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Upward expansion of fire-adapted grasses along a warming tropical elevation gradient

Courtney L. Angelo and Curtis C. Daehler

C. L. Angelo (courtneyangelo@gmail.com) and C. C. Daehler, Dept of Botany, Univ. of Hawai'i at Manoa, 3190 Maile Way, Room 101, Honolulu, HI 96822, USA.

High mountain regions in the tropics have thus far been impacted relatively little by anthropogenic activity or plant invasions, however, they are unlikely to be immune to impacts of global change, including climate change and other anthropogenic disturbances. Changes in fire regimes are known to accelerate the spread of invasive C_4 grasses and interactions between changes in fire and climate can alter species distributions. The aim of this study was to compare grass distributions along an elevational gradient in Hawai'i between 1966–1967 and 2008 to determine whether C_4 and C_3 grass distributions are shifting upward in response to alterations in fire and climate patterns. Field plots at Hawai'i Volcanoes National Park were surveyed for grass species and cover at ~150 m elevation intervals and compared to previous surveys done in 1966–1967. We found that the transition elevation, marking a shift in dominance between C_4 and C_3 grasses based on relative cover, shifted upward over 40 yr (95% confidence interval = 1476 m ± 130 m in 2008 versus 1200 m ± 106 m in 1966–1967). On the other hand, maximum elevations of all C_4 or C_3 grasses as a group were not significantly greater than 1966–1967 elevations; however, a subset of C_4 (and fewer C_3) grasses moved to substantially higher elevations, and these were the species adapted to fire. 100% of fire-adapted grasses moved up in elevation compared to 29% of non-fire adapted species, and the change in elevation of those species ($\bar{x} = +454$ m) was significantly greater than the change in elevation of non-fire adapted species ($p = 0.003$). Our study documents an upward expansion of fire-adapted grasses at high elevations in the tropics as an important threat that seems to be compounded by warming trends.

Climate change has been predicted to increase invasions in tropical montane environments more so than in temperate montane environments (Bortenschlager 1991), however, current research has primarily addressed the influence of climate change on plant distributions in temperate ecosystems. Previous studies have investigated expanding elevational ranges of plants in response to climate change (Kullman 2002, Penuelas and Boada 2003, Kelly and Goulden 2008, Lenoir et al. 2008, Parolo and Rossi 2008), but these studies were at high latitudes outside the tropics. Only a few studies on contemporary range shifts in the tropics have been published (Peh 2007, Seimon et al. 2007, Raxworthy et al. 2008, Chen et al. 2009, Juvik et al. 2011); most of these studies have not investigated changes in plant distributions. Even though the IPCC (2007) documented that temperature changes have been smaller at tropical latitudes in comparison to higher latitudes, bioclimatic modeling has shown that distributional patterns of tropical vegetation will ultimately be altered with changes in climate (Colwell et al. 2008, Feeley and Silman 2010). Studies of contemporary plant range shifts in the tropics are needed to test predicted influences of climate change.

Studies comparing species distributional shifts between C_4 and C_3 species in response to climate change are lacking. The physiological characteristics of C_4 plants such as a high optimum temperature range and minimal photorespiration give them an advantage in warm environments compared to C_3 plants, which dominate under cooler conditions (Long 1999). As a result, C_4 and C_3 plant distributional patterns are significantly correlated with temperature (Cabido et al. 1997, Wan and Sage 2001, Mo et al. 2004). Tropical mountain systems, with C_4 grass dominance at lower elevations and C_3 dominance at higher elevations, are ideal environments for studying plant responses to climate change in relation to photosynthetic pathways. The Poaceae (grass family) is one of the largest families of angiosperms found in the tropics with species comprised of both C_4 and C_3 photosynthetic pathways, making it a model group for investigating potential shifts in plant distributions in response to climate change; furthermore, because of known associations between many grasses and disturbance we may expect substantial shifts in grass distributions in response to global change.

Disturbance has been shown to disrupt dominant vegetation patterns and promote changes in species distributions

(Sousa 1984). In particular, fire can cause important changes in species distributions and composition (D'Antonio et al. 2001, Ainsworth and Kauffman 2010, Fonda and Binney 2011). In many cases, fire can shift vegetation to favor non-native, invasive species (reviewed by D'Antonio 2000). In areas that become invaded by grasses, a feedback cycle enhancing fire and grass expansion can occur (the grass-fire cycle) (D'Antonio and Vitousek 1992). In Hawai'i Volcanoes National Park for example, 36 fires burned an average of 4.5 ha/fire over a 40 yr period before the invasion of fire-adapted grasses. After the invasion of fire-adapted grasses, 93 fires have burned an average of 149 ha/fire in <30 yr (Smith and Tunison 1992). Furthermore, the impacts of global climate change and altered disturbance regimes are predicted to interact in altering distributional patterns of many invasive species (Kriticos et al. 2003a, b).

Tropical elevation gradients are excellent sites for investigating ongoing impacts of climate change in the tropics (Malhi et al. 2010). The broad elevation ranges of Hawaiian volcanoes (0–4000 m) combined with a wide assortment of C_4 and C_3 grasses makes Hawai'i a valuable tropical location for analyzing species distribution patterns and exploring underlying factors responsible for those patterns. The aim of this study was to compare grass distributions across an elevation gradient in Hawai'i over a forty year period between 1966–1967 (Newell 1968) and 2008 to determine if C_4 and/or C_3 grass distributions have shifted upward in elevation and if the species composition or dominance of grasses has changed. We hypothesized that C_4 and C_3 grasses are now established at higher elevations due to climate warming and increased fire frequency over the past forty years (Smith and Tunison 1992, Giambelluca et al. 2008). We also hypothesized that fire-adapted grasses would be a more dominant component of the landscape compared to initial surveys in 1966–1967.

Methods

During June 2008, field plots were surveyed along an elevation gradient on Mauna Loa, Hawai'i (Fig. 1). Our field surveys were done within Hawai'i Volcanoes National Park (HAVO) along the Chain of Craters and Mauna Loa Roads. Original surveys were also done along these two roads from June–September 1966, with a few surveys being done in January and June 1967, documenting the earlier vegetation along this transect (Newell 1968). Forty-three plots were surveyed at 100–150 m elevation intervals from sea level to 2000 m along the road and in natural habitats (undisturbed habitats) ~30 m away from the road. For comparisons over time, only off road sites ($n = 21$) were used because original survey sites were similarly located off road; however, we also compared our roadside plots with off-road results. The locations of survey plots were matched as closely as possible to those used by Newell in 1966 and 1967. Newell (1968) used variable plot sizes (225 m^2 up to 500 m^2) while we used a fixed plot size of 50×2 m divided into five 10×2 m subplots. In all cases, our 2008 plot size was smaller in size to that used by Newell (1968) so that any detected upward shift in plant range in 2008 represents a conservative estimate of the shift.

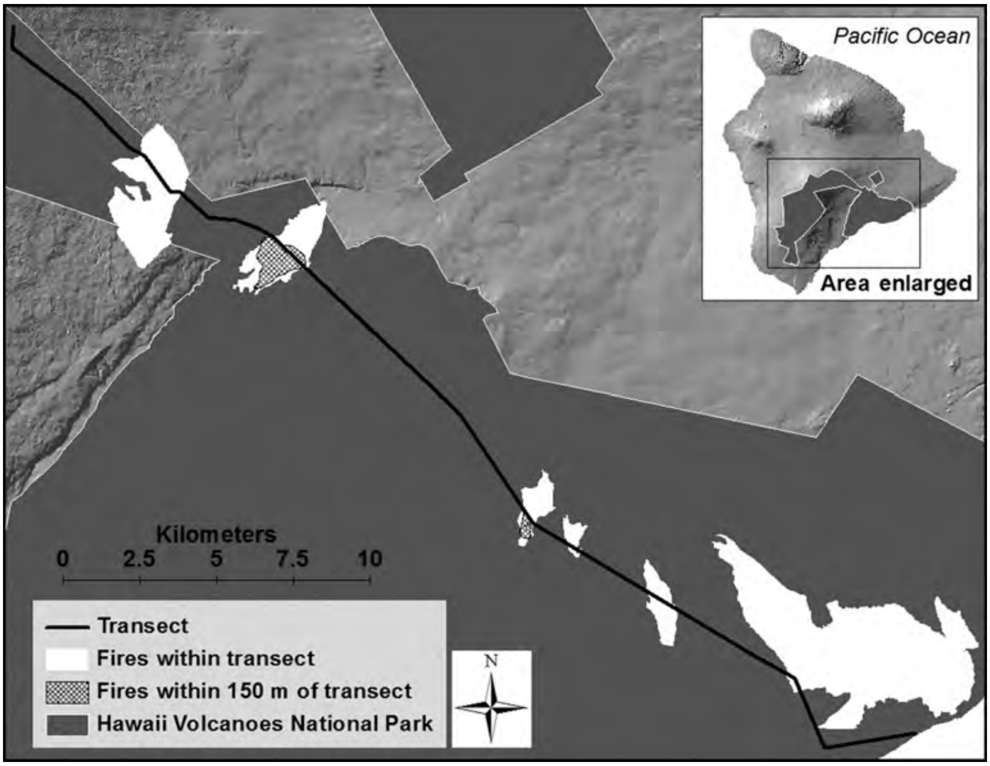

Figure 1. Survey sites (black line, 2008) and fires sites (checkered and white, 1966–1967–present) on the island of Hawai'i, all within Hawai'i Volcanoes National Park.

All grass species found in the plots were recorded and visual cover estimates for each species were made in sub-plots based on one of six percent cover categories: 0–1, 2–5, 6–25, 26–50, 51–75, 76–100 and converting categories to mid-point cover classes (Mueller-Dombois and Ellenberg 1974), which were then averaged across the five sub-plots to obtain a mean plot cover. Only relative covers of C_4 versus C_3 grasses were compared between 1966–1967 and 2008 so that an observed difference or trend cannot be accounted for by a (possible) systematic difference in cover interpretation between observation periods. The photosynthetic pathway of all grasses was determined using Brown (1977). The transition point between C_4 and C_3 grasses, defined as the elevation where C_4 and C_3 grasses both equal 50% in relative cover or richness, was calculated from the inflection point of a best fit three parameter logistic regression model (Sigma Plot ver. 10, SSPS, Chicago, IL) and compared to the 1966–1967 transition point calculated in the same manner. The logistic regression model was:

$$Y = a/(1 + (x/x_0)^b) \quad (1)$$

In Eq. 1, x is elevation (m), x_0 is the crossover elevation, Y is the proportion of C_3 grasses, $a = 1$, and b is a fitted shape parameter. Significant differences in transition elevations between 1966–1967 and 2008 were determined using 95% confidence intervals calculated by the supporting plane method (PSI-Plot ver. 8, Polysoft Software, Pearl River, NY).

In addition to examining the overall transition elevation for C_4 and C_3 grass cover and species richness, distributions of individual grass species recorded in both the 1966–1967 and 2008 surveys were compared. Paired t-tests were used to compare maximum elevations between 1966–1967 and 2008 among all C_4 species groups or all C_3 species grouped, and to compare the size of the elevation ranges in 1966–1967 and 2008. One-sample t-tests were used to determine if changes in C_4 or C_3 species distributions were different from zero. Species were also classified as either increasing or decreasing in elevation maxima, and the null expectation that half of the species would increase and half would decrease in elevation was tested using a bionomial probability test.

Average temperatures and annual precipitation were obtained for HAVO Park Headquarters and the Mauna Loa Observatory for January and July 1965–2009 (Western Regional Climate Center 2006, Pacific Island Network 2012) to compare climate conditions between survey dates. Using GIS data (Loh 2011) for fires in HAVO, the number and size of fires along our transect over time were determined. Fire-adaption status of a species was determined from Smith and Tunison (1992), which discussed fire-adapted species located in HAVO. An exact chi-square test (StatExact 4.0, Cytel Software) was used to determine if the proportion of fire-adapted species that moved up in elevation was different than the proportion of non fire-adapted species. A Kruskal–Wallis test was used to determine if the average change in elevation for fire and non-fire adapted species was different, while a t-test comparing dates of introduction (Wester 1992) was used to test the hypothesis that fire-adapted grasses were introduced more recently than non-fire adapted grasses.

Results

Temperature and precipitation trends over time

Warming trends in the immediate vicinity and at an elevation above our transect (Fig. 2A, B, C, D) provide local support for broader warming patterns across the Hawaiian Islands documented by Giambelluca et al. (2008). The average temperatures at HAVO Park Headquarters (1200 m) for July (1965–1968) and July (2005–2008) were 17.3°C ± SD = 0.5°C and 18.0°C ± SD = 0.2°C, respectively. The average temperature for January (1965–1968) and January (2005–2008) were 14.0°C ± SD = 0.3°C and 14.7°C ± SD = 0.7°C, respectively (Pacific Island Network 2012). The average temperatures at the Mauna Loa Observatory (3400 m) for July (1965–1968) and July (2005–2008) were 8.8°C ± SD = 0.9°C and 9.5°C ± SD = 0.2°C, respectively. The average temperature for January (1965–1968) and January (2005–2008) were 5.1°C ± SD = 0.7°C and 6.0°C ± SD = 1.4°C, respectively (Western Regional Climate Center 2006). Overall temperature trends from 1965 to 2009 were significant for both locations and months (Fig. 2A, B, C, D). Annual precipitation trends from 1965 to 2009 for HAVO Park Headquarters (1200 m) were not significant over the time period ($p = 0.542$), although, precipitation patterns appear to be in the downward direction (Fig. 3A). However, precipitation trends from 1965 to 2009 for Mauna Loa Observatory (3400 m) were significantly decreasing ($p = <0.001$) over the time period (Fig. 3B).

Number and size of fires

There were six large fires along our transect from 1969 to 2000 that ranged in size from 225 to 1620 ha (Fig. 1). Additionally, there were six smaller fires (1977–2000) within 150 m of our transect, ranging in size from 0.04 to 156 ha (Fig. 1). All of the fires that were directly along our transect were larger in size than fires that occurred prior to the 1966–1967 survey date (1924–1966, 8 fires, averaging < 10 ha) (Loh 2011).

Comparison of grass distributions between 1966–1967 and 2008

In the 1966–1967 surveys, Newell (1968) documented 33 grasses species, 19 C_4 and 14 C_3, 9 of which were native species (Table 1). As expected due to smaller plots sizes of our surveys, in 2008 we found fewer species (22 grass species, 13 C_4 and 9 C_3, 5 of which were native species). The vast majority of species that we failed to detect in our 2008 survey (14 of 17 species) were rare in the 1966–1967 survey (averaging 1% cover). We also found six new species in the 2008 survey. Four species that were found in the 1966–1967 surveys were only found along the road in 2008 (Table 1).

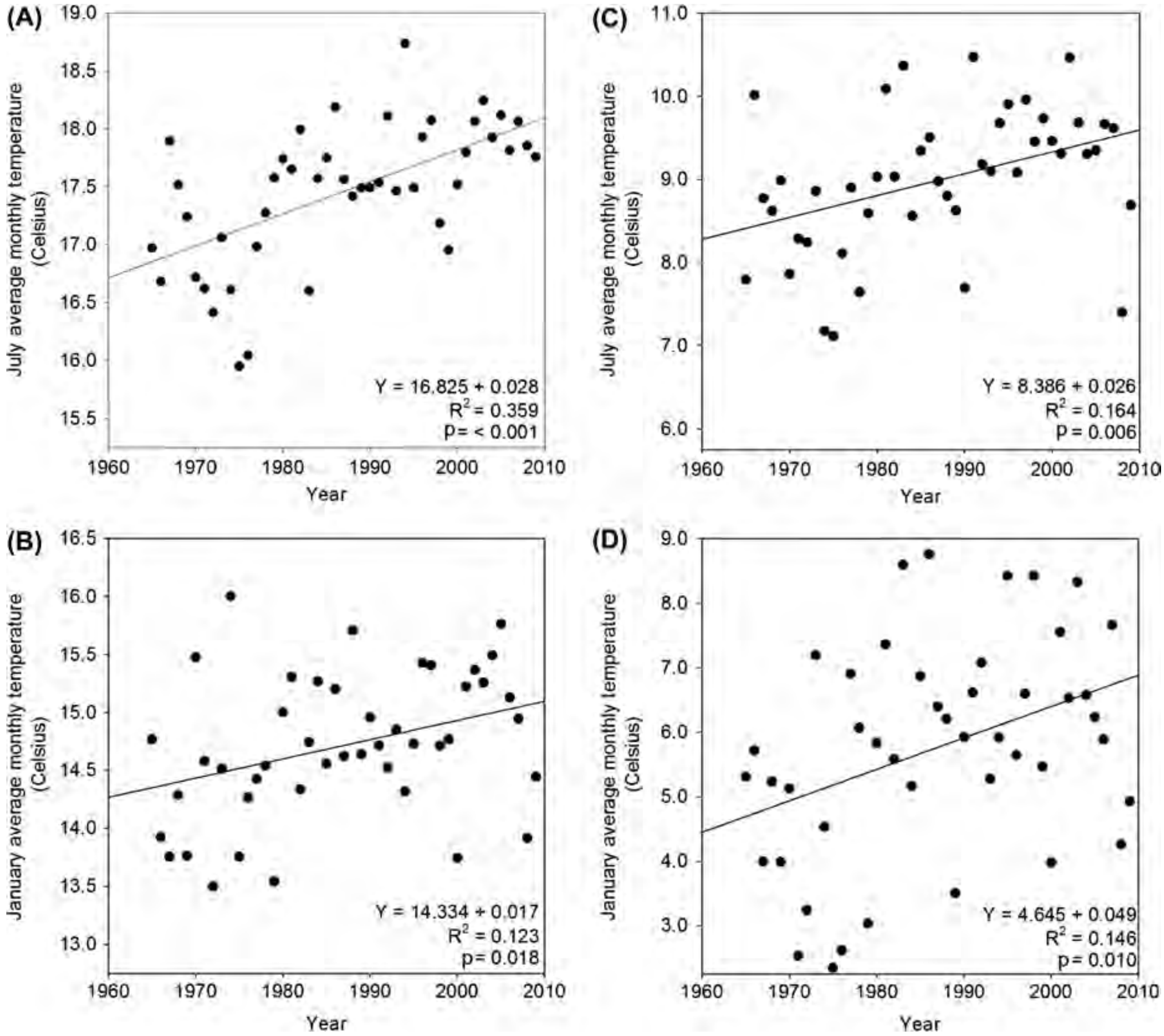

Figure 2. Temperature averages for Hawai‘i Volcanoes National Park headquarters (1200 m) in (A) July and (B) January 1965–2009 and Mauna Loa Observatory (3400 m) in (C) July and (D) January 1965–2009.

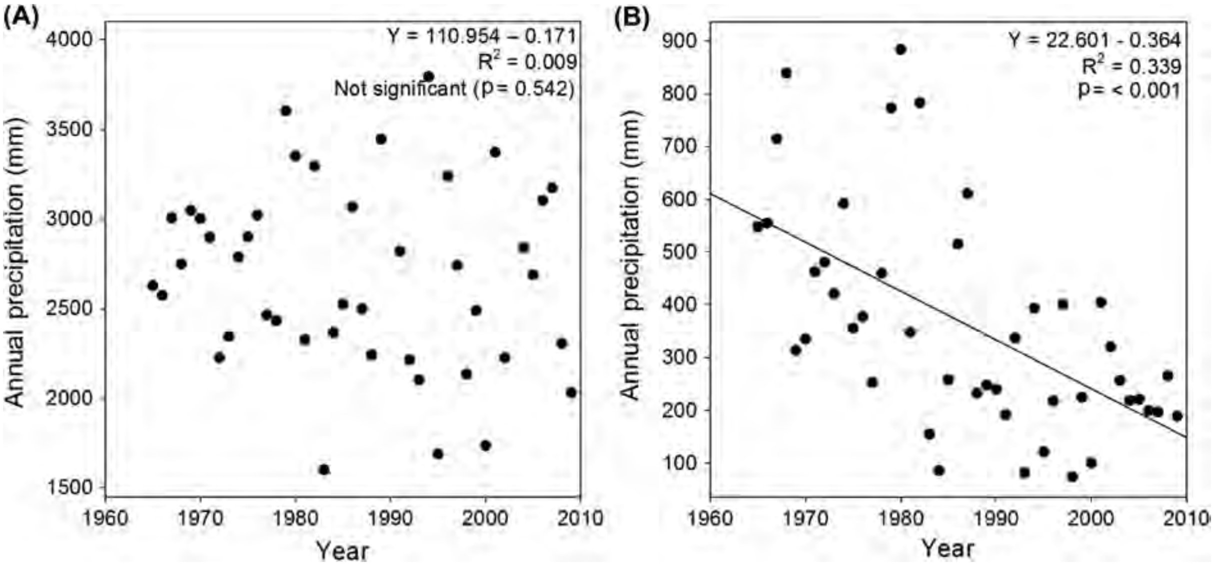

Figure 3. Annual precipitation trends for (A) Hawai‘i Volcanoes National Park headquarters (1200 m) 1965–2009 and (B) Mauna Loa Observatory (3400 m) 1965–2009.

Table 1. List of species found in 1966–1967, 2008, and roadside 2008 surveys along HAVO transect. Species dates of introduction from Wester (1992). Grass species are ordered alphabetically.

Species name	PP	Native/ non-native	DI	No. of plots 1966–1967	Average % cover/plot 1966–1967	No. of plots 2008	Average % cover/plot 2008	No. of plots RS 2008	Average % cover/plot RS 2008
Agrostis avenacea	C_3	native	–	3	2	1	1	–	–
Agrostis sandwicensis	C_3	native	–	5	1	–	–	–	–
Andropogon virginicus	C_4	non-native	1924	14	20	–	–	–	–
Anthoxanthum odoratum	C_3	non-native	1907	3	8	3	7	10	9
Axonopus fissifolius	C_4	non-native	1912	–	–	–	–	14	12
Bothriochloa pertusa	C_4	non-native	1916	1	1	–	–	–	–
Briza minor	C_3	non-native	1840	2	1	–	–	–	–
Bromus diandrus	C_3	non-native	1910	–	–	1	1	1	16
*Bromus willdenowii**	C_3	non-native	1909	2	1	–	–	3	14
Chrysopogon aciculatus	C_4	native	–	7	4	3	1	–	–
Cynodon dactylon	C_4	non-native	1888	2	21	1	1	3	8
Dactylis glomerata	C_3	non-native	1911	1	1	2	1	4	18
Deschampsia nubigena	C_3	native	–	13	17	6	15	5	15
Digitaria ciliaris	C_4	non-native	1912	2	6	–	–	–	–
Digitaria fuscescens	C_4	non-native	1852	3	1	–	–	–	–
Digitaria setigera	C_4	non-native	1826	–	–	–	–	1	4
Digitaria violascens	C_4	non-native	1916	4	1	1	1	8	3
Ehrharta stipoides	C_3	non-native	1916	–	–	3	7	4	12
Eleusine indica	C_4	non-native	1940	–	–	–	–	1	16
Eragrostis brownei	C_4	non-native	1916	–	–	–	–	3	8
Eragrostis cilianensis	C_4	non-native	1864	–	–	–	–	2	21
Eragrostis elongata	C_4	non-native	1949	–	–	–	–	5	7
Eragrostis tenella	C_4	non-native	1895	3	1	–	–	–	–
Eragrostis tenuifolia	C_4	non-native	1969	–	–	–	–	3	2
Heteropogon contortus	C_4	native	–	3	25	2	27	1	16
Holcus lanatus	C_3	non-native	1909	10	21	10	4	15	14
Hyparrhenia rufa	C_4	non-native	1933	–	–	5	20	7	7
Isachne distichophylla	C_3	native	–	5	3	–	–	–	–
Melinis minutiflora	C_4	non-native	1913	1	1	3	14	14	10
Melinis repens	C_4	non-native	1895	5	6	5	5	13	8
Oplismenus hirtellus	C_3	non-native	1841	1	1	–	–	–	–
Panicum tenuifolium	C_4	native	–	4	7	4	5	–	–
Paspalum conjugatum	C_4	non-native	1840	2	1	–	–	–	–
Paspalum dilatatum	C_4	non-native	1911	4	30	2	44	6	8
Paspalum orbiculare	C_4	native	–	1	1	–	–	–	–
*Paspalum urvillei**	C_4	non-native	1914	1	1	–	–	5	2
Pennisetum clandestinum	C_4	non-native	1924	–	–	2	46	4	40
Poa pratensis	C_3	non-native	1911	–	–	2	1	–	–
*Sacciolepis indica**	C_3	non-native	1908	1	1	–	–	4	1
Schizachyrium condensatum	C_4	non-native	1924	2	1	7	14	8	10
Setaria parviflora	C_4	non-native	1895	2	1	1	4	6	6
*Sporobolus africanus**	C_4	non-native	1911	2	1	–	–	11	4
Sporobolus diander	C_4	non-native	1911	–	–	1	1	1	16
Stenotaphrum secundatum	C_4	non-native	1840	–	–	–	–	1	4
Trisetum glomeratum	C_3	native	–	9	1	–	–	–	–
Vulpia bromoides	C_3	non-native	1911	–	–	–	–	4	1
Vulpia myuros	C_3	non-native	1911	5	1	1	10	4	1
Vulpia octoflora	C_3	non-native	1966	2	1	–	–	–	–

* = Species found in 1966–1967 and only on the roadside in 2008; DI = date of introduction; RS = roadside.

Using a best fit three-parameter logistic regression based on Newell's (1968) original data, we found that the C_4 to C_3 transition point in 1966–1967 was at 1200 m (relative cover data, $n = 24$) and 1137 m (species richness data, $n = 24$) versus 1476 m ($n = 21$) and 1407 m ($n = 21$) in 2008, respectively. Although both trends were in the predicted direction of an upward elevational shift in C_4 dominance, the difference was statistically different only for relative cover, based on 95% confidence intervals ($p = 0.04$) (Fig. 4A, B). Most grass species had higher elevation maxima in 2008 (Fig. 5, 6), but a few species, both C_4 and C_3, declined in elevation between 1966–1967 and 2008, making the overall pattern statistically non-significant (paired t-test, $t = 0.811$, $DF = 9$, $p = 0.43$ for C_4 grasses and $t = -0.038$, $DF = 4$, $p = 0.97$, for C_3 grasses). Although the number of species with increased elevation maxima (10) versus decreased elevation maxima (4) was in line with predictions based on warming, this difference was not statistically different from the random expectation of 50% ($p = 0.09$). Species total elevational ranges were

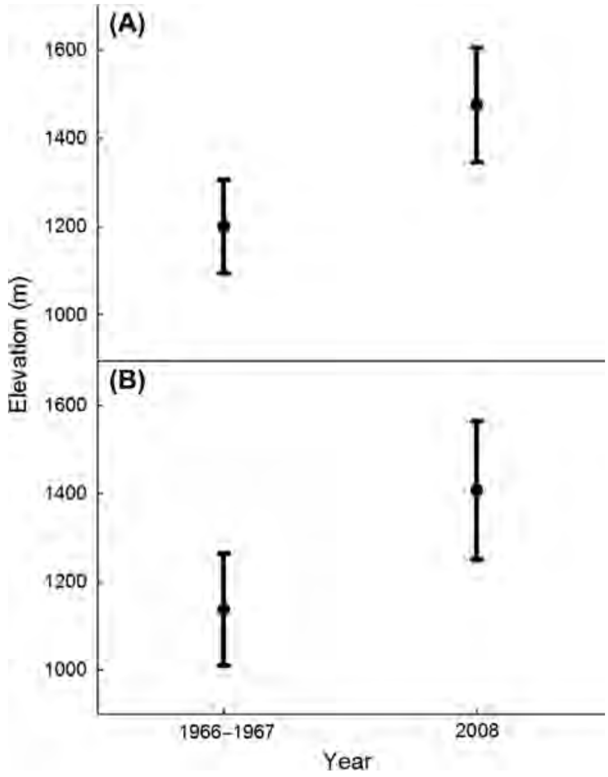

Figure 4. (A) Transition elevations for % relative cover of C_3 and C_4 grasses with 95% confidence intervals, and (B) Transition elevations for relative species richness of C_3 and C_4 grass species with 95% confidence intervals (1966–1967 and 2008 surveys).

also not significantly broader between 1966–1967 and 2008 for either C_4 or C_3 grasses (paired t-test, $t = 1.43$, $DF = 9$, $p = 0.18$ and $t = 0.073$, $DF = 4$, $p = 0.94$, respectively).

Despite the lack of statistical support for overall increases in elevation among all C_4 or C_3 grass species, a clear trend was apparent among the grass species adapted to fire (Table 2). Significantly more fire-adapted species moved up in elevation compared to non-fire adapted species (exact chi-square test, $p = 0.007$). In addition, when comparing change in elevation for fire and non-fire adapted species, the fire-adapted species moved up in maximal elevation by a significantly greater amount ($\bar{x} = 454$ m) than non-fire adapted species ($\bar{x} = -273$ m, Kruskal–Wallis, $p = 0.003$) (Table 2). This difference was not due to more recent introductions of the fire-adapted species, as species introduction dates were not significantly different between fire (mean = 1910) and non-fire adapted grasses (mean = 1904) (t-test, $t = -0.87$, $DF = 9$, $p = 0.40$, native species excluded).

Discussion

Our study was limited by the number of plots originally used by Newell (1968) and thus, our small sample size leads to limited power of inference. However, despite this we do find statistically significant patterns that document changes over time. This study revealed an increase in elevation of the C_4-C_3 transition point, consistent with a plant response to warming over the past forty years (Fig. 2), although we can't exclude a role of changing fire regime (see further discussion below). Considering that 4-yr average monthly temperatures at HAVO differed by 0.7°C in the summer and 0.7–0.9°C for the winter between the survey periods (1965–2009; Western Regional Climate Center 2006, Pacific Island Network 2012), and using a lapse rate of 0.3°C 100 m^{-1} elevation up to ~ 1500 m (Doty and Mueller-Dombois 1966), the observed warming is equivalent to a 233–300 m change in elevation. This is within the range of the mean difference we saw in our transition elevations between 1966–1967 and 2008 (a mean increase of 276 m

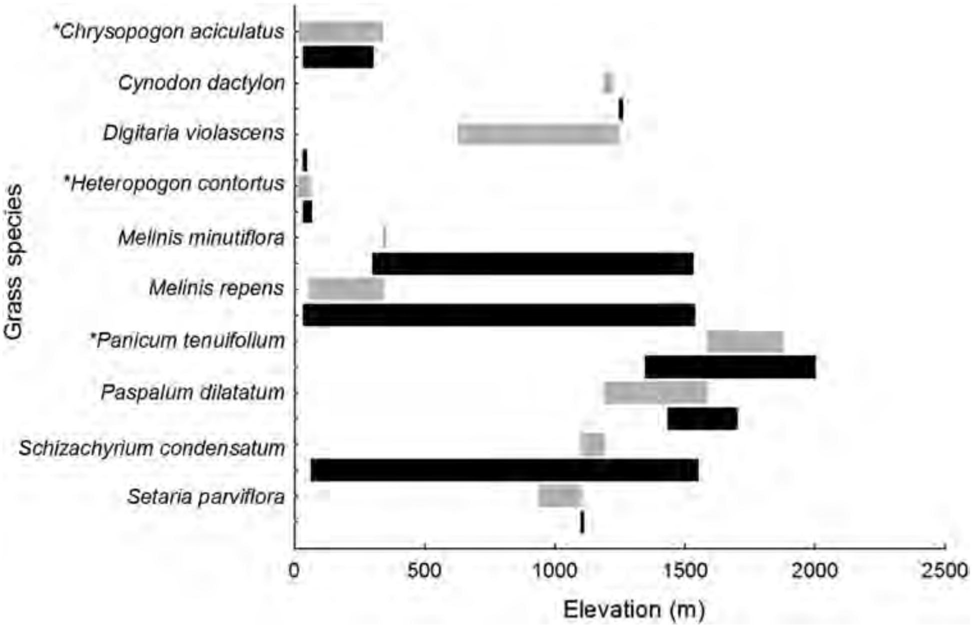

Figure 5. C_4 grass distributions based on data observations in 1966–1967 (gray bars) versus 2008 (black bars), ordered alphabetically from top to bottom. Asterisk indicates native Hawaiian grass.

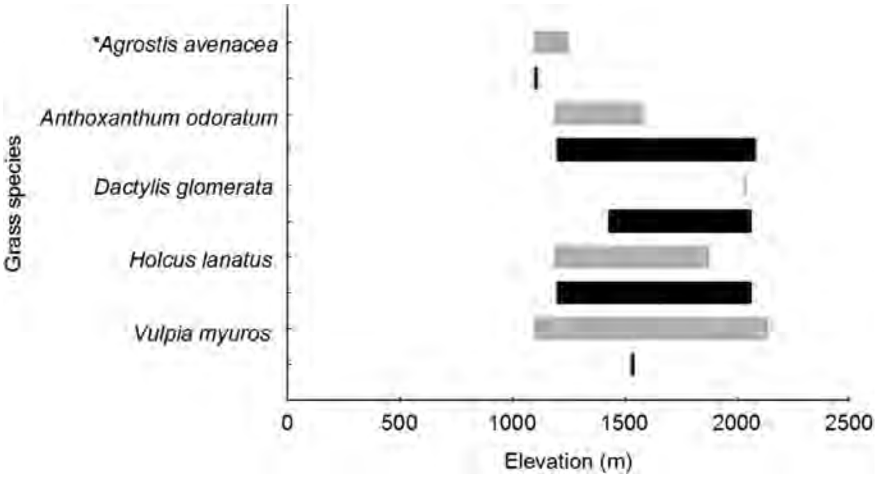

Figure 6. C_3 grass distributions based on data observations in 1966–1967 (gray bars) versus 2008 (black bars), ordered alphabetically from top to bottom. Asterisk indicates native Hawaiian grass.

using relative cover data and 270 m using species richness data). Rundel (1980) used data from Newell (1968) to visually estimate the transition point as 1400 m in 1966–1967, however our estimation method based on fitting a logistic equation provides a consistent and less subjective means of comparing transition points over time.

Changes in tropical vegetation may be lagging behind vegetation trends at higher latitudes (Kullman 2002, Penuelas and Boada 2003, Kelly and Goulden 2008, Lenoir et al. 2008, Parolo and Rossi 2008). The IPCC (2007) reported that high latitudes in the Northern hemisphere are warming faster than tropical latitudes, with temperature changes in the tropics half of what higher latitudes are experiencing. Furthermore, previous studies that have documented plant distribution shifts have reported on average a change in temperature of 0.3°C/decade (Penuelas and Boada 2003, Parolo and Rossi 2008), while, we only observed a change in temperature of 0.18°C/decade (1965–2009) for mid-elevations (from local weather station data) or 0.16°C/decade since 1975 (based on island-wide trends reported by Giambelluca et al. (2008)). Thus, in addition to a relatively small sample size of survey plots (n = 21), smaller temperature changes at our tropical site may have made some statistical patterns difficult to detect. Nevertheless, significant and non-significant trends in plant distributions were all in the predicted upward direction. As climate warming continues to increase in the future (IPCC 2007), tropical vegetation may more clearly mimic trends seen at higher latitudes.

Table 2. Elevational changes documented over a 40 yr time period for fire-adapted vs non-fire adapted C_3 and C_4 grass species in Hawai'i, ordered alphabetically and by photosynthetic pathway (PP) (Smith and Tunison 1992).

Grass species	PP	Maximum elevation change (m)
Anthoxanthum odoratum	C_3	**+495**
Holcus lanatus	C_3	**+185**
*Agrostis avenacea**	C_3	−138
Dactylis glomerata	C_3	+20
Vulpia myuros	C_3	−587
Heteropogon contortus**	C_4	**+5**
Melinis minutiflora	C_4	**+1150**
Melinis repens	C_4	**+1195**
Panicum tenuifolium**	C_4	**+125**
Paspalum dilatatum	C_4	**+115**
Schizachyrium condensatum	C_4	**+360**
*Chrysopogon aciculatus**	C_4	−40
Cynodon dactylon	C_4	+40
Digitaria violascens	C_4	−1205
Setaria parviflora	C_4	+0

*Native Hawaiian grass.
Bolded species are fire-adapted grasses.

Since 1966–1967, fires have tripled in frequency and have increased in size in HAVO (Smith and Tunison 1992), and most of these fires have been anthropogenic. Our data suggest that increased fire frequency is linked to upward range expansion of fire-adapted grasses (grasses that promote and/or tolerate fire, Table 2). These upward grass expansions are associated with reduced ranges of other grasses, usually lower stature grasses that have minimal cover compared to fire-adapted grasses. Thus, fire may selectively diminish or reduce the ranges of some grasses, perhaps indirectly via competition with fire-adapted grasses, resulting in high overall variance in distribution changes over time when all C_4 or C_3 grasses were considered together as a group.

Road habitats are frequently prone to disturbances and thus contain open niches for species establishment (Rentch et al. 2005, Alexander et al. 2009, Arteaga et al. 2009). Roadsides in HAVO were disturbed by automobile usage, human trampling, and vegetation cutting. Some species that were found off road in 1966–1967 were apparently restricted to the roadside in 2008 and species richness along the road in 2008 was also more similar to 1966–1967 values, suggesting that the competitive nature of fire-adapted grasses found in the natural habitat (away from the road) may have reduced the abundance of some grass species, although successional trends away from the road might also account for this pattern.

In addition to upward expansion, one of nine C_4 grass species (*Schizachyrium condensatum*), had substantial downward expansion in elevation. Two other studies, Kelly and Goulden (2008) and Lenoir et al. (2008), also found downward shifts of 10 and 31% of the studied species, respectively, with climate warming. Although, Lenoir et al. (2010) suggested that downslope range shifts of species may be biotic responses to habitat modifications, in the case of *S. condensatum*, it is likely related to its dominance after fire. Thus, fire may have a more immediate influence on grass distribution patterns than climate warming, but it is difficult to separate these drivers as increased fire frequency often accompanies climate change (Hemp 2005, Schumacher and Bugmann 2006, Pechony and Shindell 2010). Juvik et al. (2011) also proposed that anthropogenic impacts along with climate warming may be impacting floristic composition and range changes along Mauna Loa. In HAVO, cattle were removed from our study area by 1948 (Cuddihy 1984), while other feral animal populations were controlled before 1968. It is possible that release from grazing prior to 1968 may have facilitated an ongoing expansion of fire-adapted grasses after 1968. Juvik et al. (2011) further suggested that the dry conditions on Mauna Loa could possibly shift species' distributions downslope as a result of increased water stress at higher elevations. A decreased elevation maxima on Mauna Loa were seen among some species by Juvik et al. (2011) above the trade wind inversion layer (TWI). The TWI limits cloud formation above it, thus creating a moist layer below it and dry air above (Giambelluca and Nullet 1991, Cao et al. 2007). The TWI may explain why we did not see more C_3 species expand upward in elevation along our transect, as the upper sites are often above the trade wind inversion layer (TWI) and they can experience extreme droughts. Along with dry conditions caused by the presence of the TWI, we see a trend of decreasing annual precipitation above the TWI since 1965, making habitat conditions for C_3 grass species less likely at these elevations. Crausbay and Hotchkiss (2010) found that C_3 grass species were restricted to the highest elevations below the TWI, further suggesting that C_3 grasses may be limited in their movement upward in elevation by precipitation in Hawai'i, such that they may not be able to take advantage of warming temperatures at their upper range limits.

Our study found a significant increase in the C_4-C_3 transition elevation in terms of plant cover and the C_4-C_3 transition elevation for species richness was also in the upward direction, and grasses adapted to fire have shifted upwards in elevation in the last 40 yr. Many of these grasses pose threats to native ecosystems due to their promotion of fire (D'Antonio and Vitousek 1992, D'Antonio 2000). Tropical mountain systems are known to be very diverse in plant taxa (Laurance et al. 2011), supporting endemic montane species found nowhere else in the world (Chen et al. 2009, Crausbay and Hotchkiss 2010), and Hawaiian montane ecosystems are no different (Loope and Giambelluca 1998). Our study documents an upward dominance of C_4 grasses and expansion of fire-adapted grasses as important threats to Hawaiian montane ecosystems that will be compounded by further warming. Similar patterns are expected for montane ecosystems elsewhere in the tropics, where invasion by fire-adapted grasses at lower elevations is already well documented (D'Antonio and Vitousek 1992).

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