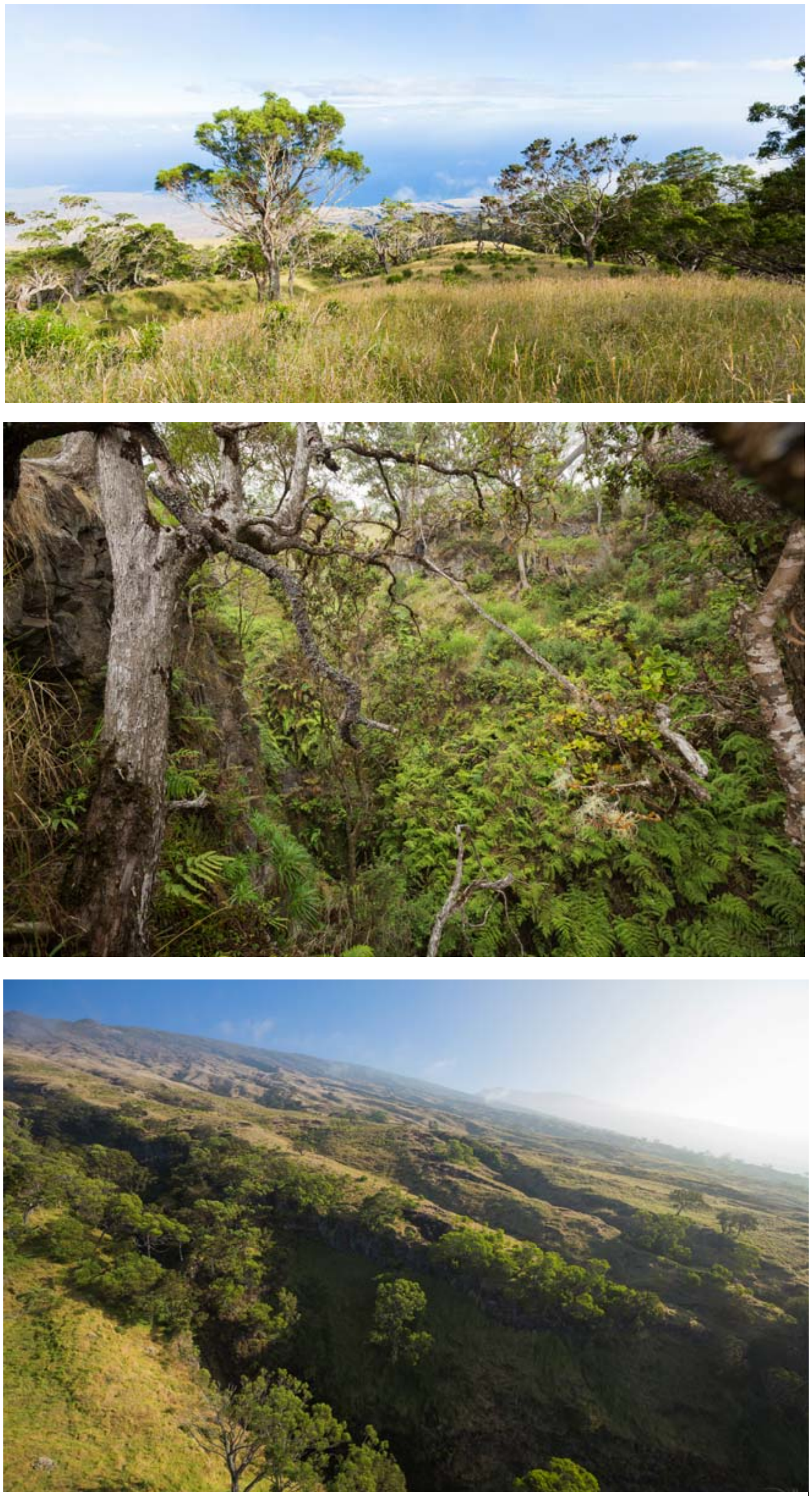

Figure 2. Photos demonstrating general habitat characteristics of the Wailaulau unit of Nakula NAR showing open grassland and savanna (top) to intact forest patches (middle). The lower photo is an aerial shot from Wailaulau facing east showing sparse canopy cover.

Kiwikiu Reintroduction

The Kiwikiu is a small (20-26.5 g), insectivorous passerine endemic to the islands of Maui and Molokaʻi but exists today in a small population in the native, montane forests of windward Haleakalā, Maui (Figure 3). The species was listed as federally endangered in 1967 and is threatened by several factors including habitat loss and introduced disease (USFWS 1967, 2006). Similar to most Hawaiian finches, the Kiwikiu is thought to be highly susceptible to avian malaria (*Plasmodium relictum*) and are now only found at high elevations (> 1200 m) where mosquitoes and the parasite are limited (Warner 1968, LaPointe 2007) (Figure 3). Based on subfossil evidence, Kiwikiu were likely found throughout the island of Maui, including low-elevation and leeward forests (James and Olson 1991). Early naturalists collected specimens in mesic, koa-dominated forests and noted their affinity for koa as a foraging substrate (Henshaw 1902, Perkins 1903). Today, Kiwikiu are restricted to the only large, contiguous native forest remaining on Maui, primarily wet ʻōhiʻa forest, which may be sub-optimal habitat (Becker et al. 2010, Stein 2007).

Kiwikiu exhibit life-history traits associated with long-lived species including single-offspring broods, which restrict the species' capacity for population growth and, combined with anthropogenic habitat changes, puts the species in danger of extinction (Simon et al. 1997, Mounce et al. 2013, 2014, 2015). In addition, pairs occupy large home ranges (12-14 ha) (Warren et al. 2015) comprised primarily of native forest, likely due to resource availability and their specialized foraging niche (Stein 2007) and live in low-densities compared to other sympatric, related species (Scott et al. 1986, Camp et al. 2009, Brinck et al. 2012, Judge et al. 2018). Total abundance has been estimated at 500-600 individuals (502 ± 116 [SE] from Scott et al. 1986, 590 ± 208 from Camp et al. 2009) although new evidence suggests that there may now be fewer than 312 (44-312 95% CI, mean = 147) in the wild (Judge et al. 2018). Infrequent surveys, low-densities, and the species' cryptic nature have limited the assessment of long-term abundance trends (Camp et al. 2009, Judge et al. 2018). From 2006-2011 and 2012-2014, MFBRP maintained marked populations of Kiwikiu in Hanawi NAR and TNC Waikamoi Preserve, respectively, and conducted annual productivity surveys (Mounce et al. 2013, Figure 3). As well as collecting other critical demographic data, MFBRP observed high annual adult survival but comparatively low juvenile survival (Mounce et al. 2014). Stein (2007) provided a detailed assessment on habitat preference at multiple spatial scales. The greatest threat to the long-term persistence of the species is thought to be the loss of suitable habitat due to increasing temperatures that allow mosquito-borne diseases to move higher into native forest (USFWS 2006, Fortini et al. 2015). Additionally, stochastic events, such as hurricanes, are a constant threat to the species' long-term survival, particularly given that the entire species range is on the windward slopes of the island where storms are most severe. Due to these threats, the USFWS recovery plan for the species calls for the establishment of a second population of Kiwikiu (USFWS 2006).

Nakula NAR was selected as the site to begin the process of establishing a second population of Kiwikiu. The Wailaulau unit of Nakula, where the reintroduction will take place, supports some of the best remaining high-elevation native forest outside their current range. The historic presence of the species and the abundance of koa, an important foraging substrate, make Nakula a prime location to attempt to establish a new population. In addition, the continuing restoration work at Nakula and the surrounding area will result in an increase of high quality habitat.

Kiwikiu forage using their bill to extract insect larvae from stems and fruits of several native trees and shrubs (Mountainspring 1987, Simon et al. 1997, Stein 2007). This specialized foraging style and the seasonality of some foods means that the species depends on a wide variety of woody plant species. Stein (2007) found a number of important habitat attributes corresponded with Kiwikiu habitat use, specifically highlighting the importance of greater diversity and canopy cover to Kiwikiu habitat selection. Despite the relative abundance of some important tree species (e.g., koa), others are rare (e.g. ‘alani [*Melicope* spp.]) or have been extirpated from Nakula (e.g., kanawao [*Broussasia arguta*]). As such, increased canopy tree cover alone may be insufficient to ensure a successful Kiwikiu reintroduction without the restoration of understory cover as well. In preparation for the reintroduction of Kiwikiu to Nakula, NEPM and MFBRP have been planting a host of native species, including those favored by Kiwikiu, as well as conducting other restoration techniques to improve the habitat for the species (Table 1). Additional outplantings of important Kiwikiu foraging tree and shrub species will likely be needed to increase the likelihood of the long-term success of Kiwikiu in Nakula.

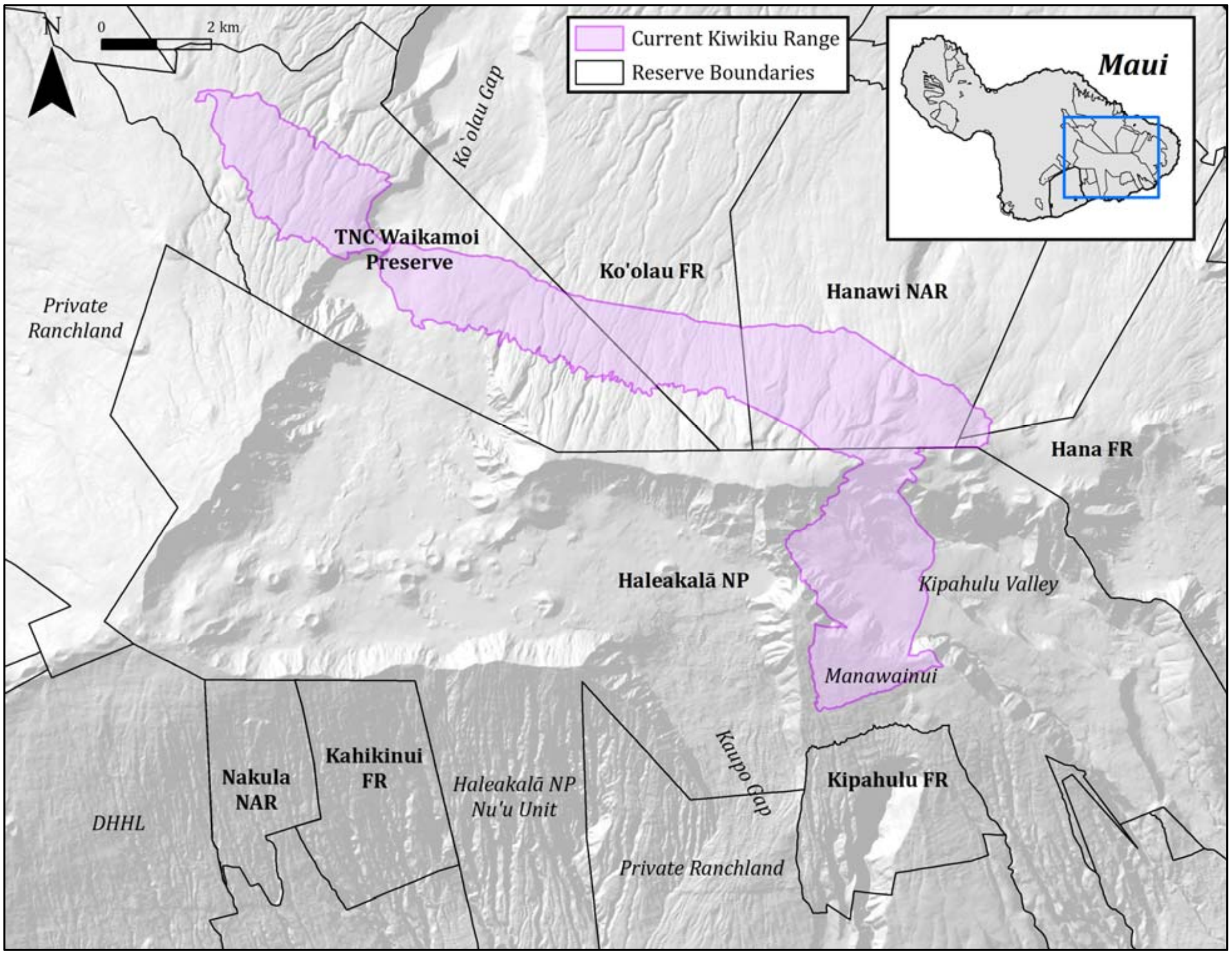

Figure 3. Current Kiwikiu (Maui Parrotbill, *Pseudonestor xanthophrys*) range in relation to management units and important topographic features.

Study Site

The 6.7 km^2 Nakula NAR is situated on the south-facing slope of Haleakalā Volcano on Maui Island. We maintained an Onset weather station in the center of the experimental area (1550 m) and recorded rainfall and temperature throughout the experimental period, March 2013 to January 2016. Based on these weather data, the Wailaulau unit of Nakula received an average 6.96 ± 5.35 cm (SD) of rain per month during the experimental period. Rainfall in this region during this period was greatest between August and March. However, occasional storms produced more than 6 cm in a single day. These storm events were not common (only 19 days recorded > 2 cm of rainfall during the experimental period) but these events contributed quite a bit to the overall rainfall throughout the year. These rainstorm events occurred most frequently in March, August, and October. Some of these storms brought high winds in excess of 80 km/hr, although these were rare. A steep moisture gradient follows elevation along this slope (Loope and Giambelluca 1998) and much of the precipitation that occurs is in the form of dew and fog (Giambelluca *pers. comm.*).

Average daily temperature was 14.7˚C (58.5˚F) in Wailaulau during the experimental period. The study site saw little seasonal changes with respect to temperature with monthly average temperatures ranging from 12.7˚C (54.9˚F) in March (the coldest month) to 16.56˚C (61.8˚F) in August (the warmest month). We recorded a minimum of 6.03˚C (42.85˚F) during the experimental period and a maximum of 23.71˚C (74.68˚F) per 30-min period. Frost was not observed during this time.

The National Conservation Service soils maps classify the experimental area as “very stony land”. The topsoil in much of the experimental area appeared to be generally nutrient-rich and > 1 m deep with the exception of some rocky areas and erosion areas where topsoil has been lost leaving dry cinder. Experimental plots were not placed in erosion areas.

In 2011, land cover within the Wailaulau unit was classified as 16.5% tree canopy, 51.7% grass, and 31.8% bare ground (exposed rock and soil) (Burnett 2015). Canopy cover was almost exclusively native trees with koa and ‘ōhi’a representing the majority. The grass cover was a mixture of mostly non-native pasture grasses, the most common being *Cenchrus clandestinus* (kikuyu grass), *Holcus lanatus* (velvet grass), and *Anthoxanthum odoratum* (sweet vernal grass). Very little is known about this forest prior to the introduction of ungulates and the damage they caused. The first territorial forester records for the region spoke of a damaged and degraded landscape with high densities of ungulates. However, it is likely that without ungulates and non-native grasses, the area would have been primarily forested with an understory and ground cover of native ferns, sedges, shrubs, and native grass (Table 1).

Experimental Restoration Trials

The positive impacts of removing ungulate pressure on native Hawaiian forest has long been established (Loope and Scowcroft 1985). Successful restoration efforts in Hawai‘i following ungulate exclusion were important guides to developing strategies to restore the forest of Nakula to a functional, diverse forest habitat (e.g. Scowcroft and Nelson 1976, Scowcroft and Hobdy 1987, Medeiros et al. 2014). Some successful techniques used elsewhere, such as soil disruption with bulldozers to promote koa regrowth as in Hakalau National Wildlife Refuge (NWR) on Hawaiʻi Island (Scowcroft and Nelson 1976), would not be possible in remote Nakula. Other sites, like those being restored by the Auwahi Forest Restoration Project a few miles to the southwest of Nakula, struggle with shallow, rocky soils, less precipitation, and a much more degraded environment than Nakula (Medeiros et al. 2014). These differences warranted local studies to determine the most effective means of restoring the Nakula forest with specific attention to the needs of Kiwikiu.

Table 1. Anecdotal relative abundance of Kiwikiu food plants, important canopy or midstory species in Nakula as of 2016, and the observed regeneration rate in the first three years following fencing based on areas where restoration activities are occurring. C = Common, UC = Uncommon, EX = Extirpated. Local = observed rarely, near mother plants. Slow = observed in low densities in several locations throughout the site. Steady = regularly observed throughout the site in low densities and/or with slow growth rates. Rapid = commonly observed throughout the site in multiple habitat types.

Common name	Scientific name	Kiwikiu food plant	Relative abundance	Regeneration (observed)
ʻaʻaliʻi	*Dodonaea viscosa*	No	C	Rapid
ʻākala ǂ	*Rubus hawaiensis*	Yes	UC	Slow
ʻalani ǂ	*Melicope* spp.	Yes	UC	Not observed
hoi kuahiwi	*Smilax melastomifolia*	Yes	UC	Slow
kanawao ǂ	*Broussaisia arguta*	Yes	EX	NA
kāwaʻū ǂ	*Ilex anomala*	Yes	C	Local
koa ǂ	*Acacia koa*	Yes	C	Rapid*
kōlea	*Myrsine lessertiana*	Yes	C	Local
māmaki	*Pipturus albidus*	No	UC	Slow
māmane	*Sophora chrysophylla*	No	UC	Slow
ʻōhelo	*Vaccinium calycinum*	Yes	UC	Steady
ʻōhiʻa	*Metrosideros polymorpha*	Yes	C	Steady
ʻōlapa ǂ	*Cheirodendron trigynum*	Yes	UC	Local
pilo	*Coprosma* spp.	Yes	C	Steady
pūkiawe	*Leptecophylla tameiameiae*	Yes	UC	Rapid

** - Regeneration of root shoots commonly observed, individuals sprouting from seeds were rare and would be classified as "slow".*

ǂ - Stein (2007) and/or Mountainspring (1987) showed preferential use of these species by Kiwikiu for foraging or strong affiliation with the presence of these species and Kiwikiu home ranges.

We designed experimental trials to examine natural seedling recruitment and survival of outplanted seedlings under a number of conditions. These trials were meant to inform managers of the efficacy of common restoration practices that may be used to restore the forest in Nakula and the surrounding area. The Nakula NAR Management Plan states that the main goal is to "return the degraded/lost past vegetation communities" and increase canopy cover and diversity (DOAFW 2015). No specific goals have been made by NEPM or MFBRP as far as densities or diversity of native woody plant species to achieve toward restoring Nakula. The majority of the species planted to date have largely been determined by availability of seeds (e.g. species still common in Nakula) and much of the focus has been on planting in grass-dominated areas.

With such a long history of ungulate damage and suppression of natural recruitment, determining the status of the native seed bank was a priority. Germination is thought to be suppressed by competition with the invasive kikuyu (*C. clandestinus*) and other non-native grasses that are common in the reserve (Denslow et al. 2006). At the outset of these trials, some limited natural regeneration was observed. However, the rarity of the regeneration of some species important to Kiwikiu (Mountainspring 1987, Stein 2007) indicated that nursery-supported outplanting would be necessary for the successful restoration of a forest capable of supporting a self-sustaining Kiwikiu population. Thus, we developed these trials to document natural regeneration following ungulate exclusion as well as to compare treatments to enhance natural regeneration and promote the growth of native, woody plant species from collected seeds and nursery stock. We broadcasted seeds and planted seedlings of eleven species in trial plots to investigate their survival and growth-rates. These species were selected based on the foraging preferences of Kiwikiu and to include common species that make up portions of the canopy, subcanopy, and shrub layers (Table 1). We established trial plots in open/savanna habitat as well as under adult koa trees to investigate natural regeneration and outplanting success in these different habitat types. Under existing tree canopy, seedlings may experience lower light intensity and have access to increased soil nutrient content and water; conditions that may be critical to the survival of certain species (Gómez-Aparicio et al. 2004, Padilla and Pugnaire 2006, Yelenik et al. 2015). We applied multiple treatments to trial plots to reduce grass cover that have been shown to increase survivorship of native seedlings elsewhere in Hawaiʻi (Cabin et al. 2000, 2002, McDaniel et al. 2011, Thaxton et al. 2012) to investigate what level of grass removal or suppression would be necessary to promote natural recruitment and what techniques would promote germination of broadcasted seeds and ensure high survival of seedlings (Hess et al. 1999, McDaniel et al. 2011, Scowcroft 2013, Medeiros et al. 2014).

METHODS

Our experimental trials were focused on the open grass-dominated savanna habitat. To meet the objectives of these trials we established 83 plots divided into four experimental factor groups. Plots were divided into natural regeneration (n = 24), outplanting (n = 27), seed broadcast (n = 16), and tree canopy (n = 16) groups (or factors). The natural regeneration plots were designed to estimate natural recruitment of woody plants after ungulate removal. The outplanting and seed broadcast plots were designed to estimate germination and survival rates of collected seeds and nursery-grown seedlings. The tree canopy plots were designed to estimate natural regeneration and the survival of outplanted seedlings under existing tree canopies. Each of these factors represented different levels of intervention and effort that may be required to restore the forest.

Plot Placement

Plot locations were selected in July 2012. All plots were placed in areas representative of the open, grass-dominated areas that characterized the majority of the Wailaulau unit. We selected sites for plot placement to minimize variation in slope (relatively flat) and elevation. Plots were placed a minimum of 10 m from another plot within the same treatment group and all plots were within an 18.5 ha area at between 1500–1650 m within the Wailaulau unit of Nakula NAR (Figure 4).

We established 24 plots to document natural regeneration. While we placed all plots, besides those in the tree canopy group, in areas with ~ 0% canopy cover, natural regeneration plots were placed at 10 m or 30 m from the crown of living koa trees to test the effect of distance from canopy trees on the recruitment of woody species. We established 27 outplanting and 16 seed broadcast plots haphazardly throughout the site. Specific distance from existing canopy trees was not considered for outplanting or seed broadcast plots, provided they had ~ 0% canopy cover.

The mature koa selected for tree canopy plots (n = 10) were largely isolated trees with few neighbors and little to no canopy continuity with other trees. Trees were selected across the entire trial area > 25 m apart to account for site variation and reduce genetic bias due to the clonal nature of koa. The boundaries of these plots were defined by the dripline of the crown of the selected trees. Dripline is defined as the outermost circumference of the tree canopy where water drips from and onto the ground. Only trees with an average crown radius (average of four radii) of < 15 m (trunk to dripline) were selected for plot placement.

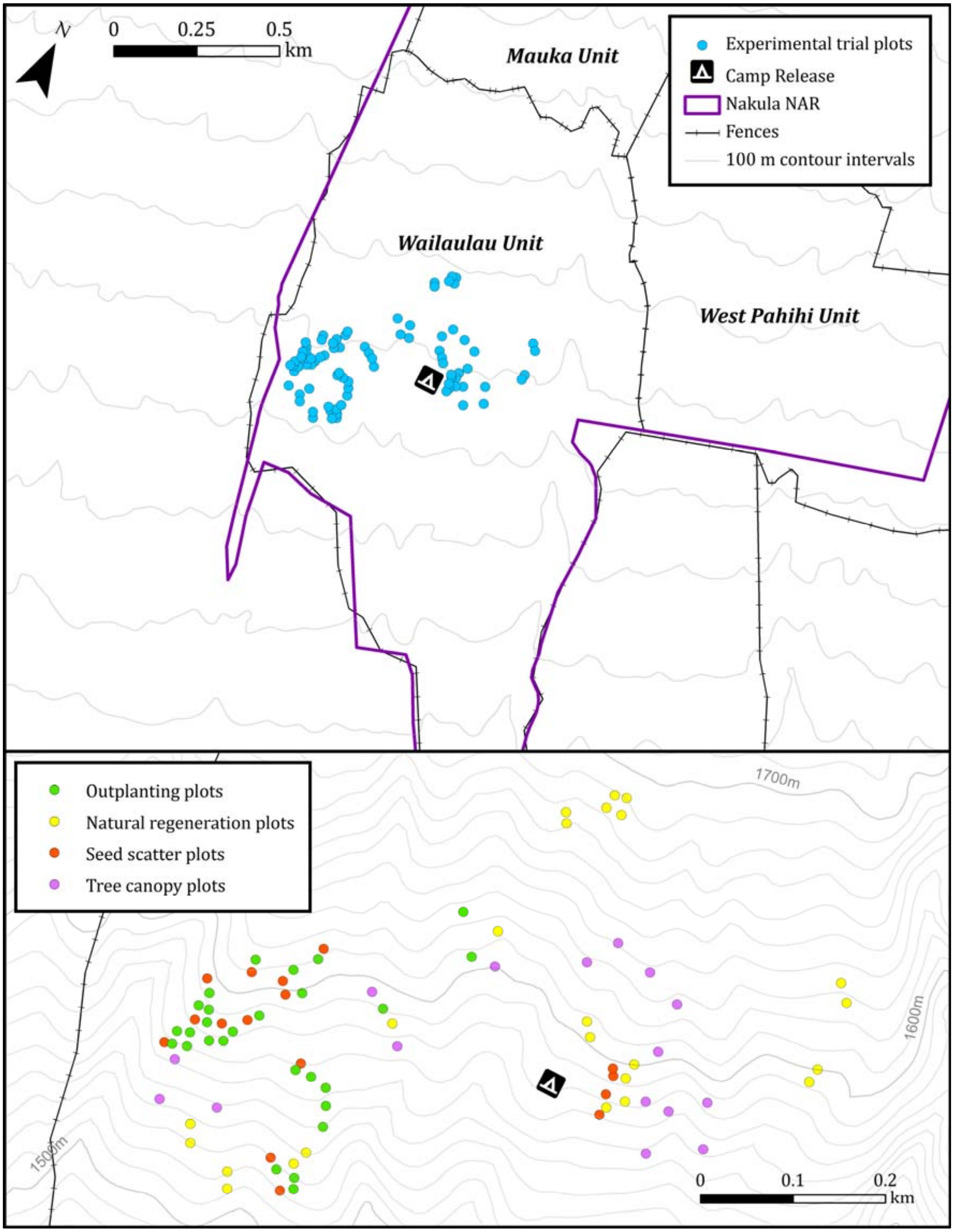

Figure 4. upper) Study site within Nakula NAR showing the Mauka, West Pahihi and Wailaulau units. lower) Experimental restoration trial plot locations within the Wailaulau unit.

Experimental Treatment Plots

Experimental plots were further subdivided into two or three treatments per factor group: herbicide application (henceforth herbicide), herbicide application in combination with biomass removal (henceforth herbicide & removal), grass biomass disruption (henceforth disruption), and control plots (Figure 5). These treatments have been applied elsewhere or were adapted from other studies examining natural regeneration and/or outplanting success. The treatments all involved the reduction or removal of non-native grasses thought to restrict germination and survival of woody seedlings (Denslow et al. 2006).

In control plots, we did not reduce grass cover following plot establishment. Plots in the herbicide and herbicide & removal treatment groups were sprayed with a mixture of glyphosate (Honcho Plus, Monsanto Co.) and imazapyr (Polaris AC, Nufarm Americas Inc.) applied at a rate of 2.24 kg of active ingredient per hectare (kg ha a.e.) and 0.56 kg ha a.e., respectively, to the entirety of each plot as per label instructions. After a minimum of 90 days following herbicide application, we removed all plant biomass (primarily necrotic grass material) from herbicide & removal plots using a gas-powered weed-whacker and rake until only exposed topsoil remained. In disruption plots, we removed portions of the grass mat from the plots, exposing topsoil in approximately 25-30% of each plot. To do this ~ 1-m^2 squares of the grass mat every 2 m were cut and removed from the plots using a Pulaski to create a checkerboard pattern (Figure 6). The herbicide & removal and disturbance treatments were applied to disturb grass and soil in the hope to stimulate natural regeneration of native seedlings (Scowcroft and Nelson 1976, Scowcroft 2013).

Natural Regeneration Plots

Three treatments were applied to the 24 natural regeneration plots, six plots per treatment: herbicide, herbicide & removal, and disruption (Table 2). Herbicide was applied in April 2013 to all herbicide and herbicide & removal plots. Ninety to 100% mortality of grasses was achieved within these plots by June 2013. We applied the disruption treatment to designated plots at the end of May 2013. All remaining grass and other plant biomass was removed from herbicide & removal plots in July 2013.

Table 2. Experimental design of plots per treatment.

Factor group	***N***	**Treatment**	***N***	**Treatment description**
Natural Regeneration	24	Control	6	nothing
10 × 10 m		Herbicide	6	herbicide
		Herbicide & removal	6	herbicide + weed-whacker/rake
		Disruption	6	checkerboard removal
Outplanting	27	Control	9	nothing
10 × 15 m		Herbicide	9	herbicide
		Herbicide & removal	9	herbicide + weed-whacker/rake
Seed Broadcast	16	Control	4	nothing
5 × 10 m		Herbicide	4	herbicide
		Herbicide & removal	4	herbicide + weed-whacker/rake
		Disruption	4	checkerboard removal
Tree Canopy	16	Control	4	nothing
$\bar{x}$ radius = 7.38 ± 2.4 m		Herbicide	4	herbicide
		Herbicide & removal	4	herbicide + weed-whacker/rake
		Disruption	4	weed-whacker/rake

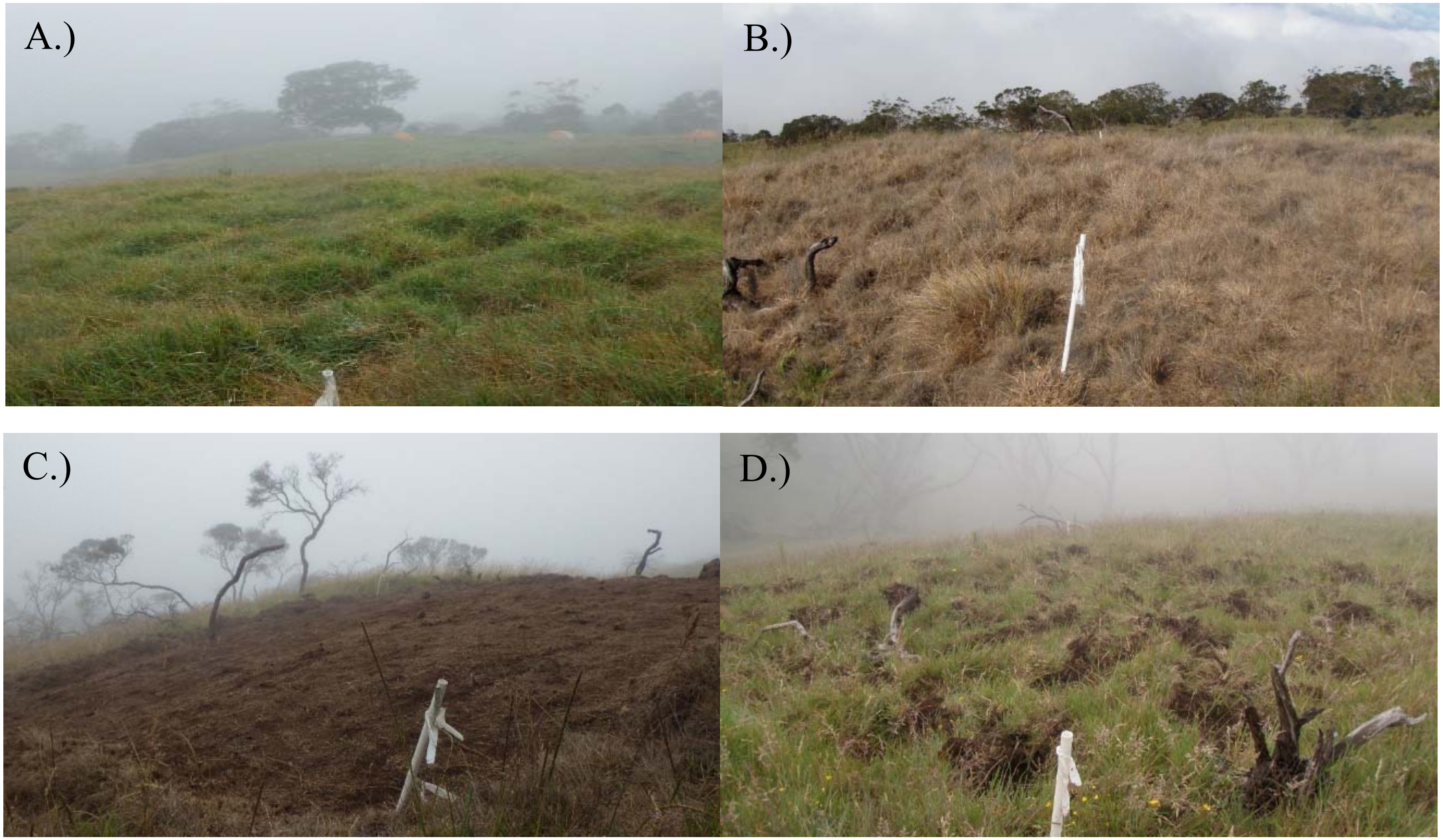

Figure 5. Examples of the four treatments applied to natural regeneration plots. A) Control, B) Herbicide, C) Herbicide & Removal, and D) Disruption

Figure 6. Close-up photo of the disturbance treatment applied to natural regeneration and seed broadcast plots.

Outplanting

Two treatments were applied to the 27 outplanting plots, nine plots per treatment: herbicide, and herbicide & removal (Table 2). The disruption treatment was not used for this group. We applied herbicide to all designated plots in May 2013. Rainfall shortly after the initial herbicide application reduced the effectiveness of the treatment and a second application of herbicide was applied to eight of the plots in July 2013 after premature grass regrowth was observed. Remaining biomass was removed from herbicide & removal plots in October – December 2013, one to three days before planting. Planting was done at least 90 days after herbicide application.

Seedlings planted in outplanting plots were grown by Native Nursery LLC. in Kula, HI from seeds sourced primarily from Nakula NAR (Table 3). Seven native woody species were selected for outplanting. These species were selected based on whether the species was known to exist or have existed in the reserve, availability of seeds, and preference was given to species that are known to provide forage habitat for Kiwikiu (Table 3). Some species that are common in leeward forests, like ‘a‘ali‘i, are not known as a foraging substrate for Kiwikiu, but this may simply be because these tree species are uncommon in windward forests. Māmaki (*Pipturus spp.*) is common in windward forests but Kiwikiu have not been observed to forage on these species. Several similar understory species are known to provide forage habitat for Kiwikiu, like kanawao (*Broussasia arguta*), but they are difficult to produce in the nursery. Like kanawao, māmaki is a small, somewhat delicate shrub that may be found under dense canopy, as well as more open, wet gulches and riparian shrubland (Wagner et al. 1999). However, māmaki is relatively easy to grow in the nursery setting. We included māmaki in these trials to serve as an understory species similar to those typically found in leeward forests to better understand the challenges in restoring species like it to Nakula.

Table 3. Plant species selected for outplanting and tree canopy plots indicating if the species is known to be used by Kiwikiu (Maui Parrotbill, MAPA) and seed source location. 'Local' indicates that seeds were collected exclusively in Nakula NAR. 'Outside' indicates that some seeds were sourced from sites other than Nakula.

Common name	Scientific name	MAPA food plant	Seed Source[1]
ʻaʻaliʻi	*Dodonaea viscosa*	No	Local
ʻākala	*Rubus hawaiensis*	Yes	Outside
koa	*Acacia koa*	Yes	Local
māmaki	*Pipturus albidus*	No	Outside
māmane	*Sophora chrysophylla*	No	Outside
ʻōhiʻa	*Metrosideros polymorpha*	Yes	Local
pilo	*Coprosma stephanocarpa/cordicarpa*	Yes	Local

[1] see text for more details about seed source.

Seeds used to grow seedlings and for the seed broadcast group were primarily sourced within Nakula NAR for four of the seven species (Table 3). We collected some pilo from windward forests, although most were locally sourced. In 2016, Cantley et al. proposed splitting the widespread pilo species *Coprosma foliosa* into three species, two of which are found in East Maui. We have yet to confirm what species are present in the outplanting group but suspect that the planted seedlings were a mix of *C. stephanocarpa* and *C. cordicarpa,* the latter being endemic to leeward East Maui. Any seedlings from seeds collected from the windward slopes were undoubtedly *C. stephanocarpa* and those collected from Nakula may be a mixture. The remaining three species (i.e., ʻākala, māmaki, and māmane) are present in Nakula but not in sufficient abundance to provide adequate seeds for this project. For these species, seeds were sourced from Nakula and additional sites in East Maui with a preference for sites close to Nakula. Māmaki and māmane were primarily sourced from Kula FR, approximately 6 km to the west of Nakula NAR (Figure 1). In addition to Nakula NAR and Kula FR, ‘ākala was sourced from TNC Waikamoi Preserve, making this the only species where we primarily collected seeds from windward forests (Figure 3).

We collected seeds from July 2012 to March 2013 for outplanting plots, and May to August 2013 for seed broadcast plots. Seeds were given to Native Nursery LLC and were sown according to species-specific protocols developed by the nursery. For species that produce fleshy fruits (i.e., māmaki, pilo, kōlea, kāwa‘ū, ‘ākala, ‘ōhelo, ‘ōlomea) the flesh was removed and seeds were dried prior to planting or seeding. Koa seeds were scarified in 100% sulfuric acid for 2 min and then soaked in water for 24-48 hrs until swollen. Māmane seeds were scarified in 100% sulfuric acid for 45 min followed by a water soak for 24-72 hrs until swollen. ‘Ōhi‘a capsules were dried until the seeds dehisced from the capsules and ‘a‘ali‘i seeds were mechanically removed from the papery capsules. Seedlings were grown for 6-12 mo in 25 cm^3 dibble tubes.

Outplanting plots were further divided evenly into three planting groups, each containing three species (Table 4). Plots were haphazardly assigned to a Species Group to reduce bias associated with plot location. Each Species Group contained at least one canopy, subcanopy, and understory species. Initially, the important Kiwikiu foraging species kōlea (*Myrsine lessertiana*) and ‘ōlapa (*Cheirodendron trigynum*) were selected as part of Species Groups 1 and 2, respectively, but these failed to germinate in sufficient numbers to be included in this study. Kōlea and ‘ōlapa were replaced with ‘a‘ali‘i and ‘ōhi‘a in Groups 1 and 2. Following treatment application, 150 seedlings of three species were planted in each plot according to the Species Group assignment.

Table 4. Experimental design of outplanting species groups and treatments. Ak = *Acacia koa* (koa), Cs = *Coprosma* spp. (pilo), Dv = *Dodonea viscosa* (ʻaʻaliʻi), Mp = *Metrosideros polymorpha* (ʻōhiʻa), Pa = *Pipturus albidus* (māmaki), Rh = *Rubus hawaiensis* (ʻākala), Sc = *Sophora chrysophylla* (māmane).

	Species Group 1				Species Group 2				Species Group 3				
	Dv	Rh	Mp	Subtotal	Ak	Mp	Cs	Subtotal	Dv	Sc	Pa	Subtotal	TOTAL
Control													
Replicate Plot 1	56	38	56	150	61	28	61	150	50	50	50	150	450
Replicate Plot 2	56	38	56	150	61	28	61	150	50	50	50	150	450
Replicate Plot 3	56	38	56	150	61	28	61	150	50	50	50	150	450
Subtotal	168	114	168	450	183	84	183	450	150	150	150	450	1350
Herbicide													
Replicate Plot 1	56	38	56	150	61	28	61	150	50	50	50	150	450
Replicate Plot 2	56	38	56	150	61	28	61	150	50	50	50	150	450
Replicate Plot 3	56	38	56	150	61	28	61	150	50	50	50	150	450
Subtotal	168	114	168	450	183	84	183	450	150	150	150	450	1350
Herbicide & removal													
Replicate Plot 1	56	38	56	150	61	28	61	150	50	50	50	150	450
Replicate Plot 2	56	38	56	150	61	28	61	150	50	50	50	150	450
Replicate Plot 3	56	38	56	150	61	28	61	150	50	50	50	150	450
Subtotal	168	114	168	450	183	84	183	450	150	150	150	450	1350
TOTAL	504	342	504	1350	549	252	549	1350	450	450	450	1350	4050

Seedlings were planted in rows at 1-m intervals with seedlings alternating by species in each plot (Figure 7). The planting arrangement was kept the same for all plots per Species Group. Holes were dug using a gas-powered auger with a 7.6-cm bit. All staff and volunteers received training prior to planting to ensure that variation in planting technique was minimized and to ensure that seedlings were planted to maximize their survival. Specific attention was given to ensuring that the roots of each plant were not exposed to air (i.e., from insufficient planting depth and/or lack of soil compression). No water was added after planting seedlings. Fifteen staff and volunteers planted all of the seedlings in outplanting and tree canopy plots.

A subset of all seedlings were enclosed within 30.5-cm BLUE-X® tree shelters. These shelters have been shown to provide increased growth rates through protection from desiccation, harmful UV radiation, and physical disturbance (e.g., Devine and Harrington 2008, McCreary et al. 2011). For most species, 20 seedlings per plot were randomly selected to be planted with a tree shelter (Figure 7). Shelter placement was randomized per species per plot. In Species Groups 1 and 2, 50% of ʻākala and ʻōhiʻa seedlings, respectively, were randomly selected to receive a tree shelter. We did this because 20 seedlings would have been > 50% of seedlings planted for these species per plot (ʻākala = 19 and ʻōhiʻa = 14). Tree shelters were placed around a seedling at the time of planting and anchored with bamboo chopsticks. Shelters were replaced or repositioned during the 6-month monitoring period as needed. All shelters were removed at 12 months due to the concern that they were increasingly becoming dislodged, constraining or otherwise harming the plants, and littering the site. As such, shelters were in place for one-half of the experimental trial period.

P07	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
A	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs
B	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp
C	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs
D	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp
E	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs
F	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp
G	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs
H	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp
I	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs	Mp	Ak	Cs	Ak	Cs
J	Ak	Cs	Ak	Cs	Cs	Ak	Cs	Ak	Cs	Ak	Ak	Cs	Ak	Cs	Mp

Figure 7. Top) An example of the planting arrangement of an outplanting plot (labelled P07). This plot was in the Species Group 2 (koa [Ak], ʻōhiʻa [Mp], and pilo [Cs]). Planting arrangement was kept constant for all plots per Species Group but tree shelter placement (shaded blue) was randomized per species per plot. Bottom) Plot P07 after treatments (herbicide) were applied and seedlings were planted. The photographer is standing at position row A, column 1 of the map at top.

Seed Broadcast

Three treatments were applied to the 16 seed broadcast plots, four plots per treatment; herbicide, herbicide & removal, and disruption (Table 2). Herbicide was applied to designated plots in May 2013. As in a small number of outplanting plots sprayed at the same time, three seed broadcast plots were re-sprayed in July 2013 due to rainfall immediately following the initial herbicide application. Necrotic biomass was removed from herbicide & removal plots and living grass was disturbed in disruption plots in January 2014. Immediately following the final treatment application at a given plot in January, a single staff member broadcasted seeds by hand evenly throughout each plot. Plots all received the same mixture of seeds containing ʻōhiʻa, ʻākala, kāwaʻū (*Ilex anomala*), ʻōlomea (*Perrottetia sandwicensis*), kōlea, koa, māmane, and ʻōhelo (*Vaccinium reticulatum/calycinum*). ʻAʻaliʻi was excluded from this mixture because of the large number of naturally regenerating seedlings near plots early in the experiment. Thus, it would have been impossible to determine if a recorded ʻaʻaliʻi seedling germinated from the existing seed bank or from broadcasted seeds. Seeds of each species were divided by weight per plot to ensure that approximately the same number of seeds were applied on each plot. The precise number of seeds per species per plot varied based on the size of the seeds. For example, approximately 20 māmane seeds were spread on each plot compared to > 100 ʻōhiʻa seeds. Seeds were sourced exclusively from Nakula NAR, with some exceptions (see above), and given to Native Nursery to scarify prior to seeding.

Tree Canopy

Three treatments were applied to the 16 tree canopy plots, four plots per treatment: herbicide, herbicide & removal, and disruption (Table 2). Herbicide was applied to plots selected for the herbicide and herbicide & removal treatments in May 2013. All biomass was removed from the herbicide & removal plots from October-December, 2013. The disruption treatment was applied differently to the tree canopy plots due to concern over harming the roots of the host koa tree if Pulaskis were used to physically disturb the grass mat within the plot. Instead, staff used weed-whackers and rakes to remove all aboveground grass in each plot. This treatment was similar to that used in the herbicide & removal treatment, except herbicide was not applied to these plots.

These plots were designed to test the effect of both natural regeneration and outplanting success under existing koa canopy. However, due to the natural variation in the area below the dripline of the selected trees, and thus plot area, plots were not assigned to either natural regeneration or outplanting (Figure 8). Instead, each plot was divided in half. Seedlings were planted in half of each plot and the other half was monitored for natural regeneration. The plots were divided in half with respect to the prevailing slope (left and right rather than up- and down-slope) to ensure that both halves contained roughly the same topography and watershed (Figure 8).

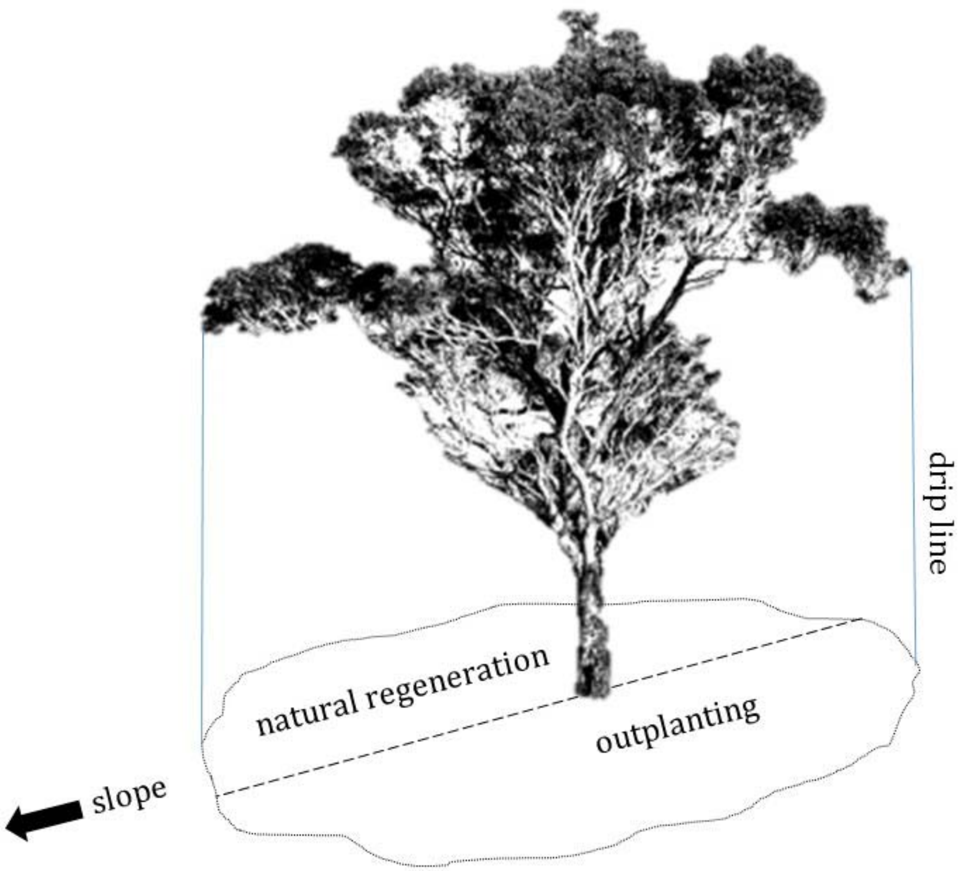

Figure 8. A demonstration of a tree canopy plot showing the irregular nature of the plot boundaries and how the plots were divided between natural regeneration and outplanting halves (approximate) with respect to the prevailing slope.

Seedlings were planted in tree canopy plots from October to December 2013. Plots were randomly assigned to one of the same three Species Groups as in the outplanting plots. However, there were insufficient numbers of ‘ākala and ‘ōhi‘a seedlings available to adequately source both the outplanting and tree canopy plots selected for Groups 1 and 2. As such, tree canopy plots assigned to these groups received only a few ‘ākala and ‘ōhi‘a seedlings. In addition, fewer seedlings were available as a whole from Species Group 2 and, as such, 75 seedlings were planted in each Group 2 tree canopy plot and 90 seedlings were planted in each Group 1 and Group 3 tree canopy plot. Just as in the outplanting plots, seedlings were planted in an alternating pattern with respect to species in tree canopy plots. The irregular shape of the plots, however, meant that the number of rows (and thus neighbor seedlings) was more variable in these plots than in the outplanting plots. BLUE-X® Tree shelters were not used in tree canopy plots.

Monitoring

Plots were monitored at 6- to 12-month intervals beginning in January 2014 (Table 5). The purpose of monitoring the experimental plots was to estimate natural regeneration and/or the survival and growth of planted seedlings. At each monitoring interval, we recorded the number of naturally regenerated woody seedlings > 15 cm in height in all plots. At this height, seedlings were considered to have survived the initial selection events affecting seedlings in the first few weeks following germination. Height was defined as the maximum length of the plant from soil level to the apical meristem farthest from the plant base. The greatest height measurement was often to the most upright branch but also included side branches of a length exceeding the most vertical branch (Figure 9). ʻĀkala sometimes grew from multiple points below the soil surface. In these cases, the length of the longest "cane" was measured.

Table 5. Dates of when the final treatments were applied and when plots were monitored.

		Monitoring			
Factor	Treatments applied	6-mo	12-mo	18-mo	24-mo
natural regeneration	July, 2013	Jan., 2014	July, 2014	Jan., 2015	July, 2015
outplanting	Dec., 2013	May, 2014	Nov., 2014	May, 2015	Dec., 2015
seed broadcast	Jan., 2014	July, 2014	Jan., 2015	July, 2015	Jan., 2016
tree canopy	Dec., 2013	n/a	Nov., 2014	n/a	Dec., 2015

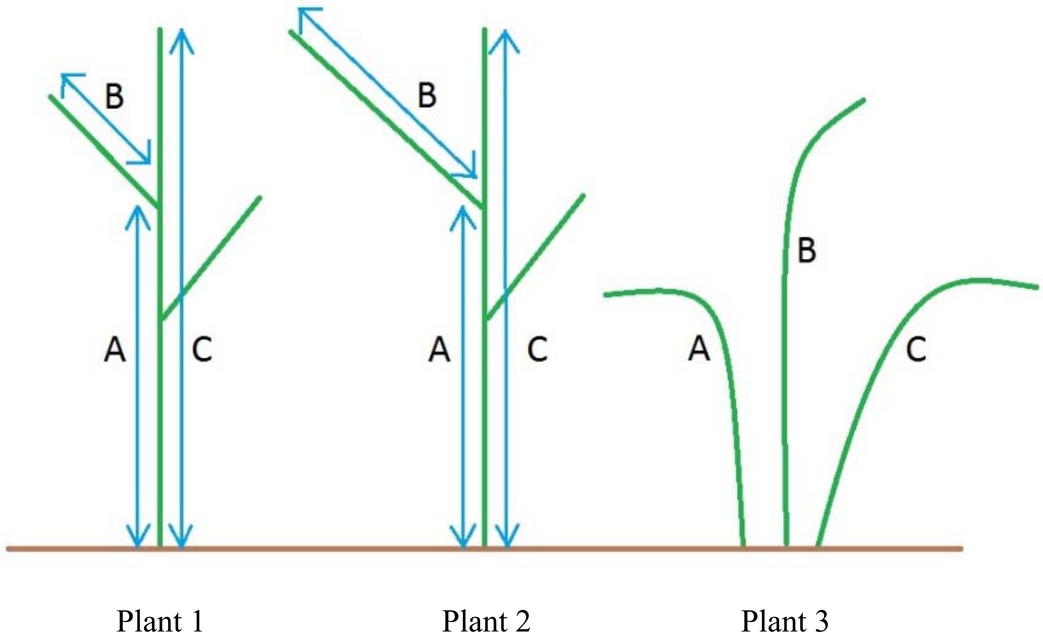

Figure 9. Demonstration of height measurement of seedlings. Plant 1 shows a scenario when the greatest height is from the soil level to the apical meristem of the most upright branch (C); C > A + B. This was the most common scenario for most species. Plant 2 shows a scenario where a side branch is included in the height measurement; A + B > C. This was a common scenario in māmane but uncommon among other species. Plant 3 shows a species that has multiple stems growing from the ground. In this case, common in ‘ākala, the length of the longest “cane” was measured (B).

During each monitoring period, an observer methodically walked back and forth through each plot multiple times and recorded height (and therefore presence) of seedlings > 15 cm in height encountered making sure all individuals were recorded and individuals were counted only once. To minimize the chance of double-counting in plots with a large number of seedlings, brightly colored string was used to make clearly defined rows for the observer to follow. All woody species were recorded, including native and non-native species. In addition to recording woody species, relative percent ground cover was recorded for each plot at each monitoring interval in the following categories: grass, tree/shrub, forb, rock/stick, and bare ground/duff. Relative percent ground cover was defined as the tallest cover classes that define the total cover (100%) of a plot. In this context, the tree/shrub generally trumped all other categories because it was taller.

We recorded survival and height of all planted seedlings (no minimum size) in outplanting and tree canopy plots. Natural regeneration was recorded for the entire plot in outplanting and tree canopy plots. To monitor outplantings, an observer walked along each row of planted seedlings in each plot and recorded height and survival of each seedling. Tree shelter status (present, fallen, missing) was recorded for all seedlings that received a shelter. The observer was provided a map of each plot locating each individual planted and whether it received a tree shelter (Figure 7). In this way, all planted seedlings were tracked throughout the trial period. Toward the end of the trials, some planted seedlings, particularly koa, reached a height of > 2 m, making precise height measurement to the nearest cm difficult for the typical observer. As such all seedlings > 2 m in height were recorded as "> 200 cm."

All naturally regenerating woody seedlings encountered were also recorded (height and number). In some cases, individual naturally regenerating seedlings were flagged if that same species was planted in a given plot (e.g., a naturally regenerating ʻaʻaliʻi encountered in a Species Group 1 plot) to distinguish these individuals from planted individuals.

Analyses

At each monitoring period, we recorded the number, species, and height of all woody seedlings ≥ 15 cm in height present in all plots except outplantings where all seedlings > 1 cm were recorded. We calculated mean height per species to serve as a measure of relative growth rate for comparison among treatment groups. At the 24-month monitoring period, some seedlings reached a height that was difficult to measure accurately. During this period, we recorded a total of 217 seedlings (5.3% of seedlings planted in outplanting plots) as being > 200 cm in height and very few of these seedlings approached 300 cm. No seedlings were this tall during any of the earlier monitoring periods. For analysis purposes, the height of these seedlings was assumed equal to 200 cm, less than their true height. Thus, average height of these seedlings during the 24-month monitoring period should be considered a minimum number. No seedlings reached 200 cm in tree canopy plots.

We tested for variation among treatments for the response variables "number of wild seedlings recorded" and "average height of wild seedlings" using repeated measures analysis of variance (ANOVA) for all factor types in R 3.3.0 (R Core Team 2013). We did this using linear mixed effects models blocking by plot ID using the “lme” function of the “nlme” package (Pinherio et al. 2013) followed by a Type I ANOVA. We performed similar analyses for the response variables “proportion of surviving individuals” and “mean plant height” for each species planted in outplanting and tree canopy plots. For tree canopy plots, we did not have enough seedlings of all species to plant sufficient numbers in multiple plots within each treatment group to adequately assess survivorship among all groups in a fully crossed fashion. In addition, no ‘ōhi‘a were planted in herbicide & removal plots and no māmaki or māmane were planted in disruption tree canopy plots. Some species were planted in only one plot per treatment group. As such, we ran Type III ANOVA using the “anova.lme” function following the linear mixed effects regression for all analyses of outplantings in tree canopy plots. Separate ANOVA were run for these variables in each factor group, natural regeneration, seed broadcast, outplanting, and tree canopy.

RESULTS

When these experimental trials began in early 2013, little natural regeneration was observed within much of the Wailaulau unit of Nakula NAR. Trial plots were established in open areas dominated by non-native grasses and large, widely-spaced koa and other trees. Only a few months following the removal of all ungulates and the beginning of the experiment, the first naturally regenerating ‘a‘ali‘i were documented in the trial area. Shortly after, koa seedlings (largely clonal root shoots) began to appear as well as occasional pūkiawe (*Leptecophylla tameiameiae*) and ‘ōhelo seedlings. A handful of ‘ōhi‘a seedlings were recorded in open areas but these remained rare throughout the trial period. The abundance of ‘a‘ali‘i and koa seedlings transformed the trial area over the experimental period, noticeably increasing the canopy cover throughout the site (Figure 10, Appendix 1). However, while natural regeneration was documented throughout the site, regeneration was sparse or absent across large areas. Natural recruitment of many species, including kōlea, kāwa‘ū, and ‘ōlapa, remained limited and localized throughout this period. Seedlings of these species were usually only found within intact forest patches in gulches, often near potential parent trees.

Figure 10. A photo point showing a representative view of the Wailaulau Unit of Nakula NAR at the beginning (January 2013) and the end of the trials (January 2016) demonstrating the amount of natural regeneration that occurred throughout the area during the experimental period. See *Appendix 1* for photos of all photo points.

Ground Cover

Grass covered nearly > 90% of all experimental plots prior to treatment application. After treatments, grass cover was significantly reduced in the herbicide and herbicide & removal treatments and remained below 30% six months after the initial treatments (Figure 11). During treatment application in herbicide & removal plots, we removed ~ 100% of all grass cover, living and dead. At six months, we recorded lower relative grass cover in the herbicide plots compared to the herbicide & removal plots. However, it is possible grass growth may have been occurring at the same pace in both these treatments. By removing the necrotic grass material in the herbicide & removal plots, the grass regrowth may have been more visible in these plots compared to the herbicide plots. In herbicide and herbicide & removal plots grass cover returned to approximate pre-treatment levels (no difference between treatment and control groups) by 18- and 24-months, respectively. Physically removing the grass biomass following herbicide application in the herbicide & removal treatment may have slowed the grass regrowth more than just herbicide only. While the intention was to reduce the amount of grass cover manually in the disruption treatment, grass returned very quickly in these plots and showed no difference in relative grass cover from the control group by 6 months post treatment (Figure 11).

One of the major concerns to reducing grass cover is that it may create a disturbance that can be exploited by weedy species. Not too surprisingly, forb cover (including most weeds) was greater in the herbicide and herbicide & removal plots early in the experiment (6- and 12-months) than the control group. However, likely due to the grass returning at the same time, forb cover dropped to the levels seen in the control group by 18 months. This reduction in forb cover once the grass returned is good news if managers are concerned about the spread of these weeds due to restoration activities. Most forb species observed were common pasture weeds such as *Cirsium vulgare* and *Plantago lanceolata* but also included the invasive *Senecio madagascariensis*.

Relative tree/shrub cover was generally greater in the herbicide & removal treatment compared to all other treatments, but only differed significantly from the other treatments at 18 months, 20.7 ± 12.5% (SE) (Figure 11). In the other treatments average tree/shrub cover remained below 5% throughout the trial period.

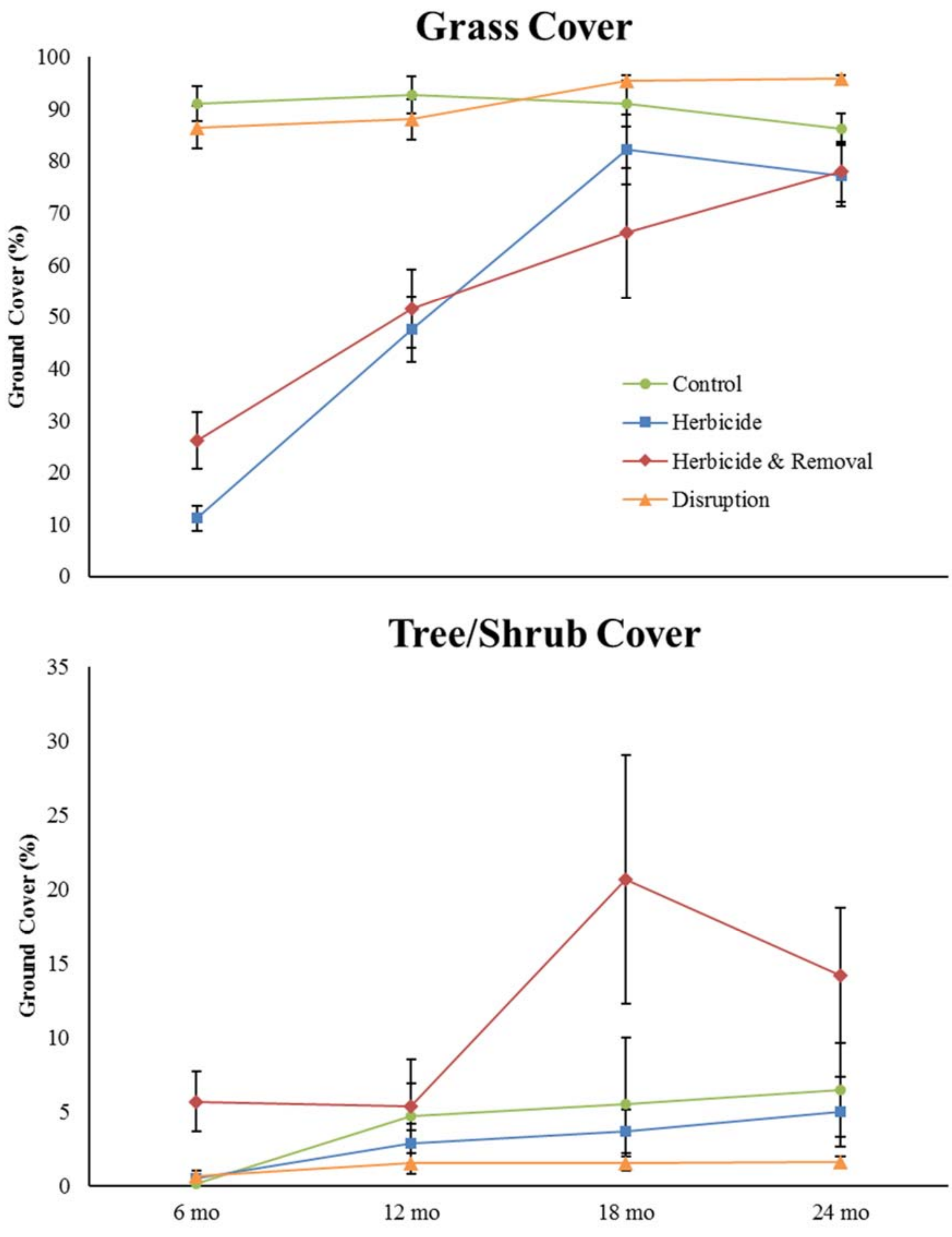

Figure 11. Relative percent grass cover (top) and tree/shrub cover (bottom) classes in natural regeneration plots throughout the trial period.

Natural Regeneration

Species

Despite the presence of dozens of native woody species in the reserve and observed natural regeneration of several species, the diversity of naturally regenerating seedlings within the trial plots was low. Only three species were found within the natural regeneration plots, ʻaʻaliʻi, koa and pūkiawe. Of these species, ʻaʻaliʻi was by far the most common and abundant, occurring in 87.7% of plots (21 of 24 plots) and accounting for 84% of all measured seedlings throughout the experimental period. Koa was recorded commonly in plots (15 of 24 plots) but the number of individuals was comparatively low, 15.5% of measured seedlings. The third species, pūkiawe, was rare in plots (2 of 24 plots) representing only 0.3% of measured seedlings in natural regeneration plots. Given their size, most pūkiawe seedlings were likely present prior to the experimental period. Overall, these results reflect the pattern observed throughout the majority of the site in that ʻaʻaliʻi seedlings, in particular, were germinating throughout the area but few other species were observed. Only two additional species were observed as naturally regenerating outside of plots during the trial period in the same open, grassy habitat, ʻōhiʻa and ʻōhelo, and only a few individuals were observed of each.

Seedling abundance

The number of seedlings recorded in natural regeneration plots was strongly affected by treatment wherein the herbicide & removal treatment produced by far the greatest number of naturally regenerated seedlings ($F = 4.79$, $p = 0.011$, $df = 20$; Figure 12). The variation in seedling abundance was driven by ʻaʻaliʻi abundance alone as ʻaʻaliʻi seedlings varied among treatments ($F = 4.9$, $p = 0.01$, $df = 20$) but koa abundance did not ($F = 1.08$, $p = 0.38$, $df = 20$). By 12 months, overall seedling abundance was an order of magnitude greater in the herbicide & removal treatment compared to the control and disruption plots and remained so until the end of the trial period. Although lower than the average in the herbicide & removal treatment, the number of seedlings was greater in the herbicide treatment compared to the control or disruption treatments during the second half of the experiment. While the average number of seedlings continued to increase in the herbicide treatment throughout the experiment (unlike the other treatments), seedling abundance was still more than three times greater in the herbicide & removal treatment at 24 months. Additionally, the increase in seedling abundance in herbicide treatment plots was reflective of an increase in koa seedlings. No corresponding increase in ‘a‘ali‘i seedling abundance was seen herbicide plots. The disruption treatment did not result in more seedlings than the control treatment at any point in the experiment.

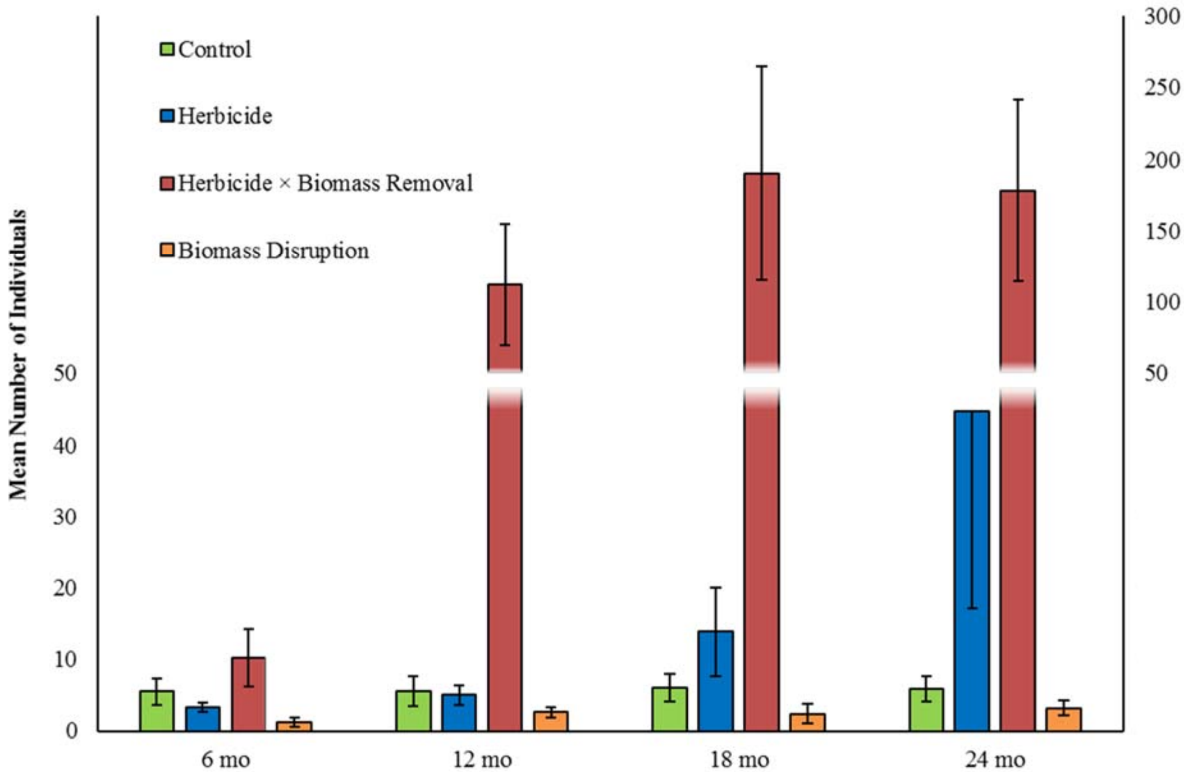

Figure 12. Average number of naturally regenerating native woody seedlings recorded in natural regeneration plots among four treatments throughout the trial period.

Growth rate

There were enough individuals to compare average plant height for two of the three species recorded in natural regeneration plots: ‘a‘ali‘i and koa. Seedling height did not vary among treatments in either ‘a‘ali‘i ($F = 1.79$, $p = 0.182$, $df = 20$) or koa ($F = 0.39$, $p = 0.76$, $df = 20$).

Distance from koa

The majority of seedlings recorded were ‘a‘ali‘i, a species that is primarily wind dispersed and not likely to be affected by distance from koa. Comparatively few koa were found in plots and we saw a fair amount of variation among plots. As such, it is not surprising that we also found no effect of distance from koa on the number of wild ‘a‘ali‘i ($F = 0.14$, $p = 0.716$, $df = 19$) or koa seedlings ($F = 1.18$, $p = 0.195$, $df = 19$, Figure 13). Although there was not a significant overall effect, koa seedlings were not recorded in disruption plots at the 30-m distance category. Additionally, seedling height was not affected by distance from mature koa in ‘a’ali‘i ($F = 0.7$, $p = 0.412$, $df = 19$) or koa ($F = 2.19$, $p = 0.155$, $df = 19$).

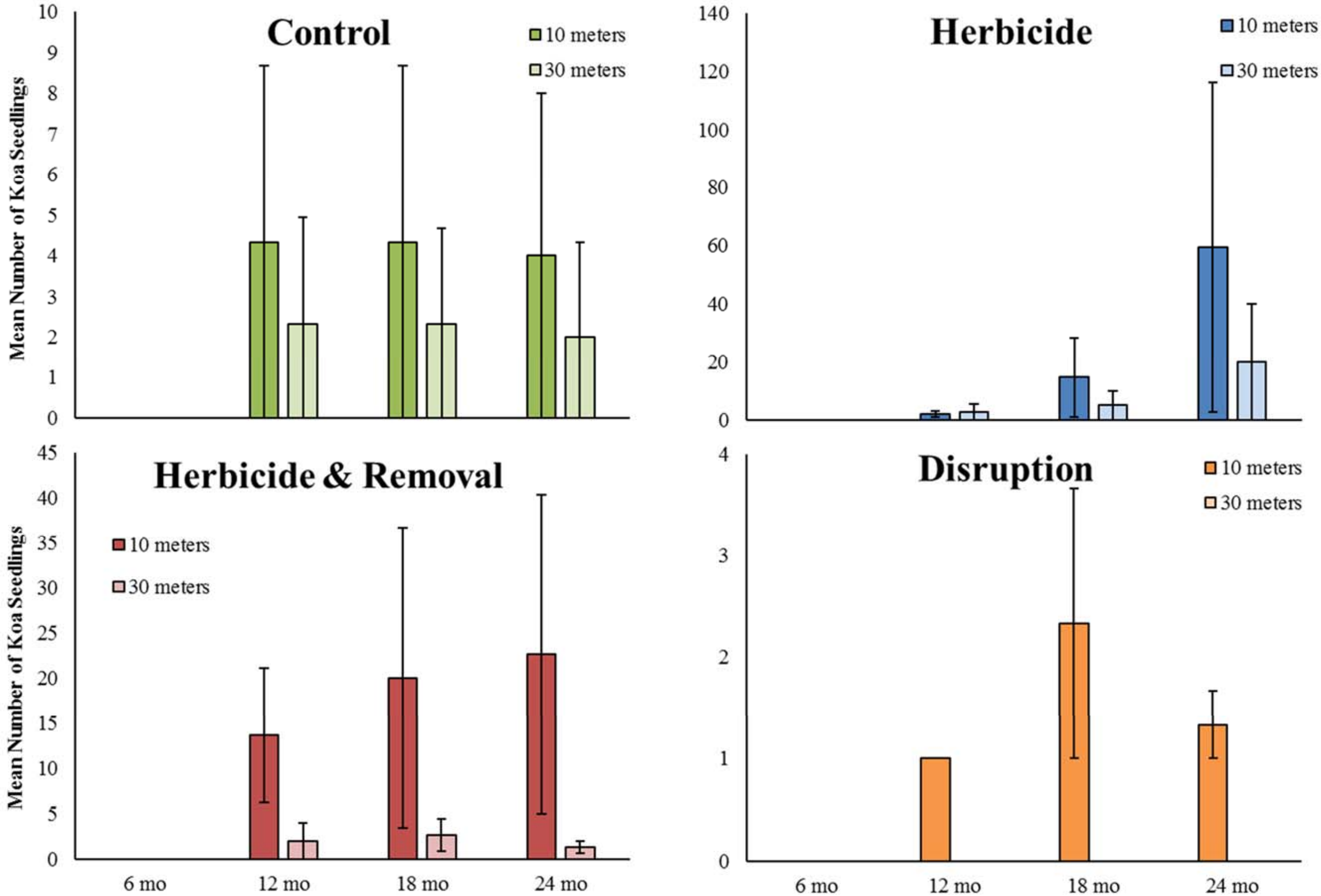

Figure 13. Mean number of wild koa seedlings in natural regeneration plots in the near (10 m) and far (30 m) distance categories from mature koa canopy trees. Y-axes vary between plots.

Figure 14. Progression of a natural regeneration plot from 6 months post-treatment (herbicide & removal in this case) to 24 months post-treatment. Of note is the timing of grass recursion, proliferation and then decline in herbaceous cover, and naturally regenerating ‘a‘ali‘i seedlings. Figure 33 shows this same plot from a distance and at a later date.

Natural regeneration in other plot types

We recorded the number and height of all naturally regenerating woody seedlings in all plots. Similar to the natural regeneration plots, we only recorded three naturally regenerating woody species in outplanting and seed broadcast plots, ‘a’ali‘i, koa, and pūkiawe. In addition to the three species recorded in the other plot types, we recorded the presence of three other species, pilo (*Coprosma cordicarpa*), ‘ōhelo (*Vaccinium reticulatum*) and tree poppy (*Bocconia frutescens*), in tree canopy plots. Pilo, ‘ōhelo, and pūkiawe were rare in these plots, collectively accounting for only five seedlings recorded. However, their presence is notable given the low diversity of wild seedlings found in other plots. The highly invasive *Bocconia* is actively controlled within the reserve and all individuals found were removed during monitoring. In total we found (and removed) 11 *Bocconia* individuals > 15 cm in height from four plots at 12 months. No additional individuals > 15 cm in height were found at 24 months. We also removed six small (< 15 cm) *Bocconia* seedlings from five plots at 12 months and seven seedlings from two plots at 24 months.

Unlike in the designated natural regeneration plots, we found no significant variation in the number of natural regenerating seedlings among treatments in outplanting plots ($F = 1.61$, $p = 0.22$, $df = 24$) or tree canopy plots ($F = 1.63$, $p = 0.235$, $df = 12$; Figure 15). However, in the tree canopy plots, the herbicide treatment had a marginally greater number of natural regenerating seedlings ($t = 1.87$, $p = 0.086$). Seedling abundance did vary among seed broadcast plots ($F = 6.16$, $p = 0.009$, $df = 12$) but abundance was greatest in the control plots rather than the herbicide & removal plots as seen in the natural regeneration plots and overall abundance was much lower than in other plot types.

In outplanting plots, natural regenerating ‘a‘ali‘i seedlings were larger in control plots compared to those in herbicide ($t = -2.06$, $p = 0.051$) and herbicide & removal plots ($t = -3.95$, $p < 0.001$). Natural regenerating ‘a‘ali‘i seedlings were also marginally larger in the herbicide plots over those in herbicide & removal plots ($t = -1.89$, $p = 0.071$). However, average height of ‘a‘ali‘i seedlings did not vary among treatments in seed broadcast plots ($F = 1.56$, $p = 0.25$, $df = 12$). We also found no effect of treatment on average height of naturally regenerating ‘a‘ali‘i ($F = 1.47$, $p = 0.273$, $df = 12$) or koa ($F = 0.86$, $p = 0.489$, $df = 12$) in tree canopy plots. Comparatively few naturally regenerating koa seedlings were recorded ($N_{24\ mo} = 39$ in 8 outplanting plots; $N_{24\ mo} =$

17 in 3 seed broadcast plots) and, thus, we did not compare koa seedling height among treatments in outplanting or seed broadcast plots.

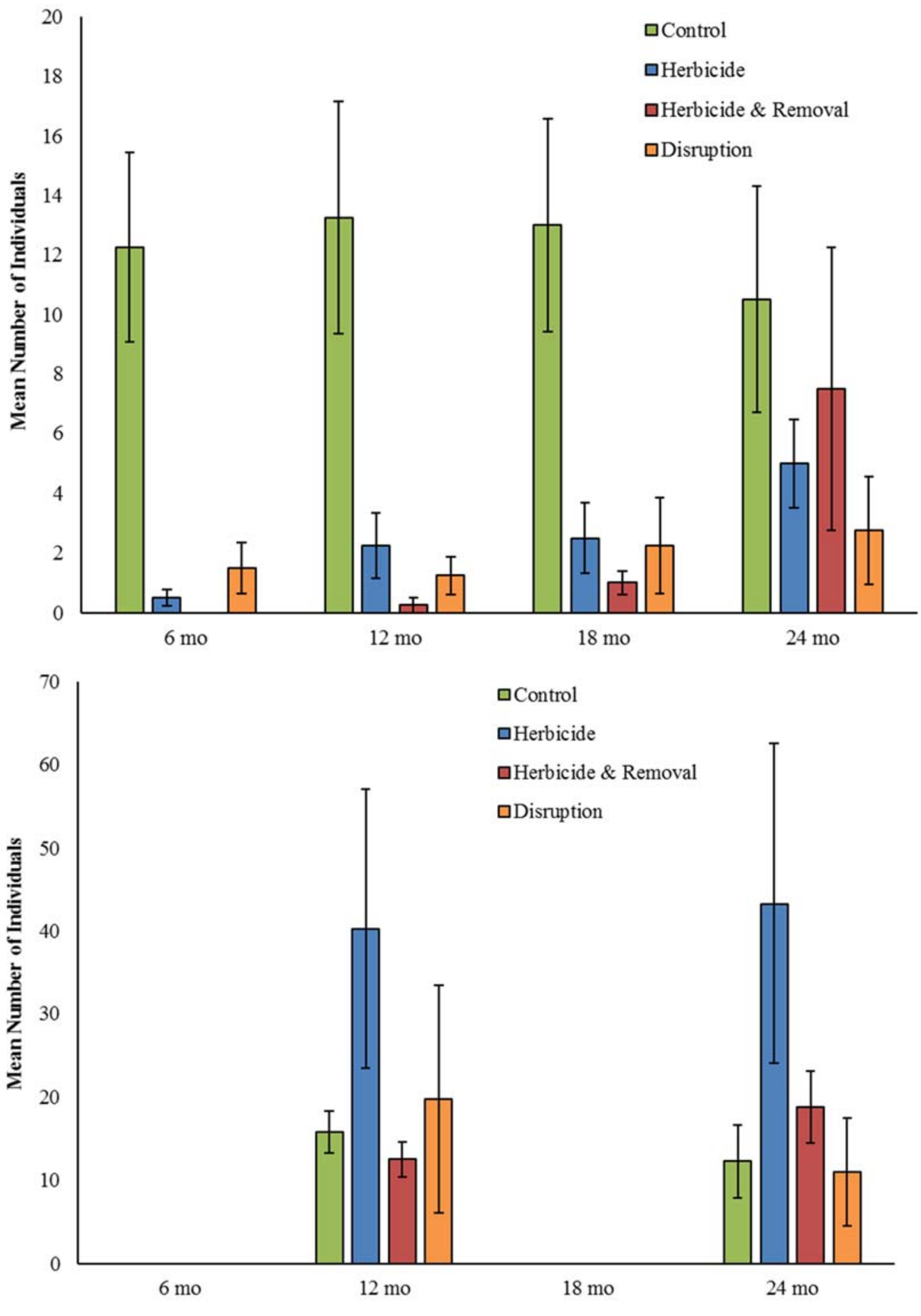

Figure 15. Average number of naturally occurring seedlings recorded in seed scatter (top), and tree canopy plots (bottom) among treatments throughout the trial period. Note: tree canopy plots were not measured at 6- or 18-mo.

Outplanting

Survivorship

Across all treatments, the two-year survival of planted seedlings exceeded 90% for; ‘a‘ali‘i (96.5 ± 9.5% [SE]), koa (95.5 ± 1.7%), pilo (94.7 ± 1.1%), and ‘ōhi’a (92.5 ± 1.7%). Māmane showed slightly lower but still high overall survivorship at 82.7 ± 3.4%. The remaining two species, ‘ākala and māmaki had comparatively low overall survivorship of 50.9 ± 7.3% and 32.2 ± 8.8%, respectively. In general, all canopy and subcanopy species showed higher survivorship compared to understory species. Across all species and treatments, overall survivorship of planted seedlings was 82.4% by the end of the 24-month trial period.

Treatment did not affect survivorship of ‘a‘ali‘i ($F = 1.437$, $p = 0.269$, $df = 15$), ‘ākala ($F = 1.07$, $p = 0.402$, $df = 6$), koa ($F = 0.61$, $p = 0.576$, $df = 6$), or ‘ōhi’a ($F = 0.5$, $p = 0.619$, $df = 15$, Figure 16). We found significant variation in the proportion of surviving planted individuals among treatments in māmaki ($F = 9.12$, $p = 0.015$, $df = 6$), pilo ($F = 4.71$, $p = 0.059$, $df = 6$), and marginally so in māmane ($F = 3.48$, $p = 0.099$, $df = 6$). Pilo survivorship was greater in the herbicide and control treatments compared to herbicide & removal (herbicide × herbicide & removal: $t = -2.76$, $p = 0.033$; control × herbicide & removal: $t = -3.1$, $p = 0.021$; herbicide × control: $t = 0.34$, $p = 0.741$). However, mean survivorship in the herbicide & removal treatment was still quite high at 95.3% compared to > 97% in the other two treatments. Survivorship of māmaki and māmane was greatest in the herbicide treatment. However, the effect was much greater in māmaki than māmane. ‘Ākala showed a similar trend of generally greater survivorship in the treatments where herbicide was used (herbicide and herbicide & removal) compared to the control group. However, we saw large variation in ‘ākala survivorship among plots, particularly in the herbicide treatment, and thus found no significant difference among treatments.

Treatment effects were most pronounced in māmaki wherein survivorship among treatment groups diverged early and continued throughout the trials: highest in herbicide followed by herbicide & removal and then control. By the end of the experiment, māmaki survivorship in the herbicide treatment was 66% compared to 8% in the control group and did not differ in the herbicide and herbicide & removal treatments until after 12 months and removal of tree shelters.

Inspection of the time interval at which mortality occurred may provide an additional perspective into the causes of death in each species (Figure 17). In some species, like māmaki, ʻaʻaliʻi, and ʻōhiʻa, seedlings died in the herbicide and control plots evenly throughout the trial period and was likely caused by factors that are likely not discernable from these data. ʻĀkala in all treatments had high early mortality and, conversely, māmane had high late mortality. Early mortality may indicate a failure of seedlings to become established or compete with the returning grasses. The high survivorship rates in the second half of the experiment may indicate that if an individual (e.g., ʻākala) survived past 12 months, their chances of long-term success were good. The pattern seen in māmane may indicate that most individuals could become established, but then could not compete in the long-term with the increasing grass presence. Indeed, many māmane seedlings had to be manually extricated from the grass to be measured, or even found, during monitoring. A similar pattern of increasing mortality later in the experiment was seen in several species in the herbicide & removal plots (e.g., koa, māmaki, ʻōhiʻa, pilo), possibly owing to the same failure to compete with increasing grass cover. In other words, the lack of grass cover early on (due to treatment application) may have allowed even the slowest-growing individuals to survive later than they may have in other treatment plots. However, once the grass returned, those individuals did not survive. Pilo showed different patterns of mortality between treatments wherein in the herbicide & removal plots mortality was high later and high early on in the control plots. This pattern likely indicates that the heavy grass cover prevented many individuals from becoming established and the returning grass later on may have affected survivorship.

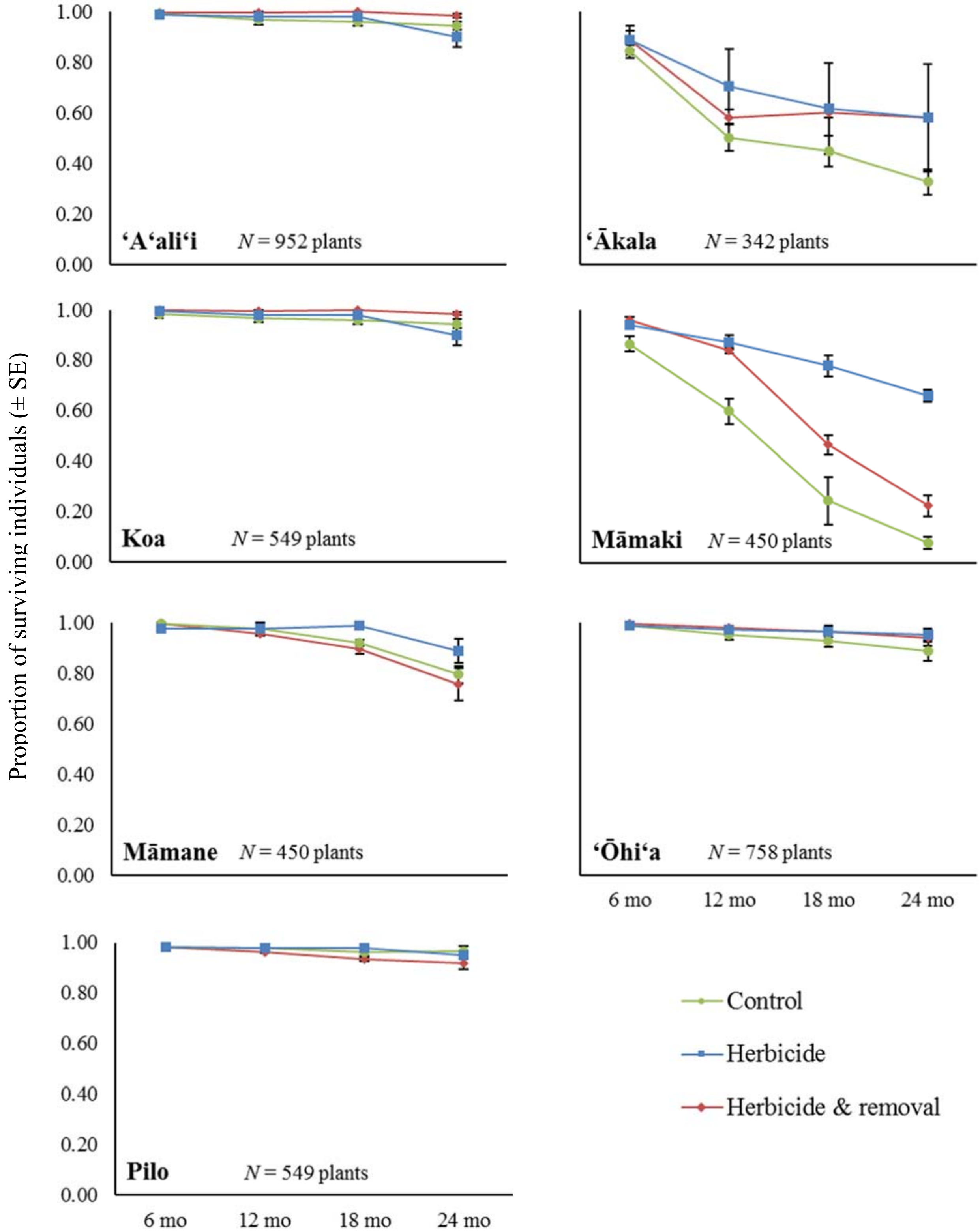

Figure 16. The average proportion of surviving individual planted seedlings (± SE) per species among plots in each of three treatments.

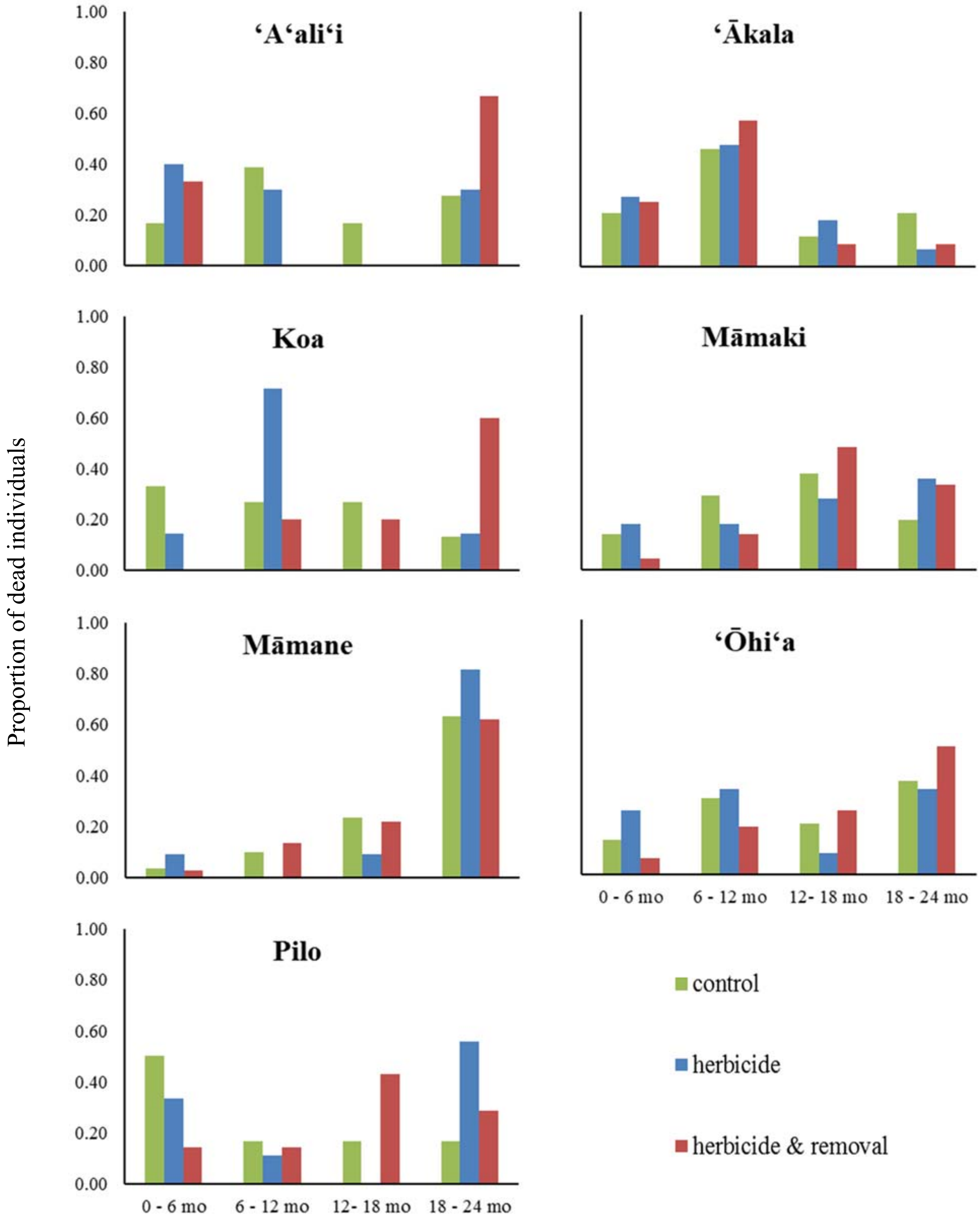

Figure 17. The average overall proportion of all dead planted seedlings per species among plots in each of three treatments during each time interval.

Plant height

Experimental treatment affected plant height in ‘a‘ali‘i, māmaki, and māmane, and had a marginally significant effect on ‘ākala (Table 6, Figure 18). No effect was seen in koa, ‘ōhi‘a, or pilo (Table 6). The herbicide treatment provided a growth advantage (compared to control) in ‘a‘ali‘i, ‘ākala, māmaki, and māmane (Table 6). These same species grown in the herbicide treatment were also larger than those in herbicide & removal plots (Table 6). Herbicide & removal plots did not differ from control plots in any species (Table 6).

In the species for which the herbicide treatment had a significant effect on growth, little to no differences were seen in average plant height at 6 months but the effect was evident by 12 months. In māmaki specifically, surviving seedlings in the control and herbicide & removal treatments were > 20 cm smaller on average from 12 months until the end of the trial period. Individual māmaki were also taller, on average, in the treatment where they had the greatest survivorship (herbicide).

Table 6. Treatment effect on planted seedling height. Treatments included herbicide (H), herbicide & removal (H & R), and control (C). Significant treatment effects and differences among treatments are shown in bold.

				H × C		H × H & R		H & R × C	
Species	*F*	*p*	*df*	*t*	*p*	*t*	*p*	*t*	*p*
‘a‘ali‘i	**7.15**	**0.007**	**15**	**3.72**	**0.002**	**2.43**	**0.028**	1.29	0.216
‘ākala	**3.89**	**0.082**	**6**	**2.59**	**0.041**	**2.19**	**0.071**	0.4	0.702
koa	1.76	0.25	6	1.85	0.114	0.66	0.536	1.2	0.277
māmaki	**21.76**	**0.002**	**6**	**6.41**	**< 0.001**	**4.99**	**0.003**	1.25	0.258
māmane	**5.64**	**0.042**	**6**	**2.98**	**0.025**	**2.84**	**0.03**	0.13	0.898
‘ōhi‘a	1.12	0.354	15	0.99	0.336	1.46	0.164	-0.47	0.647
pilo	0.03	0.972	6	-0.036	0.972	0.22	0.832	-0.19	0.859

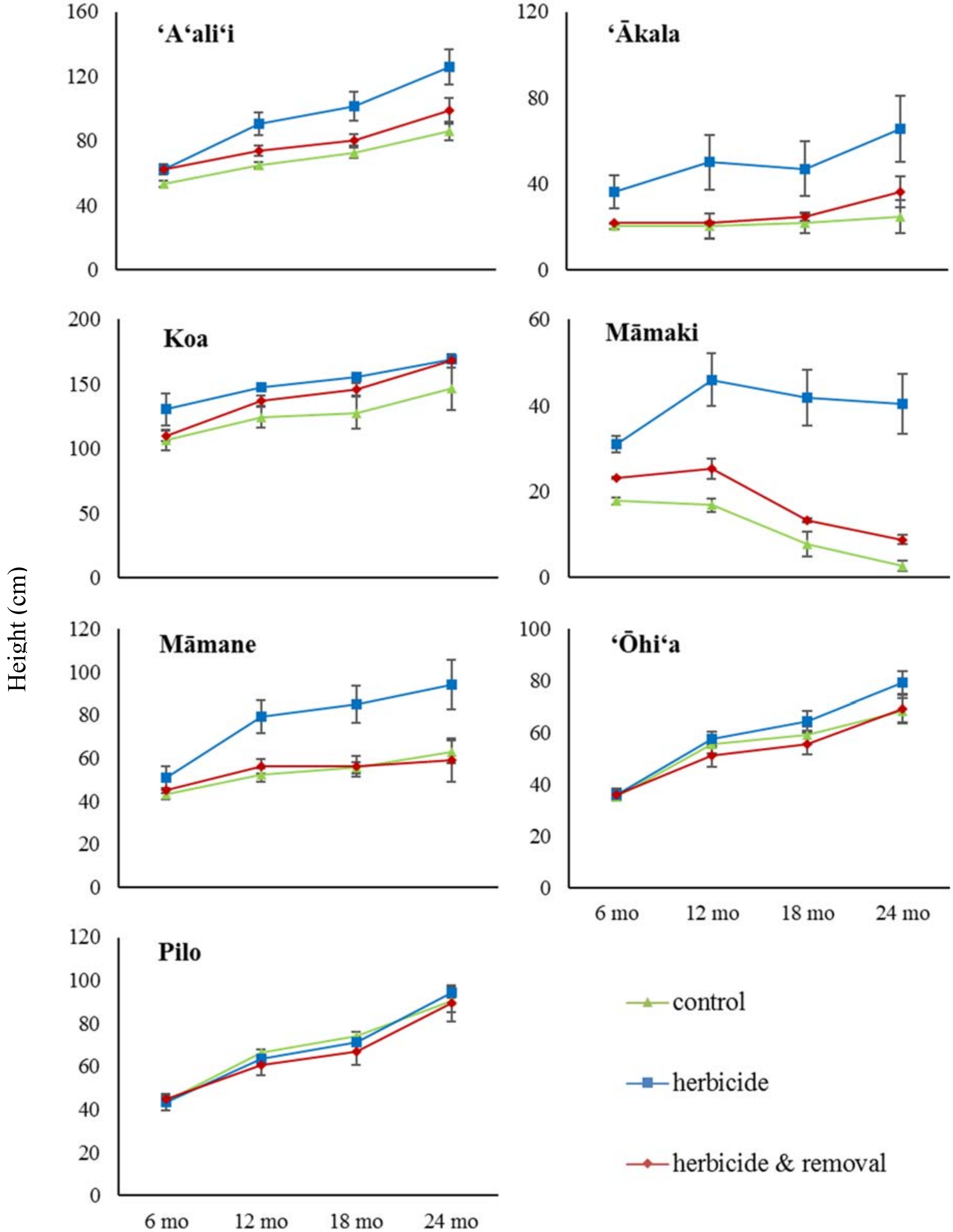

Figure 18. The average height (± SE) of seedlings in outplanting plots per species among plots in each of three treatments. Y-axes differ between plots.

Tree Shelters

The Blue-X Tree shelters had an overall positive effect on survivorship in the species with the highest overall survivorship (‘a‘ali‘i: $F = 9.2$, $p = 0.003$, $df = 125$; koa: $F = 8.17$, $p = 0.006$, $df = 62$; pilo: $F = 16.31$, $p < 0.001$, $df = 62$; Figure 19). In these species, almost all ($\bar{x} > 98\%$) sheltered seedlings survived while unsheltered individuals had slightly lower survivorship. However, survivorship of unsheltered seedlings was still high, $\bar{x} > 95\%$, in all three species. Shelters had no overall effect on survivorship in māmaki ($F = 0.7$, $p = 0.406$, $df = 62$) or māmane ($F = 2.1$, $p = 0.153$, $df = 62$; Figure 19). We found a significant interaction between treatment and shelter presence on survivorship in ‘ōhi‘a ($F = 10.7$, $p < 0.001$, $df = 123$) and ‘ākala ($F = 4.8$, $p = 0.012$, $df = 60$; Figure 20). Sheltered ‘ōhi‘a had higher survivorship in the control treatment only and sheltered ‘ākala had higher survivorship only in the herbicide & removal treatment. Although we found no significant overall effect, survivorship of māmaki and ‘ākala was greater in the control group during the first half of the experiment, but then the effect disappeared by 18 months (Figure 19 and Figure 20). This may indicate that no lingering positive effect of the shelter placement was present after the shelters were removed at 12 months.

Although shelters provided little overall benefit in terms of survivorship, there was an effect of shelter presence on growth rate in most species. Sheltered seedlings of four species were larger on average than unsheltered plants (‘a‘ali‘i: $F = 13.28$, $p < 0.001$, $df = 125$; māmane: $F = 13.98$, $p < 0.001$, $df = 62$; ‘ōhi‘a: $F = 11.28$, $p = 0.001$, $df = 125$; pilo: $F = 8.81$, $p = 0.004$, $df = 62$; Figure 21 and Figure 22). While sheltered plants were taller than unsheltered plants, the actual difference in height was not large. In these four species, sheltered seedlings were ~ 11 cm taller (16% larger) on average than unsheltered plants. On average, however, in several of these species, unsheltered plants were not significantly shorter than sheltered individuals were by 24 months. Thus, while shelters may have conferred an initial growth advantage to these species, the effect was small and did not necessarily result in larger plants by the end of the experiment. The effect of shelter on plant height varied by treatment in māmaki ($F = 3.79$, $p = 0.028$, $df = 60$) and ‘ākala ($F = 8.48$, $p < 0.001$, $df = 60$; Figure 22). In māmaki, sheltered seedlings were larger in the herbicide treatment only. In contrast to the general positive effect of shelters on height in other species, sheltered ‘ākala in the herbicide and herbicide & removal treatments were smaller than unsheltered plants. However, there was no effect in control plots. Only koa showed no effect of shelter placement on height (F = -0.054, p = 0.593, df = 62). Thus, overall the tree shelters provided a moderately positive effect on the growth of seedlings, although the effect was not uniform in degree or direction.

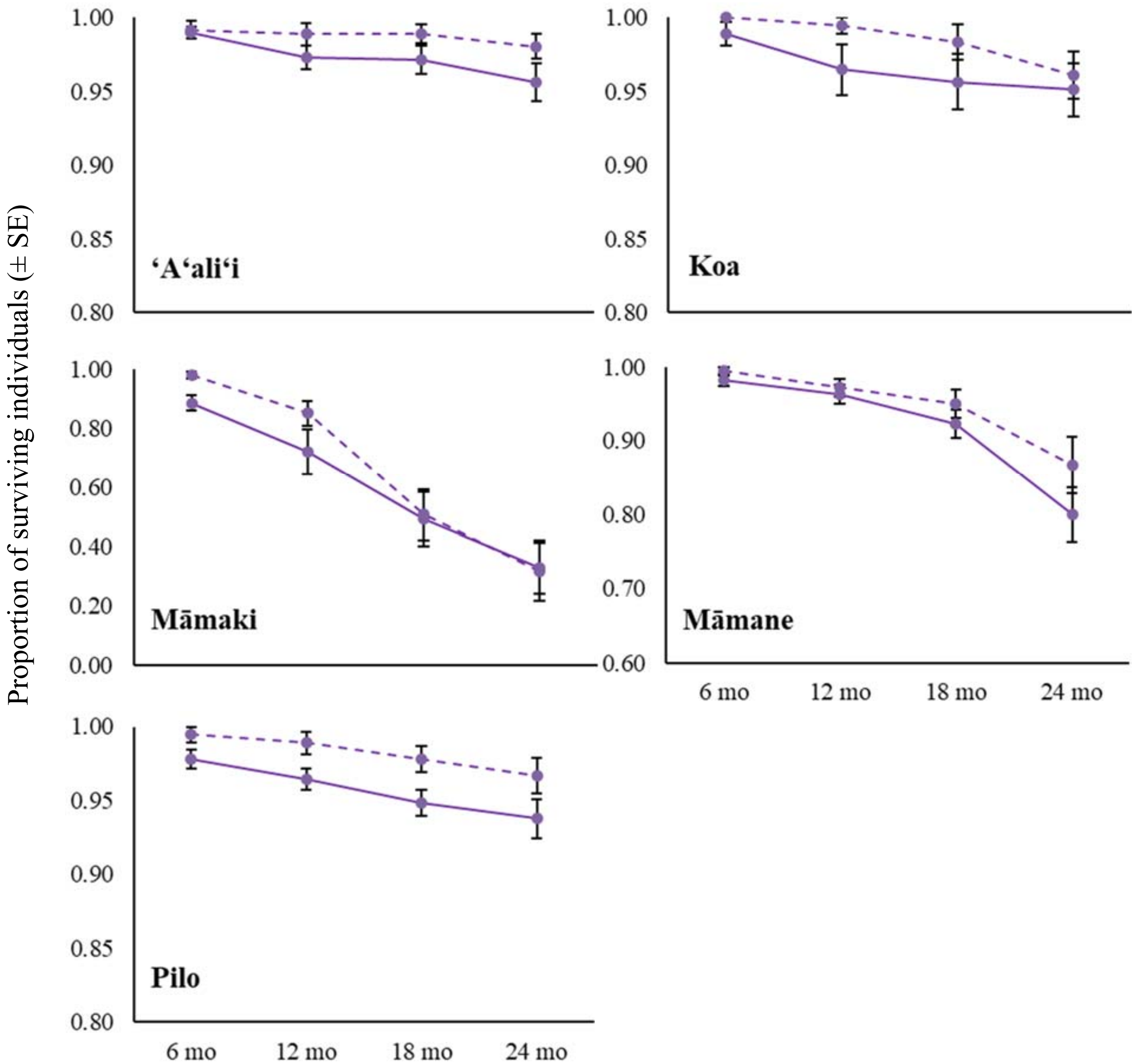

Figure 19. The average proportion of surviving individual seedlings planted in outplanting plots with shelters (dashed line) and without shelters (solid line) in each of three treatments. No effect of treatment was found in these species; treatments are showed pooled. Y-axes vary by plot.

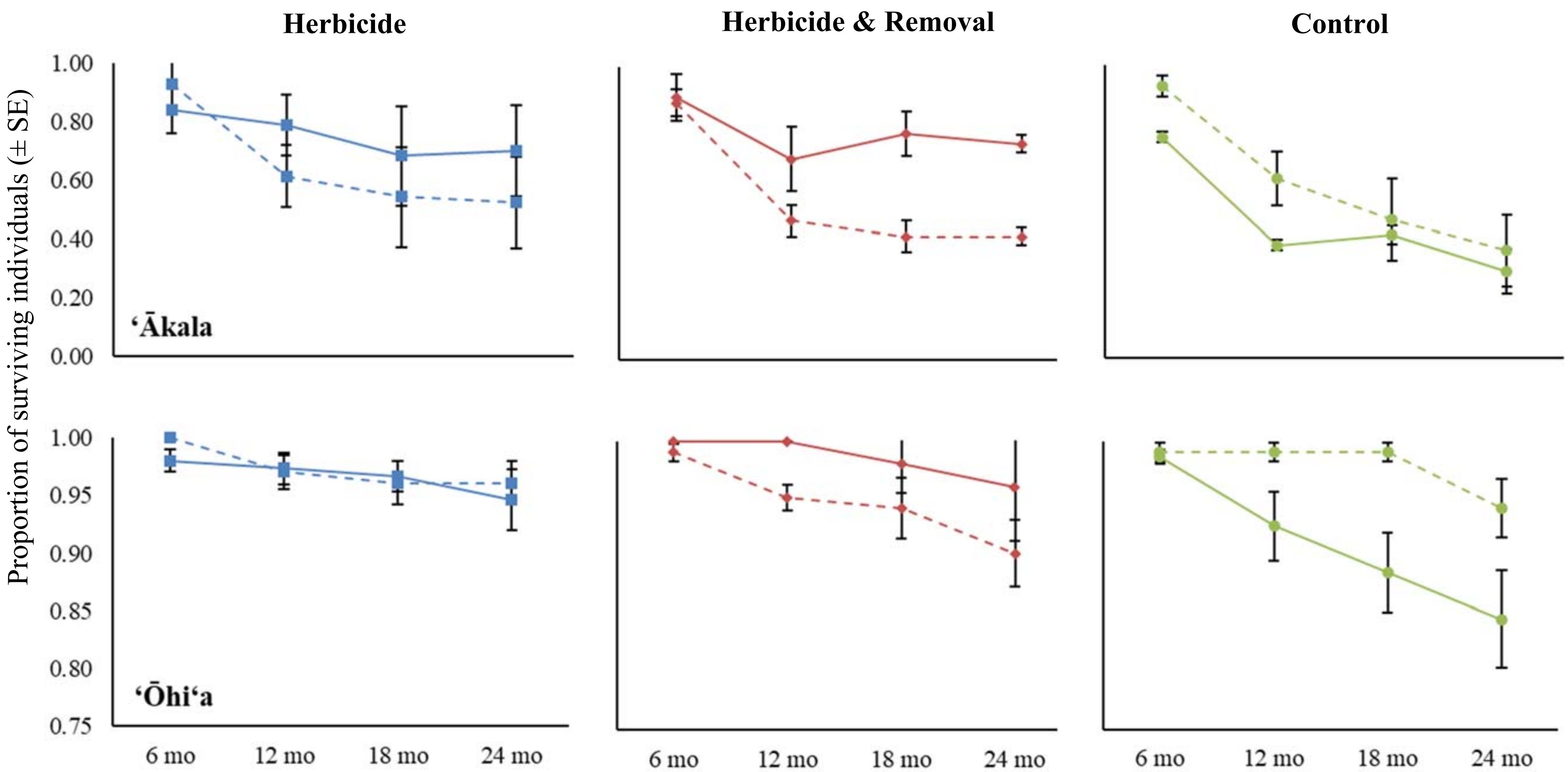

Figure 20. The average proportion of surviving individual ʻākala and ʻōhiʼa seedlings planted in outplanting plots with shelters (dashed line) and without shelters (solid line) in each of three treatments. Y-axes differ between top and bottom panels.

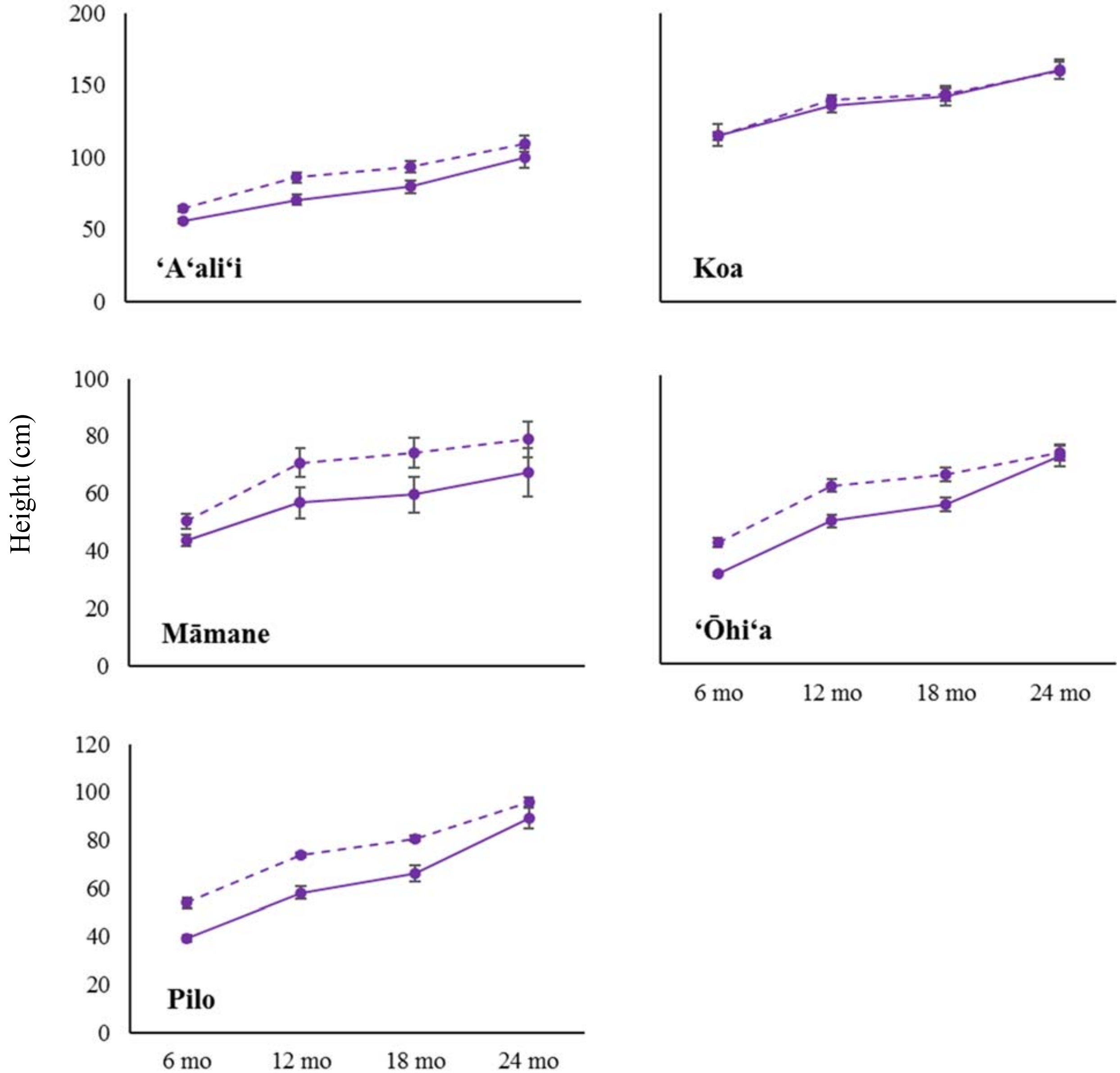

Figure 21. The average height of seedlings (cm) planted in outplanting plots with shelters (dashed line) and without shelters (solid line) in each of three treatments. No effect of treatment was found in these species; treatments are showed pooled.

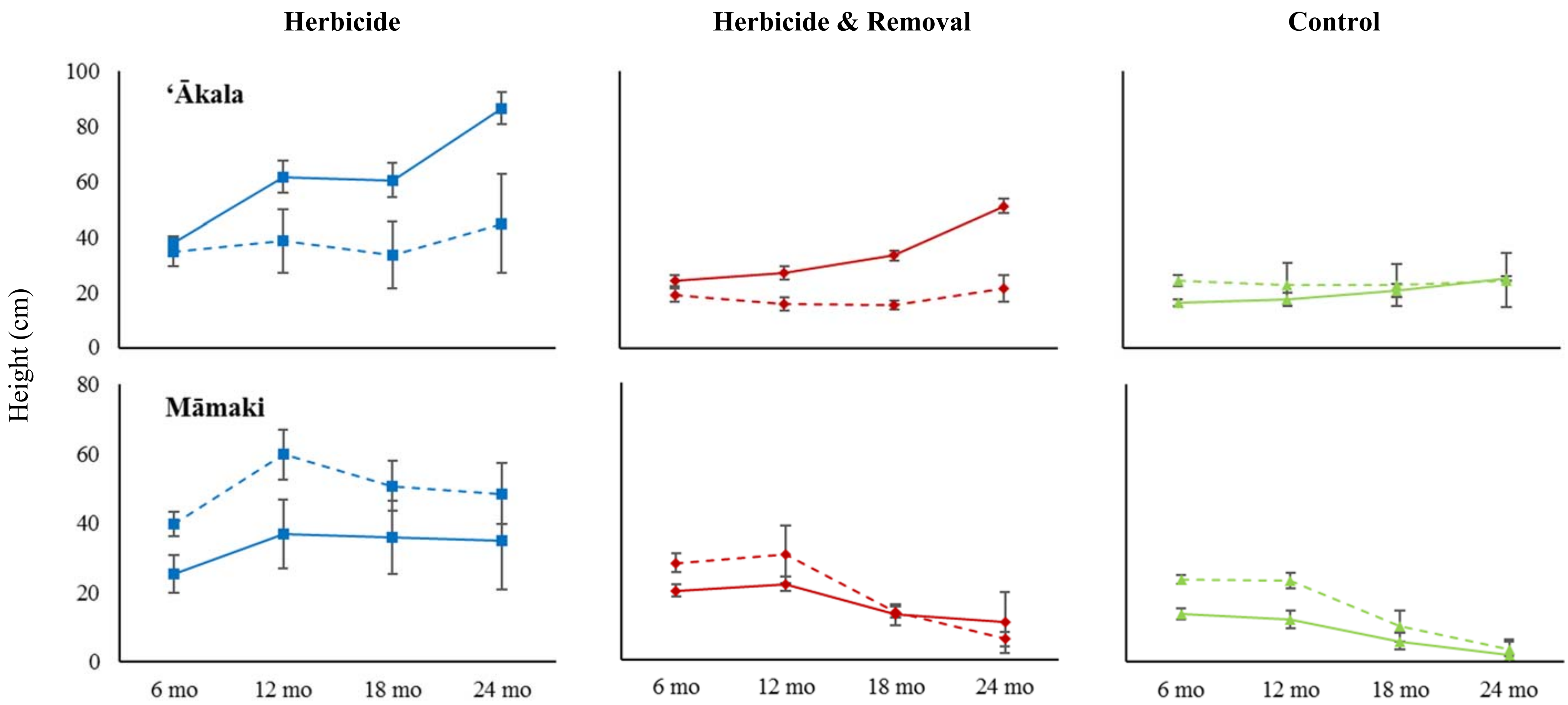

Figure 22. The average height of seedlings (cm) planted in outplanting plots with shelters (dashed line) and without shelters (solid line) in each of three treatments. Y-axes differ between top and bottom panels.

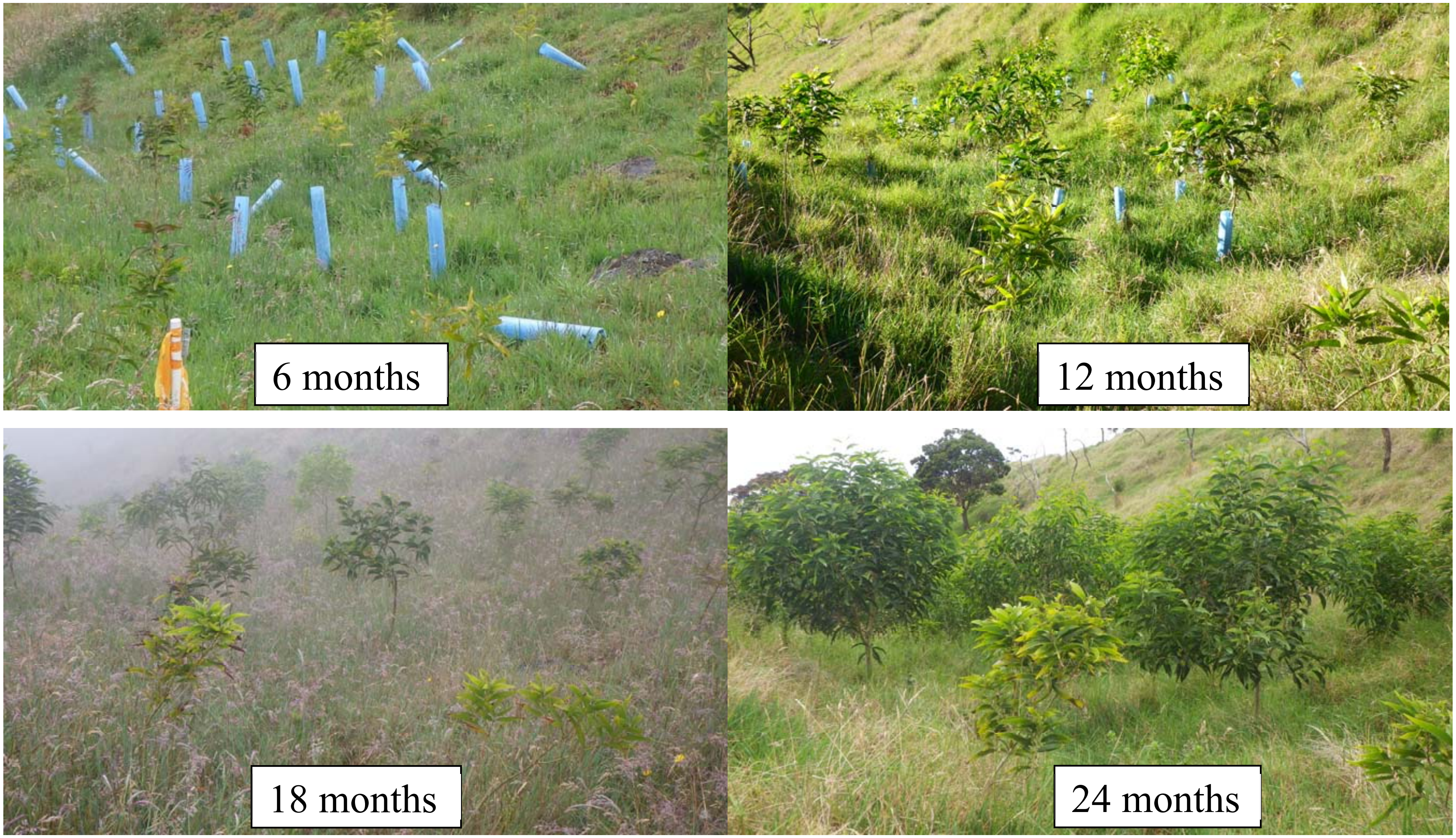

Figure 23. Progression of an outplanting plot from 6 months post-treatment (herbicide & removal in this case) and planting to 24 months post-treatment and planting. This plot received koa (*Acacia koa*), ʻōhiʻa (*Metrosideros polymorpha*), and pilo (*Coprosma stephanocarpa/cordicarpa*). Blue-X tree shelters were removed at 12 months.

Seed Broadcast

Seedling abundance and growth rate

Of the species recorded as seedlings in seed broadcast plots, only koa was among the species applied to the plots. We do not know if these seedlings resulted from broadcasted seeds, the seed bank, or from root shoots. Among koa seedlings, the predominant difference between treatments was the near complete absence of the species in any plots besides those in the control treatment (Figure 24). The only exception was two seedlings found in a single herbicide plot at 24 months. It should be noted, however, that the overall abundance of koa seedlings in the seed broadcast plots was low (n = 17 at 24 months) and these were found in a total of three plots, two control and one herbicide. As such, the apparent difference in koa seedling abundance between the control plots and other treatments is based on very few plots and may still be a result of chance with respect to plot placement. The three plots that ultimately contained koa seedlings may have simply been placed in a location with koa roots beneath the soil, providing the possibility of root shoots.

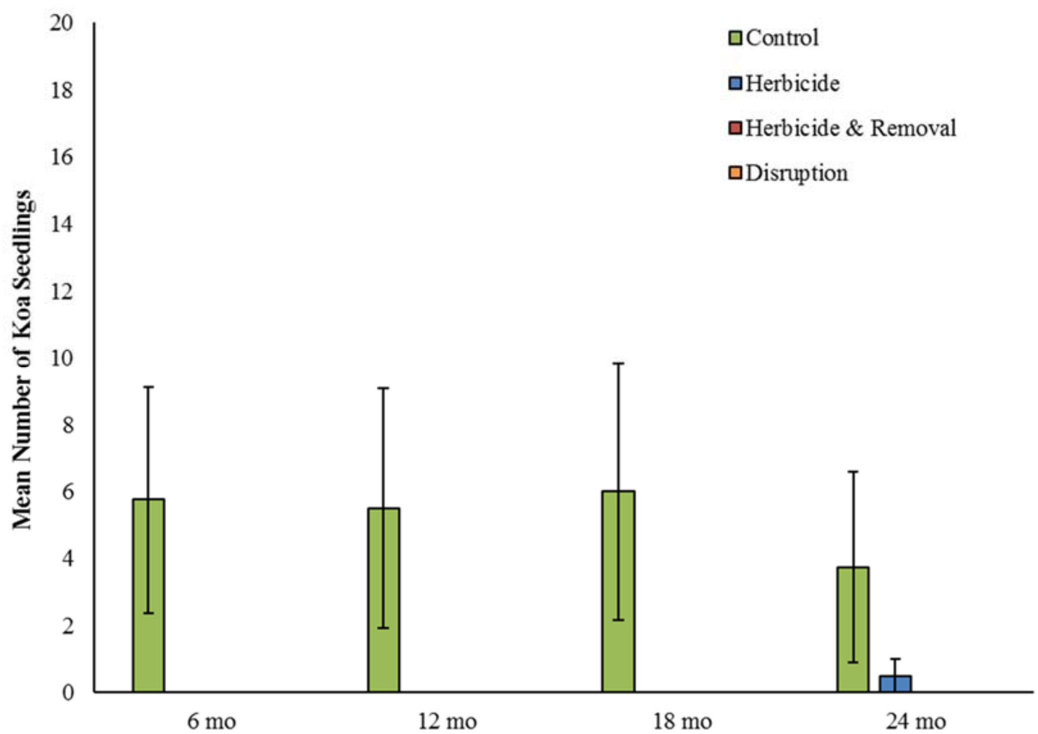

Figure 24. Average number of naturally occurring, koa seedlings recorded in seed scatter plots among four treatments throughout the trial period.

Tree Canopy

Plot size and variation

Given that tree canopy plots were defined by the dripline of adult koa trees, the size of these plots was not uniform (Table 7). The average area of tree canopy plots was 182.96 ± 130.38 m^2 (SD) based on a circular area using the average of four radii measured. Although the area of the plots varied quite a bit in size, they did not vary among treatments ($F = 1.24$, $p = 0.336$, $df = 3$).

Table 7. Area and average radius of tree canopy plots. Radii were measured from the trunk to the dripline of each tree at the approximate center of each plot. Four radii were measured to incorporate variation in the crown spread of each tree. Area is based on a circular area using the average radius for each plot.

Plot ID	Treatment	Radius	Area (m^2)
3	control	11.88	443.01
4	control	9.00	254.47
7	control	6.73	142.08
8	control	8.89	248.15
2	herbicide	6.50	132.73
11	herbicide	5.55	96.77
15	herbicide	9.15	263.02
16	herbicide	6.10	116.90
6	herbicide & removal	6.48	131.71
9	herbicide & removal	7.40	172.03
12	herbicide & removal	3.40	36.32
14	herbicide & removal	5.15	83.32
1	disruption	5.00	78.54
5	disruption	12.60	498.76
10	disruption	5.28	87.42
13	disruption	6.73	142.08
	$\bar{x}$ =	7.24	182.96 ± 130.38 (SD)

Survivorship and growth rate of outplantings

Overall, survivorship among planted seedlings in tree canopy plots was 75.8% across all plots and treatments. We found no significant variation in survivorship of five species among treatment groups in tree canopy plots (‘a‘ali‘i: $F = 0.77$, $p = 0.552$; koa: $F = 1.44$, $p = 0.435$; māmaki: $F = 0.48$, $p = 0.677$; māmane: $F = 2.87$, $p = 0.258$; pilo: $F = 0.94$, $p = 0.552$; Figure 25). Too few ‘ākala were planted in tree canopy plots to adequately compare survivorship among treatment groups. However, of the eight individuals planted in tree canopy plots, only one (12.5%) survived to 24 months. Only ‘ōhi‘a survivorship varied among the treatments in which this species was planted ($F = 385.36$, $p = 0.003$, $df = 2$; Figure 25). ‘Ōhi‘a survivorship was much lower in control treatment compared to the other two treatments (herbicide: $t = 25.95$, $p = 0.002$; disruption: $t = 24.65$, $p = 0.002$), although this species was planted in only one control plot.

Unlike outplanting plots, we found no significant variation in mean plant height among treatments in any species planted (‘a‘ali‘i: $F = 0.1$, $p = 0.958$; koa: $F = 1.07$, $p = 0.517$; māmaki: $F = 0.35$, $p = 0.743$; māmane: $F = 1.05$, $p = 0.487$: ‘ōhi’a: $F = 1.86$, $p = 0.35$; pilo: $F = 1.02$, $p = 0.53$; Figure 26).

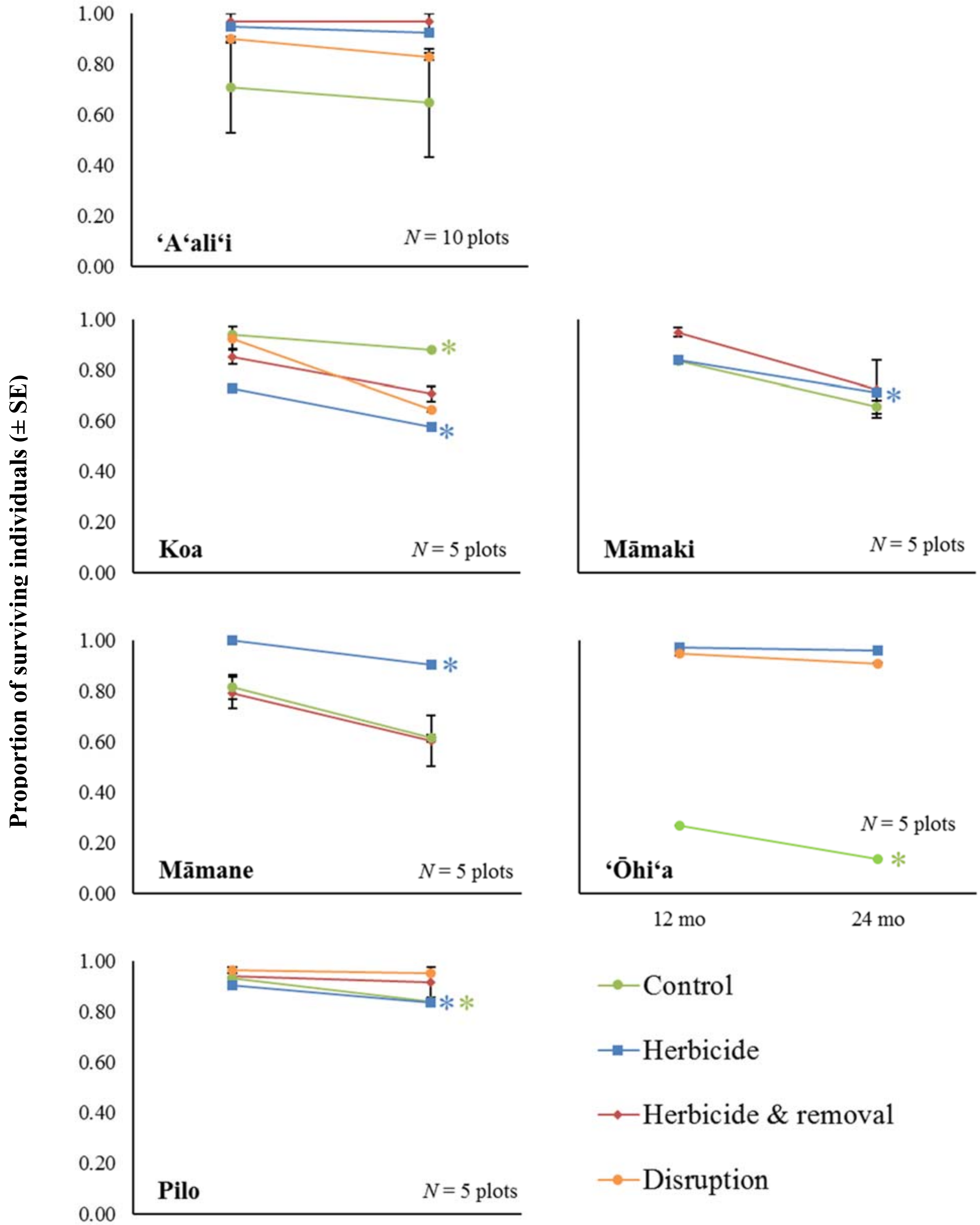

Figure 25. Mean proportion of surviving planted seedlings per treatment among seven species. Only one of eight 'ākala plants survived to 24 months. Asterisks indicate species without replication within a treatment, and, thus, the standard error could not be calculated.

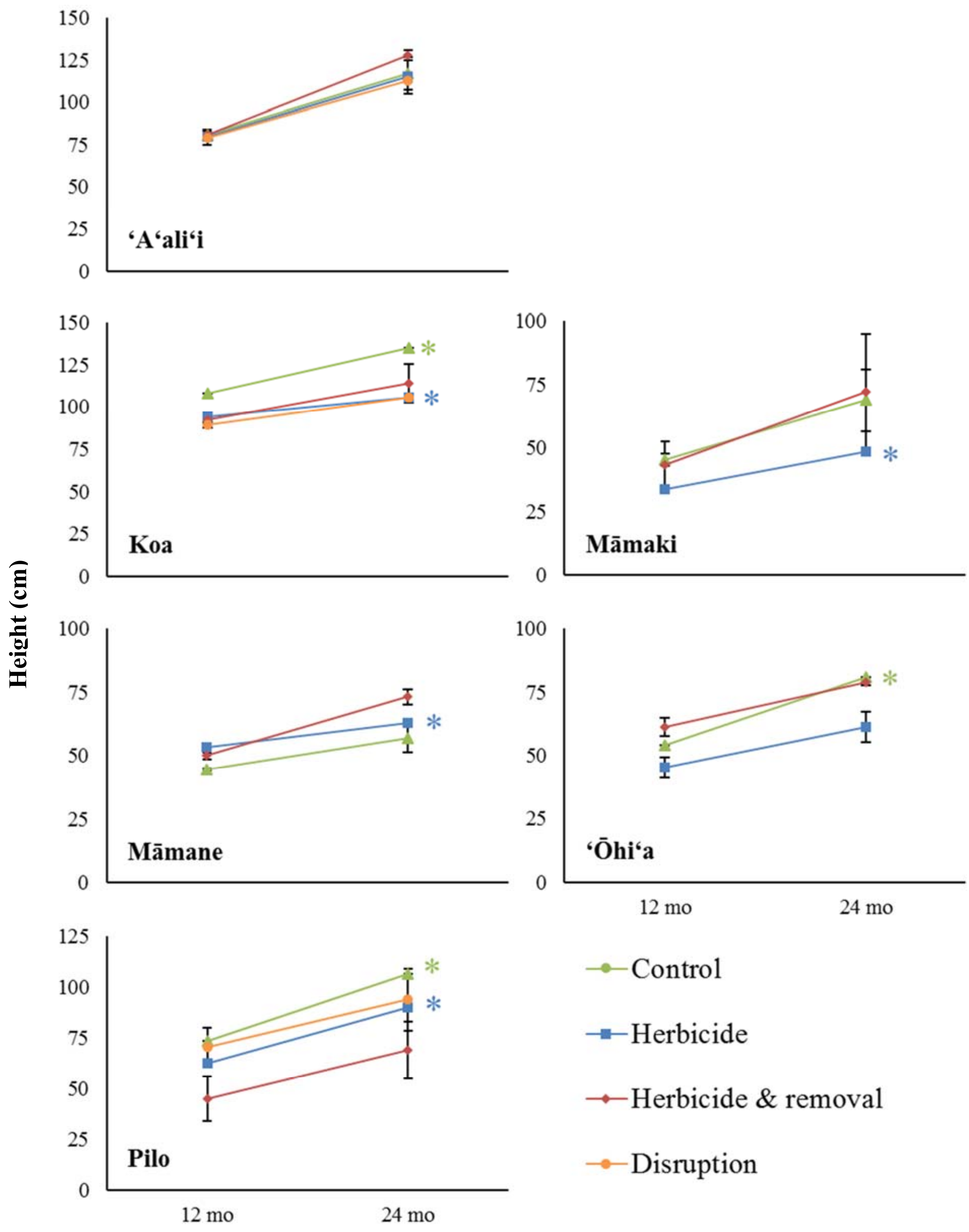

Figure 26. The average height of seedlings (cm) planted seedlings per treatment among seven species. Too few 'ākala were planted to compare among treatments. Asterisks indicate species without replication within a treatment, and, thus, the standard error could not be calculated. Y-axes differ among panels.

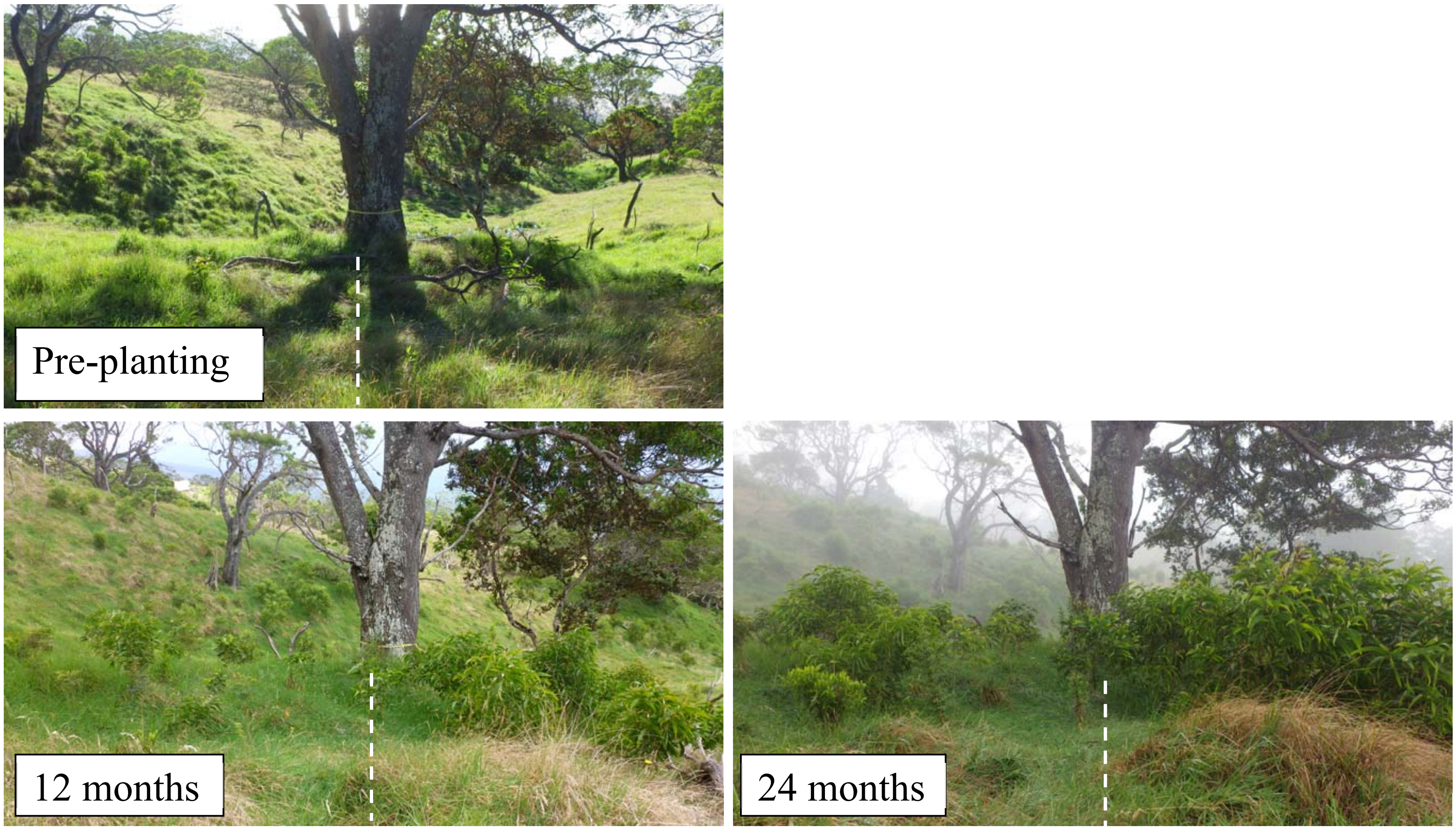

Figure 27. Progression of a tree canopy plot prior to treatment (control in this case) and planting, after 12 months post-treatment and planting, and after 24 months. The white dashed line delineates the outplanting (left) and natural regeneration (right) halves of the plot.

Comparison among Plot Types

Naturally regenerating seedling diversity

Six species of woody plants were recorded as naturally regenerating seedlings in experimental plots – five native and one invasive. The vast majority of these seedlings in all plot types were ‘a‘ali‘i. As all plots were located within the same relatively small 18.5 ha area where the species is common, it is not surprising that ‘a‘ali‘i seeds would reach most plots. However, dispersal was clearly not uniform as abundance of natural regenerating ‘a‘ali‘i varied among plots. Like ‘a‘ali‘i, koa are common in the trial area and the presence of the species would be expected in plots. The remaining species recorded primarily use animal-assisted dispersal mechanisms. The presence of pilo, ‘ōhelo, and *Bocconia* in tree canopy plots are likely the result of ornithochory where the large koa at the center of these plots provided perches for birds. The absence of these species in the other plot types may be a result of their location in the open grassland, which lack perches. As these plots mature, planted and naturally regenerating seedlings likely will provide foraging habitat and perches for birds and thus greater potential for dispersal of these species in the future. Birds can also disperse pūkiawe seeds, but most native songbirds avoid the fruit of this species (Wu et al. 2014, Pechjar et al. 2015). Nēnē (*Branta sandvichensis*) and non-native game birds regularly eat pūkiawe fruit and are typically found in open, grassy habitat (Baldwin 1947, Schwartz and Schwartz 1951, Black et al. 1994, Cole et al. 1995, Banko et al. 1999). Nēnē and ring-necked pheasants (*Phasianus colchicus*) were commonly observed foraging in experimental plots.

Growth rate and survivorship – Outplanting vs. tree canopy

Plot type (i.e., outplanting or tree canopy) affected planted seedling survivorship in most species. Survivorship was greater in outplanting, or low canopy cover, plots in three species: ‘a‘ali‘i (t = -2.22, p = 0.037), māmane (t = -4.66, p < 0.001), and pilo (t = -3.38, p = 0.008; Figure 28). In contrast, māmaki survivorship was greater in tree canopy plots (t = 2.08, p = 0.064). The effect of plot type on koa survivorship varied among treatments (F = 7.79, p = 0.017, df = 7; Figure 29). Koa survivorship was greater in outplanting plots in herbicide (t = -6.42, p = 0.004) and herbicide & removal (t = -5.39, p = 0.001), but not in control plots (t = -0.89, p = 0.403). However, we did not have plot-level replication in koa planted in herbicide and control tree canopy plots. The effect of plot type on survivorship of ‘ōhi‘a also varied among treatments (F = 148.26, p < 0.001, df = 11). Survivorship of ‘ōhi‘a was greater in outplanting plots in the control treatment (t = -15.33, p <

0.001), but did not differ in herbicide treatment (t = -0.16, p = 0.879). We did not have plot-level replication in ʻōhiʻa planted in control tree canopy plots. Overall, with the exception of māmaki, seedlings grown in outplanting plots had greater survivorship than those grown in tree canopy plots.

Plant height was affected by plot type in a few species but, as in survivorship, the effect was not uniform. ʻAʻaliʻi seedlings were larger in tree canopy plots (t = 2.95, p = 0.007; Figure 30). Māmaki height differed between plot types in two treatments, herbicide & removal and control, but not herbicide (F = 5.88, p = 0.027, df = 8; Figure 31). In both cases māmaki planted in tree canopy plots were larger on average than those in outplanting plots (herbicide & removal: t = 4.8, p = 0.001; control: t = 5.49, p = 0.006). In contrast, koa seedlings were smaller in tree canopy plots (t = -3.24, p = 0.01; Figure 30). No other species differed in height among plot types (māmane: F = 0.18, p = 0.679, df = 10; ʻōhiʻa: F = 0.004, p = 0.953, df = 12; pilo: F = 0.25, p = 0.63, df = 9).

Koa showed the most marked differences as a whole in survivorship and height among the plot types, with seedlings planted in tree canopy plots showing reduced survivorship and being > 40 cm smaller on average than in other treatments (Figure 29 and Figure 30). Outplanted koa seedlings were larger than naturally regenerated seedlings or root shoots (F = 6.23, p = 0.019) but did not differ by treatment (F = 1.24, p = 0.338). This may indicate that the negative effects of increased canopy cover are not restricted to outplanted seedlings. The other canopy species, ʻōhiʻa and ʻaʻaliʻi, both generally had greater survivorship in outplanting plots. However, ʻaʻaliʻi seedlings had increased growth in tree canopy plots, while ʻōhiʻa growth was not affected by plot type.

Māmaki was the only species that generally responded favorably to being planted in the tree canopy plots, showing increased survivorship and growth rates (Figure 28 and Figure 31). We anticipated that an understory shrub like māmaki would show optimal growth under increased moisture conditions (Cordell et al. 2009).

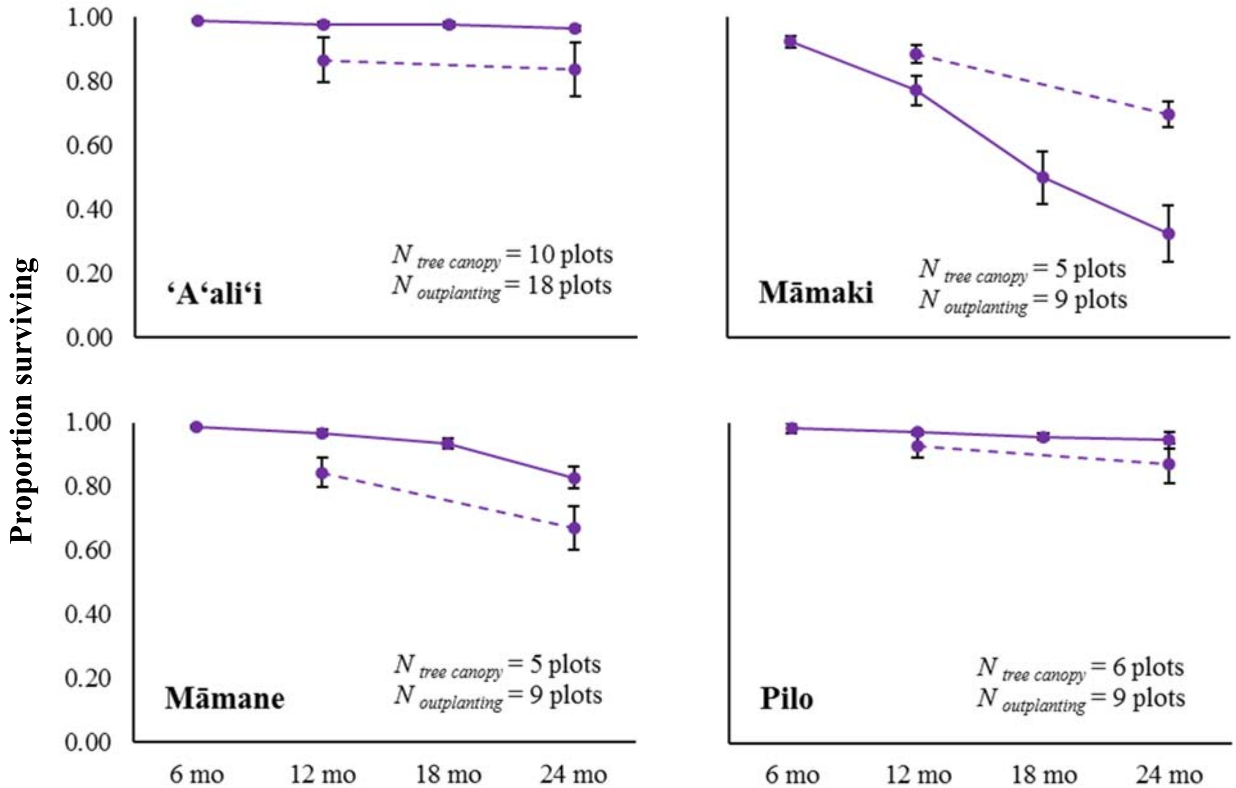

Figure 28. The proportion of surviving individuals planted in outplanting (solid lines) and tree canopy (dashed lines) plots.

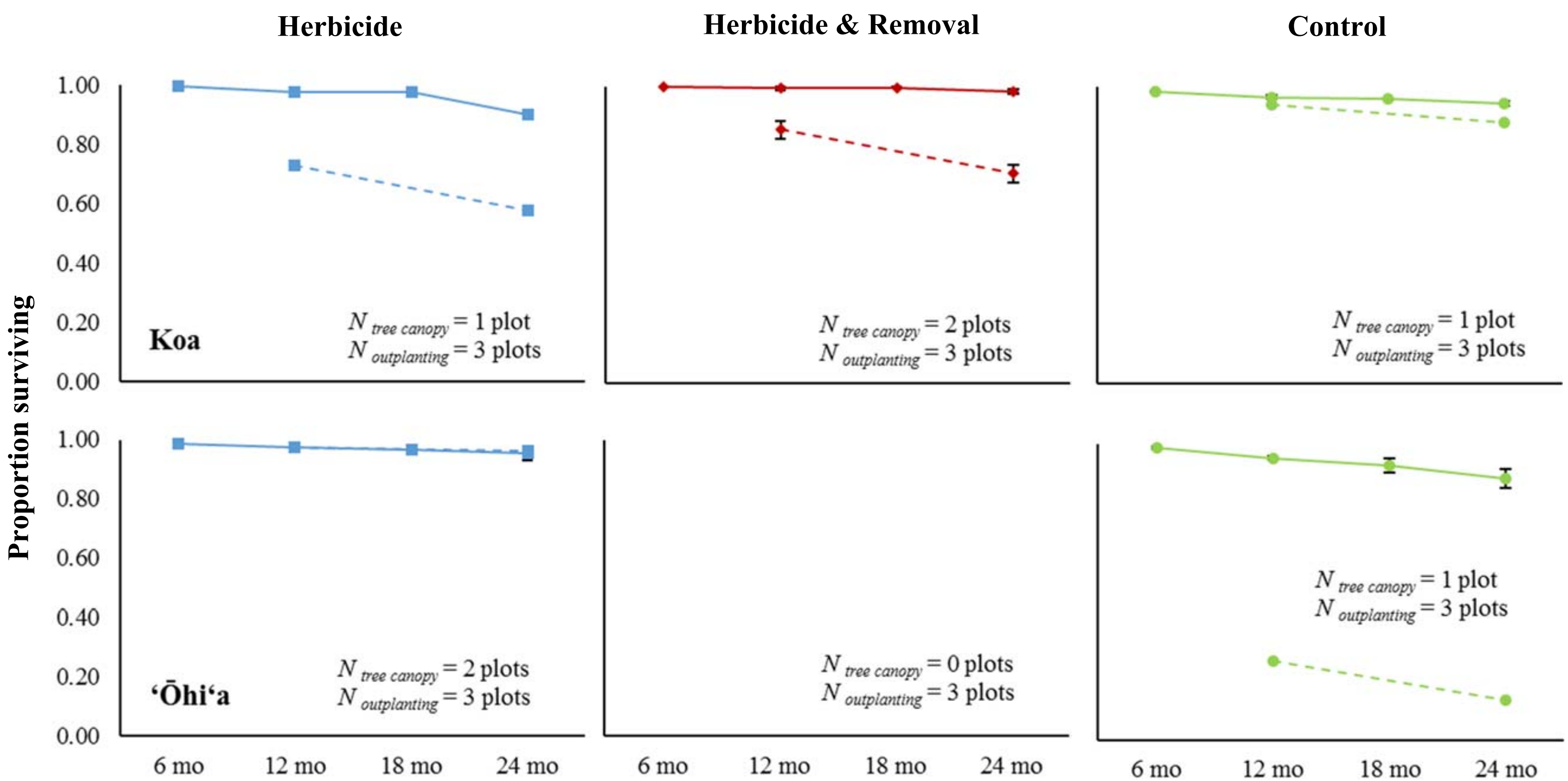

Figure 29. The proportion of surviving koa (top panels) and ʻōhiʻa (bottom panels) individuals planted in outplanting (solid lines) and tree canopy (dashed lines) plots.

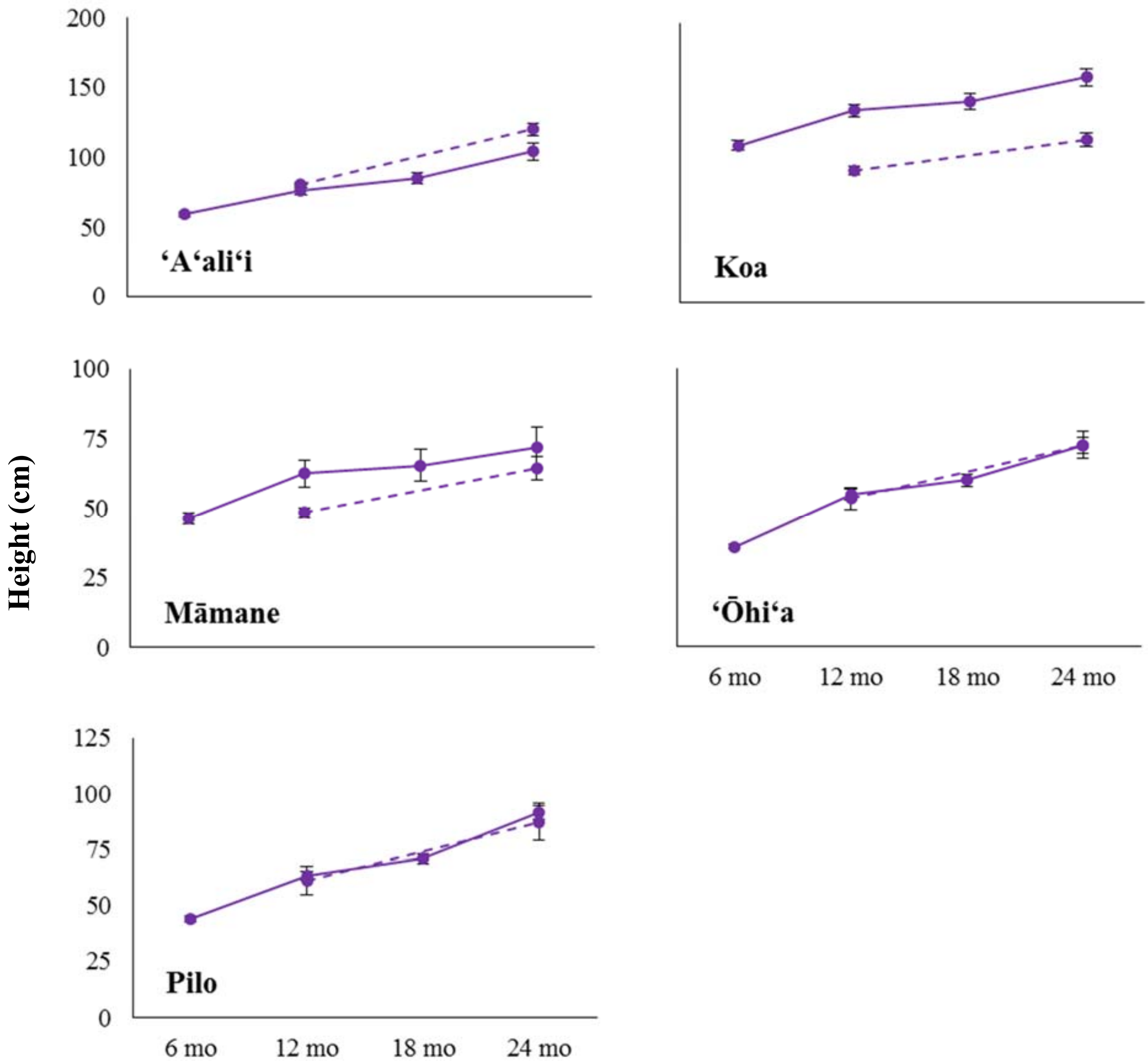

Figure 30. The average height of surviving individual seedlings planted in tree canopy plots (dashed line) and in outplanting plots (solid line) in each of three treatments.

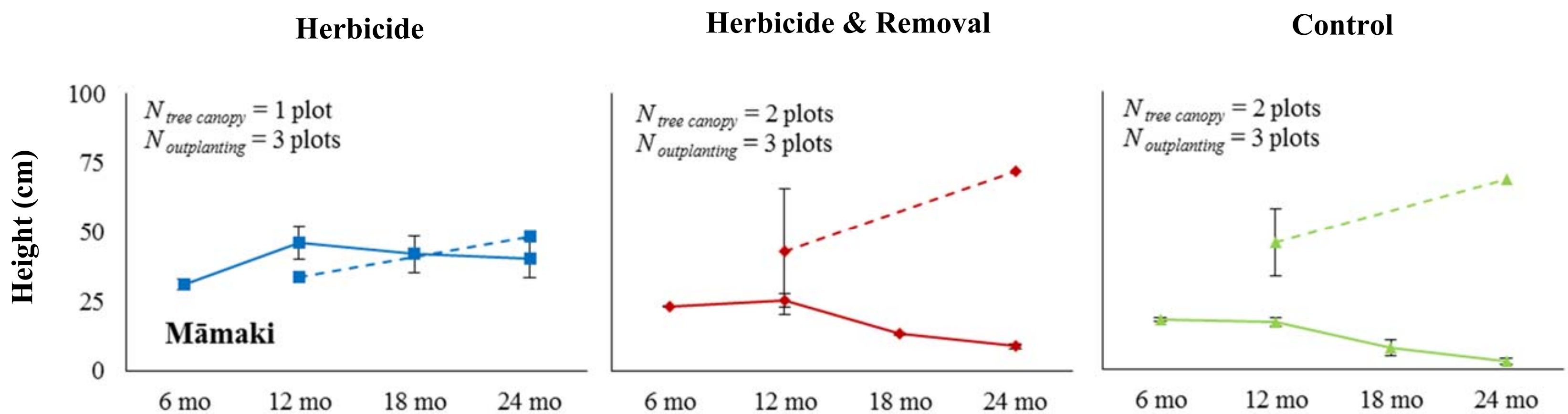

Figure 31. The average height of māmaki seedlings planted in tree canopy plots (dashed line) and in outplanting plots (solid line) in each of three treatments.

DISCUSSION

One of the primary goals of our restoration trials was to measure the natural regeneration that occurred in the initial period following ungulate removal from Nakula NAR. We found that a few species, primarily ‘a‘ali‘i and koa, were able to increase in density and overall cover in Nakula via the existing seed bank or seed dispersal into the site given sufficient time without ungulate pressure. This strongly suggests that the seed bank in the open savanna-like habitat is depauperate following more than a century of ungulate pressure. Alternatively, the seed bank may be intact but our treatments failed to stimulate germination or at least failed to do so within the 18-month window before the grass cover returned to pre-treatment levels. ‘A‘ali‘i seedlings and koa seedlings, or root shoots, appear capable of growing through the non-native grass mat to a certain extent in many areas. The natural regeneration of these species may provide microhabitats that will facilitate the germination and growth of additional native species in the future (Scowcroft and Jeffery 1999, Medeiros et al. 2014). For example, we have anecdotally observed non-native grass to become reduced under dense groves of koa root shoots which produce shade and a layer of leaf litter. However, once these root shoots grow to sufficient height to allow light to reach the ground, grass appears to re-grow quickly and may lead to a reduction in natural recruitment of other species (Yelenik 2017). The low diversity of naturally regenerating seedlings suggests that planting a wider diversity of species may be a vital to restoring function to this forest.

Regeneration of native seedlings following release from ungulate pressure has been seen in many Hawaiian forests (Loope and Scowcroft 1985, Hess and Jacobi 2011, Hess 2016), although this type of natural recovery is not always observed (e.g. Jacobi 1980). In our trials, natural regeneration was enhanced by the complete removal of grass cover to expose bare soil. This is consistent with other studies in mesic forest environments in Hawai‘i (Cabin et al. 2000, McDaniel et al. 2011, Thaxton et al. 2012). In Nakula, we observed naturally regenerating ‘a‘ali‘i seedlings over much of the site including control plots where non-native grasses were dominant. While the species appears capable of regenerating naturally, our results indicate that the abundance of naturally regenerating ‘a‘ali‘i can be increased by removal of grass. Unless natural regeneration without intervention can produce densities of ‘a‘ali‘i necessary to competitively exclude grasses, this technique provides a more efficient and likely more cost-effective solution to increasing ʻaʻaliʻi cover compared to outplanting. This technique has been replicated on a larger scale in Nakula resulting in areas with high densities of ʻaʻaliʻi, while also providing places to plant seedlings of additional species to increase diversity (Figure 32).

Figure 32. Example of enhanced natural regeneration as a result of the herbicide & removal technique applied in strips snaking down the hill.

High diversity of native trees and shrubs is thought to be an important element of Kiwikiu habitat (Stein 2007). If the seed bank in Nakula is depauperate and largely restricted to a few wind-dispersed species, native plant diversity may only increase naturally through animal-assisted seed dispersal. Much of this dispersal will likely be facilitated by two non-native passerines, the Red-billed Leiothrix and the Japanese White-eye, and to a lesser extent the native Hawaiʻi ʻAmakihi (Foster and Robinson 2007, Pejchar 2015). The proliferation of some native species like ʻoha wai (*Clermontia kakeana*), ʻolapa and ʻolomea throughout the site since 2016 suggests that bird-assisted seed dispersal is already having an impact on the diversity of the Nakula forest since this experiment was completed. Unfortunately, the non-native passerines are smaller than some of the now-extinct seed dispersers (e.g. ʻOlomao, *Myadestes lanaiensis*) and have been shown to only disperse a subset of available native seeds (Pejchar 2015), as well as several habitat-modifying invasive weeds (Woodward et al. 1990, Medeiros 2004, Chimera and Drake 2010). Some native plant species may also be dispersed by Nēnē (Baldwin 1947, Black et al. 1994, Banko et al. 1999) and non-native game birds like Ring-necked Pheasants (Schwartz and Schwartz 1951, Cole et al. 1995), especially in open areas. However, dispersal by these species will likely be limited to native shrubs such as pūkiawe and ʻōhelo, which are already present in the open areas of Nakula. Naturally regenerating ʻaʻaliʻi and koa may promote increased plant diversity not only via the suppression of grass, as we discuss above, but also by providing perches for seed-dispersing birds (Scowcroft and Jeffery 1999). Non-native rodents may also facilitate seed dispersal of smaller native and non-native seeds, but these animals are also known seed predators, especially of many vulnerable larger-seeded taxa (Shiels and Drake 2011). Rat densities have been shown to increase as forest cover increases in nearby forests (Shiels et al. 2017). Thus, their densities and potential dispersal benefits, may also increase in response to the on-going restoration and regeneration in Nakula. However, because of the well-documented detrimental effects to native birds (Atkinson 1977), invertebrates (Hadfield et al.1993, Cole et al. 2000, Hadfield and Saufield 2009), and both common and endangered plant species (Stone 1985, Sugihara 1997, Cole et al. 2000), the overall negative impact of increased rat densities to the native plant and animal community will almost certainly outweigh their dispersal benefits, and will likely threaten the survival of any native birds introduced to the area in the future

Strategic placement of restoration activities (e.g. outplanting, stimulating natural regeneration) may also increase forest cover by promoting increased bird movement throughout the site. By planting species that produce fleshy fruits (at least species known to be distributed by the resident bird species), we may be able to attract more birds to the areas with little diversity in naturally regenerating plants. Additionally, many of the seed-dispersing bird species present (e.g., Red-billed Leiothrix) are forest species that avoid open areas. Wu et al. (2014) found that Japanese White-eyes travelled on average < 200 m within the typical gut passage time in a different fragmented Hawaiian forest habitat, i.e. kīpuka habitat. The native ʻOmao (native to Hawaiʻi Island and sister to the extinct Maui species, ʻOlomao) travelled < 100 m in that time. Although not tested in Wu et al. (2014) it is possible that the Red-billed Leiothrix may behave more like ʻOmao, choosing to stay in close cover for longer periods. By planting in areas to connect existing forest patches, birds may occupy these corridors and patches and spread seeds into areas that they may have otherwise avoided. It would be important to know the minimum distance between trees that these seed dispersers will accept. However, based on the typical movement patterns of these seed dispersers, these outplanting corridors should be designed to reduce the gaps between forested areas to less than 100 m. MFBRP has strategically planned many of its landscape-scale outplantings to connect forest patches specifically to facilitate bird movements to increase outcrossing in plant species and seed dispersal. Increased movement of non-native frugivorous birds is likely to also increase the probability of the dispersal and establishment of many invasive plant species into the site (Woodward et al. 1990, Medeiros 2004, Chimera and Drake 2010). Thus, management efforts to control these weeds may need to increase as forest cover expands.

In these trials, we had no success with seed broadcast as a restoration technique for the species tested. In contrast, a similar study in Kahuku on Hawaiʻi Island had success producing seedling koa, pilo and ʻōlapa via seed augmentation (McDaniel et al. 2011). Notably, the seeding densities used by McDaniel et al. (2011) were much higher than we used in our study. These authors found seedling densities produced using this method were highest in plots where grass cover was reduced. Denslow et al. (2006) had success in producing ʻaʻaliʻi seedlings through seed broadcast, although only in areas treated with herbicide. Brooks et al. (2009) also employed a combination of herbicide treatment and broadcast seeding to successfully establish a suite of native seedlings in a montane dry forest on Hawaii island. Given these author's success, this may still be an option in Nakula, particularly in areas with low natural regeneration like the West Pahihi unit. As a technique the cost of seed broadcast is primarily in collecting and preparing seeds. ʻAʻaliʻi is a highly productive species and seeds are easily collected, making seed broadcast a potentially cost-effective technique for this species. The cost of collecting and cleaning seeds of other species is likely much higher. We did not include ʻaʻaliʻi in the seeding group in this study because of the difficulty of determining if an individual ʻaʻaliʻi seedling was a product of the existing seed bank or via seed broadcast. If managers do consider this technique for ʻaʻaliʻi, prior grass suppression is recommended given the results from Denslow et al. (2006).

When planted densely, ʻaʻaliʻi has shown the ability to resist grass reinvasion and promote natural regeneration of other native species through the seed bank and, possibly, through bird-dispersal (Medeiros et al. 2014). ʻAʻaliʻi is not known to serve as a foraging substrate for

Kiwikiu but this may be because it is currently rare in the bird's current range. Even if it is not a favored food source, it is a keystone species in Kahikinui and may be critical to restoration efforts. We found that removing grass through a combination of herbicide and manual means can produce high densities of ʻaʻaliʻi (Figure 10 and Figure 33). Natural regeneration also occurred in the untreated areas outside of the plots but tree densities were much lower in untreated areas (Figure 10). From the densities observed to date, it seems unlikely that the unassisted regeneration from the existing seedbank will be able to competitively exclude grass and thereby enhance recruitment of other species in the short-term. In comparison, the density of ʻaʻaliʻi achieved through the herbicide & removal method has the potential to promote rapid recruitment. It is important to note, however, that the effect of this treatment was not uniform. Some plots had high densities of ʻaʻaliʻi, while others produced no more seedlings than most control plots. Perhaps the addition of seed broadcast would facilitate high densities of ʻaʻaliʻi following grass removal even in areas with depauperate seed banks.

The natural regeneration seen within the plots, as well as anecdotal on-site observations, indicates the need for substantial restoration efforts to increase species diversity across Nakula. While natural seed dispersal will play an important role in the long term, outplanting may be the only way to increase abundance of many plant species in the short term. This may be particularly true for subcanopy and understory species that have shown limited recruitment to date, such as kōlea, ʻōlapa, and ʻalani (see Table 1). Outplanting may also be required for common species, like ʻaʻaliʻi and koa, in areas where natural regeneration has been minimal, for example, in the upper elevations of the Wailaulau or most of the West Pahihi unit. As much of the natural regeneration of koa appears to be through clonal root shoots, outplanting of koa seedlings may be required to promote genetic diversity of the species to protect against disease or other factors that could decimate a genetically uniform population.

Our outplanting trials showed that, although labor-intensive and expensive, outplanting is the most highly effective restoration tool for Nakula NAR. The high survivorship of most species in trial plots is encouraging given the costs required to produce, transport, and plant seedlings in the reserve. Medeiros et al. (2014) had high survivorship in ʻaʻaliʻi (> 95%) in nearby Auwahi. McDaniel et al. (2011) also saw high survivorship in koa (77%), and pilo (71%; *Coprosma pubens*), although lower than what we observed in Nakula, 95.5% and 94.7% respectively.

However, māmaki survivorship was much greater in their study at 61% compared to 32.2% in the present study. It is possible that the additional water McDaniel et al. (2011) applied to seedlings at planting provided some survivorship benefits to māmaki. McDaniel et al. (2011) found survivorship of koa and pilo to be highest in a version of the herbicide & removal treatment that included applying herbicide and then tilling the soil with an earthmover several months later. While, the use of heavy machinery would not be possible in Nakula, perhaps simply removing the dead grass material following herbicide application was insufficient to see the benefits of soil disruption on outplanting.

Given the cost of outplanting, any cost-effective methods that can improve survivorship are worth investigating. We saw little effect of treatment on overall survivorship in most species. However, patterns of mortality may tell us more about the limiting factors affecting seedlings post-planting (Figure 17). Several species included in this study (e.g. ʻākala, pilo) showed the highest rates of mortality early in the experiment, which may indicate a failure of seedlings to become established. Māmane saw the highest rates of mortality at the end of the experiment possibly indicating that this species has different limiting factors than the other species. This is in contrast to the comparatively low one-year survivorship of planted māmane on Mauna Kea; 68% (K. Asing *pers. comm.*) compared to 96.7% here. It is likely that in a colder, drier habitat like Mauna Kea, failure to establish may be a greater source of mortality than what we observed in Nakula. One explanation for the later mortality in Nakula is grass competition. This is supported by the fact that so many māmane seedlings remained small and tangled in grass throughout the experiment. However, we cannot rule out other factors affecting survivorship of this species. While māmane survivorship varied by treatment, the pattern of mortality was the same indicating that even when grass is suppressed, māmane can still struggle against grass competition in later stages. Yelenik et al. (2017) found a positive effect of removing grass on māmane seedling survival, further suggesting that the explanation for later mortality may be increasing competition with grass. The greater average height of māmane in the herbicide plots may indicate that these plots contained fewer very small, stunted individuals. If the larger individuals in the herbicide plots are large enough that grass competition (or at least “smothering”) is less of an issue, then this may be another benefit of herbicide application prior to planting. Alternatively, killing the grass (but not removing the duff) may have provided a moisture benefit to māmane seedlings allowing some individuals to grow faster and increase their chances of surviving in the long run.

Survivorship of planted seedlings is a critical element to evaluate the effectiveness of outplanting as a strategy, but measuring growth and overall quality of the planted seedlings is required to evaluate long-term success of the project. The herbicide treatment conveyed a growth advantage to ‘a‘ali‘i, ‘ākala, māmaki, and māmane (Table 6). In māmaki, this effect was most pronounced where seedlings planted in control and herbicide & removal plots were much smaller on average than those planted in herbicide plots. The herbicide treatment is also where māmaki had its highest survivorship rates. This may indicate a connection between survivorship and plant height, possibly because seedlings had passed a critical height threshold necessary to reduce grass competition. During monitoring we often located (with great difficulty at times) very small surviving māmaki deep in the grass. Many of these individuals may have been able to survive for a time with little light or other resources, but ultimately succumbed to the pressures of grass competition. In contrast, individuals that were freed from grass competition in the herbicide treatment grew at a greater rate and were of a size to be able to compete with the grass once grass cover returned to pre-treatment levels. Māmaki survivorship and height were lower in the herbicide & removal plots indicating that the removal of the dead grass material in these plots negatively affected growth rate in māmaki. It is possible that moisture loss as a result of exposing the topsoil led to direct mortality or reduced growth rates, ultimately resulting in a seedling too small to compete with the returning grasses.

A similar pattern was evident with māmane height and survivorship but to a lesser extent given the overall high survivorship of the species. However, if plant height is an indication of overall plant vigor, māmane planted in the herbicide plots may continue to appreciate greater survivorship into the future and we would expect to see a greater difference in survivorship rates over the next few years. A seedling may survive for many years, but grow so slowly that it contributes very little to the ecosystem as a whole, particularly for the native birds, and the benefits of planting that seedling are few. Māmane can be slow growing as seedlings (Hess et al. 1999), so it is possible these individuals will continue to grow over the decades, or they may linger at the same size and die later, never having contributed to the forest structure or overall ecosystem processes. Planting larger seedlings than those in this experiment may increase overall survivorship. Many ecologically important species, such as ʻōhiʻa, are slow growing and will not contribute much to forest structure for some time but this does not diminish their potential importance to the climax community. This forest was degraded over a period of over 150 years and we still know little about how long it may take the forest to return. We plan to monitor these plots at five-year intervals in the future beginning in July 2018. Continued monitoring will allow us to determine the ultimate fate of these small individuals and other factors affecting older life stages.

Results from the tree canopy plots provide additional information into potential site selection of future outplantings or other restoration activities. With the exception of koa, all species grew fairly well under existing koa canopy cover, although many did better planted out in the open. Species that are water-limited, like māmaki, may be more successful planted under trees in this fashion. Planting in these areas may also benefit species that are sensitive to high-light levels. Although treatment had little effect on planted seedlings in tree canopy plots, it may still be important to suppress grass prior to planting to balance out increased grass growth under koa canopy as has been seen in the koa-dominated forest in Hakalau NWR (Yelenik 2017). In choosing future outplanting sites, existing canopy cover should not be avoided wholly, but the species planted in these conditions should be carefully selected. We planted species that occupy the canopy, subcanopy, or understory in Hawaiian forests. The successional nature and specific optimal conditions of each species likely play a large role in the success of a planted seedling (Yelenik et al. 2015). For example, an understory species, like māmaki, may survive and grow best in high moisture environments. In this case, our results seemed to confirm this in that māmaki showed higher survivorship and growth in tree canopy plots than outplanting plots out in the open. Primary succession species or canopy species, like koa, did comparatively poorly in the tree canopy plots. This kind of intraspecific competition may have ramifications for restoration plantings, indicating that koa, at least, should not be planted under mature canopy and do best when planted in the open.

The success of a species in any given environment is also dependent on the plasticity of the species to the conditions of that environment. We planted seedlings in outplanting and tree canopy plots, which can be classified as low canopy cover and high canopy cover, respectively. Comparing growth rates and survivorship among the different species in these two factor groups may tell us more about the general conditions in which each species does best as outplantings. This may also offer a window into the plasticity exhibited by a given species for traits relating to growth and survivorship in relatively high- and low-light and moisture conditions. Survivorship of pilo and māmane were lower in tree canopy plots but height was not affected by plot type in either species. Given that pilo, in particular, is naturally almost exclusively found under canopy cover, it is somewhat surprising that this species did not do as well in the tree canopy plots. Other pilo species, like *Coprosma montana* and *C. ernodioides*, are often found in exposed habitats away from canopy cover. Our results may indicate that *Comprosma stephanocarpa* and *C. cordicarpa* retain traits that make the species plastic and grow well in a variety of environmental conditions and that while these species may be shade-tolerant, they are not restricted to these conditions. Despite often being found in the understory in forested habitats, māmane can also be a primary succession species in shrubland habitat or even the climax forest in subalpine zones, indicating that the species has a high tolerance for high light, low moisture conditions. The lower survivorship of māmane in tree canopy plots may indicate that the environmental tolerances of the species are more like those of a primary succession canopy species, such as koa. Additionally, Yelenik et al. (2017) found reduced māmane survivorship when nitrogen was experimentally elevated. This could indicate that a high nitrogen soil environment, such as under a koa, may be detrimental to māmane success.

A comparison of seedling density and diversity among the plot types included in this study can be helpful in determining the level of effort that may be required to meet certain expectations and restoration goals. In outplanting plots, we planted 150 seedlings, a seedling density of 1.5 seedlings per 1 m^2. This density was influenced by naturally regenerating seedlings and by mortality of planted and wild seedlings. Overall, survivorship in outplanting plots was 82.8 ± 2.5%, approximately 124 individual planted seedlings. Additionally, an average of 5.25 ± 1.3 naturally regenerating seedlings were found in outplanting plots at 24 months. Thus, after 24 months, outplanting plots had approximately 129 individual seedlings or a density of 0.86 seedlings/m^2. By-and-large no other factor type resulted in a seedling density as high as that found in the outplanting plots. Overall, we found 65.04 ± 22.3 naturally regenerating seedlings on average in natural regeneration plots for a density of 0.65 seedlings/m^2. However, in natural regeneration plots in the herbicide & removal treatment we found an average density of 1.78

seedlings/ m^2. Thus, by using the herbicide & removal technique we were able to produce a higher density of seedlings than any factor and treatment tested, including outplanting. However, even though we only planted three species in each plot, the extremely low diversity in the naturally regenerating seedlings meant that the outplanting plots had higher species diversity. The positive effect of the herbicide & removal treatment was also not uniform, even among plots within this treatment group. Thus, application of this treatment does not guarantee high density of seedlings compared to outplanting.

Figure 33. Photo of a natural regeneration plot that received the herbicide & removal treatment taken about mid-way through (top) and after (bottom) the trial period in January, 2015 and November 2017, respectively. The dashed line indicates the approximate borders of the plot. This photo shows the difference between the unassisted natural regeneration outside of the plot and the assisted regeneration inside the plot.

Figure 34. Photo showing an example of how grasses may be suppressed via shading and leaf litter in an outplanting plot.

CONCLUSIONS

The forest in Nakula NAR has shown a remarkable ability to rebound from over a century of ungulate damage, but without additional management, progress will likely be slow in returning the area to a diverse, functional forest ecosystem. Establishing ultimate restoration goals (e.g. % canopy cover) toward returning Nakula to a pre-ungulate state is hampered by the fact that this forest saw considerable damage prior to any historical biological descriptions of the habitat. As a result, we only have a partial picture of the "natural state" of the Kahikinui mesic forest. Naturally regenerating ʻaʻaliʻi and koa have already transformed much of the Wailaulau unit and forest cover will continue to increase through the seed bank without additional intervention. However, increasing diversity may only be achieved, at least in the short term, through outplanting. This diversity may be crucial to restoring a functional ecosystem capable of sustaining species like Kiwikiu (Stein 2007). Whether the habitat in Nakula is currently sufficient to support Kiwikiu is unknown. Based on the habitat preferences measured in its current range, increasing diversity and density of native tree and shrub species will undoubtedly increase the chance of Kiwikiu being successful in Nakula. These trials indicate the need for continued management to support this goal.

The results of these trials likely are most applicable to the grass-dominated habitats characteristic of large areas of Kahikinui, particularly the western half of the region. Many other areas in the region have seen significant erosion. In the most extreme cases the topsoil has been completely lost. These "erosion scars" become more common east of Nakula and cover large areas of eastern Kahikinui and Nuʻu. Clearly, additional strategies will be needed to restore these areas beyond what our trials addressed. MFBRP has experimented with outplanting in the smaller erosion scars within the Wailaulau unit of Nakula NAR. In this unit, the erosion scars can span for several hundred meters down a ridge but are rarely more than a few meters wide. ʻAʻaliʻi planted in these scars seem to have an extremely delayed establishment period (> 3 years to see vertical growth) but have high survivorship. Even the largest of these plants, however, do little to slow erosion. Additional techniques like establishing berms, planting native grasses, transplanting ferns, and planting species that grow vegetatively, like ʻākala, may help slow erosion. These methods are currently being tested by LHWRP and MFBRP.

These trials make it clear that in this fragmented mesic forest, the non-native grass mat negatively affects the germination and growth rates of native woody plants and that reduction of this grass leads to increased seedling survivorship and growth. Herbicide application can reduce these effects to aid in the establishment of wild and planted seedlings, but the effect is only temporary. Increasing canopy cover and density of woody plant species and/or ferns may be the only way to produce enough shading and leaf litter to control grasses. Landscape-scale outplantings have the potential to transform the area and increase the abundance of species that have so far shown minimal recruitment within the reserve (Figure 35). However, outplanting is not the only technique available to managers. Removal of grass cover through herbicide application followed by weed-whacking and raking is labor-intensive but the results can be very positive. The costs of this technique are likely to be much lower than outplanting and can result in dense stands of ‘a‘ali‘i capable of producing shade and leaf litter sufficient to reduce grass cover. Removing grass to promote natural regeneration followed by outplanting of target species may be the most effective and cost-efficient method of restoring this forest.

Figure 35. Photos showing several outplanting plots (highlighted in red) approximately half-way through the trials in February 2015 (top) and nearly four years after planting in August 2017 (bottom). The ʻaʻaliʻi in the foreground and between the plots are naturally regenerated seedlings germinating from the seed bank without intervention. The comparison between the densities of unassisted naturally occurring seedlings and outplanting plots is instructive of the short-term differences between a high-effort restoration method and allowing succession with no intervention.

RECOMMENDATIONS

The following are recommendations to managers based on the results of these trials for restoring the montane mesic forest in Wailaulau, Nakula NAR and the surrounding areas. This is designed to help managers choose the appropriate method for the desired effect.

1. Passive restoration
    a. Low-density native woody species
        i. No action required. Will result in a predominately ʻaʻaliʻi and koa forest in the short-term.
    b. High-density native woody species
        i. Apply herbicide & removal technique to achieve high densities of ʻaʻaliʻi.
2. Seed broadcast
    a. Not recommended for ʻākala, kāwaʻū, koa, kōlea, ʻōhelo, ʻōhiʻa, ʻōlomea, māmane, māmaki, or pilo.
    b. Possibly effective for ʻaʻaliʻi following pre-seeding herbicide application and/or disruption of grass mat.
3. Outplanting
    a. No pre-treatment
        i. Expect good results from koa, ʻōhiʻa, and pilo.

            Note: It is physically more difficult and inefficient to plant in dense grass.

        ii. Expect good survivorship but <u>reduced</u> growth rates in ʻaʻaliʻi and māmane.
        iii. Do <u>not</u> plant māmaki or ʻākala in areas without pre-treatment.
    b. Apply herbicide prior to planting
        i. <u>Highly recommended</u> for planting any species tested here.
        ii. Expect <u>high survivorship</u> in all species.
        iii. Expect <u>increased</u> growth rates in ʻaʻaliʻi, ʻākala, māmaki, and māmane.
    c. Remove grass duff following herbicide application
        i. Not recommended for māmaki.
        ii. Expect high survivorship in ʻaʻaliʻi, ʻākala, koa, māmane, ʻōhiʻa, and pilo.

        iii. Expect <u>reduced</u> growth rates in ‘a‘ali‘i, ‘ākala, and māmane compared to just herbicide alone without biomass removal.

    d. Choosing planting location

        i. Low canopy cover (high light)

            1. Expect <u>high</u> survivorship for ‘a‘ali‘i, koa, māmane, ‘ōhi‘a, and pilo.
            2. Expect <u>reduced</u> survivorship and growth rate in māmaki

        ii. High canopy cover (low light)

            1. Expect <u>reduced</u> survivorship for ‘a‘ali‘i, koa, māmane, ‘ōhi‘a, and pilo.
            2. Expect <u>increased</u> growth rates in ‘a‘ali‘i, and māmaki.
            3. Not recommended for koa. Expect <u>reduced</u> survivorship and growth rates.

4. Outplanting and promoting natural regeneration

    a. No pre-treatment

        i. Not recommended. Will likely have reduced outplanting success and only low densities of wild ‘a‘ali‘i and koa.

    b. Apply herbicide prior to planting

        i. Recommended for planting <u>all species.</u>
        ii. Expect elevated wild ‘a‘ali‘i seedling densities.

    c. Remove grass duff following herbicide application

        i. Not recommended for planting ‘a‘ali‘i, ‘ākala, and māmane due to reduced growth rates in these species.

            Note: In areas with good water retention and rich soils, ‘ākala can do very well.

            Note: There is no need to plant ‘a‘ali‘i due to likelihood of naturally germinating seedlings

        ii. Recommended for planting koa, ‘ōhi‘a, and pilo and can result in <u>high densities</u> of wild ‘a‘ali‘i seedlings.

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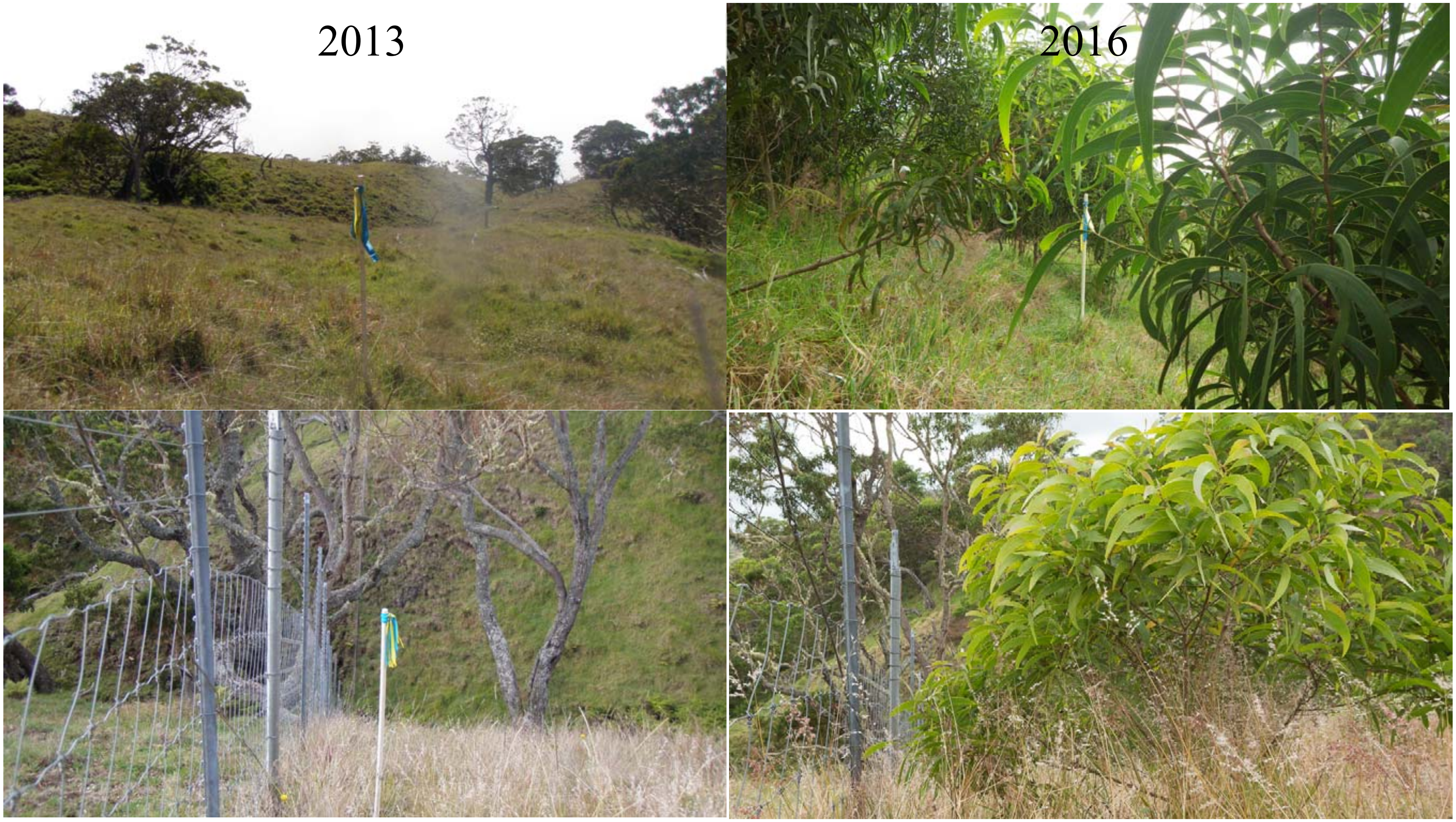
Appendix 1. Photo points showing progression of natural regeneration in the Wailaulau unit of Nakula NAR throughout the trial period. Each of the six photo points are shown in January 2013 (left panels) and in January 2016 (right panels) representing the beginning and the end of the experimental trials.


2013
2016


2013
2016