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FACILITATING ADAPTATION IN MONTANE PLANTS TO CHANGING PRECIPITATION ALONG AN ELEVATION GRADIENT

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ABSTRACT

Montane plant communities throughout the world have responded to changes in precipitation and temperature regimes by shifting ranges upward in elevation. Continued warmer, drier climate conditions have been documented and are projected to increase in high-elevation areas in Hawai'i, consistent with climate change effects reported in other environments throughout the world. Organisms that cannot disperse or adapt biologically to projected climate scenarios *in situ* may decrease in distributional range and abundance over time. Restoration efforts will need to accommodate future climate change and account for the interactive effects of existing invasive species to ensure long-term persistence. As part of a larger, ongoing restoration effort, we hypothesized that plants from a lower-elevation forest ecotype would have higher rates of survival and growth compared to high-elevation forest conspecifics when grown in common plots along an elevation gradient. We monitored climate conditions at planting sites to identify whether temperature or rainfall influenced survival and growth after 20 weeks. We found that origin significantly affected survival in only one of three native montane species, *Dodonaea viscosa*. Contrary to our hypothesis, 75.2% of seedlings from high-elevation origin survived in comparison to 58.7% of seedlings from low elevation across the entire elevation gradient. Origin also influenced survival in linearized mixed models that controlled for temperature, precipitation, and elevation in *D. viscosa* and *Chenopodium oahuense*. Only *C. oahuense* seedlings had similar predictors of growth and survival. There were no common patterns of growth or survival between species, indicating that responses to changing precipitation and temperature regimes varied between montane plant species. Results also suggest that locally sourced seed is important to ensure highest survival at restoration sites. Further experimentation on larger spatial and temporal scales is necessary to determine the empirical responses of species and communities to changing climate in the full context of highly degraded Hawaiian ecosystems.

INTRODUCTION

Montane plant communities in widely separated intact natural environments of the world have responded to changes in precipitation and temperature regimes by shifting ranges upward in elevation (Lenoir et al. 2008). The average elevation of dominant plant species in the Santa Rosa Mountains of Southern California shifted ~65 m upward over a 30-year period (Kelly and Goulden 2008). An upward shift in optimum elevation of 29 m per decade occurred in plant species of west Europe (Lenoir et al. 2008). Reduced evapotranspiration rates in cooler climate zones at higher elevation may compensate for less precipitation and higher temperatures within species' former ranges. Plants with short generation times and faster population turnover, such as grasses, may be able to quickly disperse upward (Lenoir et al. 2008); however, longer-lived plants that disperse more slowly may consequently adapt poorly to rising elevation of climate zones (Aitken et al. 2008).

Several studies have reported warmer and drier climate conditions in Hawai'i consistent with climate change reported in other environments throughout the world. Changes include a rapid rise in surface temperature since about 1975 (Giambelluca et al. 2008), downward trends in annual precipitation since 1905 (Kruk and Levinson 2008), upward trends in drought indexes since the 1950s (Chu et al. 2010), and long-term (1913–2008) downward trends in streamflow and groundwater discharge to streams (Bassiouni and Oki 2013). Moreover, frequency changes in the trade wind inversion that limit upward movement of prevailing moisture-laden trade

winds indicate a long-term shift toward drier conditions for high-elevation areas in Hawai'i (Cao et al. 2007). Indeed, prolonged severe drought conditions have occurred since 2008, affecting native biota in subalpine environments of Hawai'i (Banko et al. 2013). Rainfall in 2009, 2010, and 2011 on Hawai'i Island was 67.8%, 46.2%, and 65.7% of the long-term annual mean rainfall at 21, 34, and 31 stations, respectively (National Weather Service, Honolulu, Hawai'i). Surface air temperatures are projected to increase at greatest topographic heights, in locations such as upper Mauna Kea (Zhang et al. 2016).

Mountain parklands are among the most degraded ecosystems in Hawai'i (Cuddihy 1984). Centuries of adverse land use practices have caused deforestation, fragmentation, and genetic isolation in montane plants, disrupting biological connectivity between high-elevation subalpine woodlands and lower-elevation montane wet and mesic forests. The loss of montane forest cover also breaks an important positive feedback mechanism by interrupting fog-drip interception whereby convection commonly delivers additional precipitation to higher-elevation forests. A cyclic diurnal influx of low-elevation humid air forms afternoon fog on leeward subalpine Mauna Kea that contributes 38% additional precipitation under woodland tree canopies at 2,600 m asl (Juvik and Nullet 1993), and an estimated 43% additional precipitation at 1,985 m asl on windward Mauna Kea (J. Juvik, pers. comm.). The restoration of dry forest cover on Maui has also more than doubled infiltration and distribution of water in soil and its availability to plants relative to adjacent deforested areas (Perkins et al. 2012).

There is now substantial evidence that non-native ungulates have degraded native ecosystems throughout Hawai'i, and that recovery of native plant communities cannot occur in the continued presence of ungulates (Price et al. 2009). Several species of non-native ungulates are known to directly inhibit regeneration and cause mortality in many native tree and understory plant species through herbivory, digging, and bark stripping (Spatz and Mueller-Dombois 1975, Scowcroft and Sakai 1983, Merlin and Juvik 1992, Drake and Pratt 2001). To date, ungulates have been completely excluded or removed from roughly 750 km² of important terrestrial ecosystems throughout the Hawaiian Islands (Hess and Jacobi 2011), including the Kanakaleonui Bird Corridor (KBC) of windward Mauna Kea. Although these management actions have demonstrated beneficial effects for native ecosystems (Loope and Scowcroft 1985, Loh and Tunison 1999, Cole et al. 2012, Cole and Litton 2013), some areas like KBC may require intensive restoration efforts to recover ecological integrity and ecosystem function where few native plants remain (Perkins et al. 2012), particularly during a regime of changing climate.

Organisms that cannot disperse or adapt biologically *in situ* to rapid environmental changes may decrease in distributional range and abundance. Moreover, fragmented forest habitats may have little gene flow due to limited seed dispersal, further reducing species' ability to adapt naturally. Several native plant species in mountain parkland ecosystems are found naturally over a broad range of elevation, but may become range-restricted if environmental conditions shift rapidly as a consequence of climate change (Fortini et al. 2013). Recovery of previous plant populations may no longer be suitable within mountain parklands; however, conspecifics from more distant seed sources may grow more vigorously and have greater survival at higher elevation if altitudinal climate zones have shifted upward. In other words, if climates are shifting uphill faster than plants can disperse, the "ideal" genotype is most likely located below a given habitat. Genetic enrichment from more appropriate elevation climate zones may benefit such species. One potential management approach is to transplant conspecifics from low-elevation locations to small fragmented populations in higher-elevation zones. Transplanting in higher-

elevation zones encourages evolutionary change by moving climate compatible variants to more appropriate zones faster than they can disperse naturally (Kilpatrick 2006).

The evolution of plant species in Hawai'i has resulted in both dramatic speciation events, but in contrast, many species span large environmental gradients. Ecotypic variation tracking with clinal patterns has been documented in numerous plant species (Etterson 2004, Carlson et al. 2011), and may be a factor allowing persistence of Hawaiian species across diverse environmental conditions. Ecotypic variation has been documented in Hawai'i, with differences in germination, seedling growth, and survival for *Alyxia stellata* populations (Wong 2011), and differences in nutrient cycling across populations of *Metrosideros polymorpha* (Treseder and Vitousek 2001). Therefore, appropriate selection of seed sources may enhance the success of restoration efforts.

Objectives

Our objective was to determine if important native Hawaiian montane plant species may benefit from enrichment with seeds projected to be from climatically appropriate sources to enhance survival, growth, and adaptation to changing precipitation patterns by relocating conspecifics to more favorable higher elevation climate regimes. We sought to identify local sources of each species from appropriate climate zones to restore mountain parkland ecosystems where these species were absent, thereby increasing tolerance to contemporary and future climate conditions, and connectivity between existing high-elevation subalpine woodlands and lower-elevation montane wet and mesic forests. We hypothesized that plants from a lower-elevation forest ecotype would have higher rates of survival and growth compared to high-elevation forest conspecifics when grown in common plots along an elevation gradient.

METHODS

Study Area

The 'āina mauna (mountain land) of windward Mauna Kea is a culturally important area historically used by travelers making their way along traditional trails between Laupāhoehoe to Waipunalei and Kanakaleonui to Mauna Kea. The area was frequented by indigenous practitioners and is still important for cultural practices. This landscape provides important services to native practitioners such as sacred areas to worship; places to bury human remains (Kanu iwi) and umbilical cords (Kanu piko); places to gather stones, food, medicinal plants and to catch birds, and; safe areas for those who were traversing from one region to another (Raymond 2005). Traditional uses declined after the introduction of non-native ungulates and subsequent degradation of the area. European explorers viewed the Hawaiian Islands as strategic re-supply outposts for ships on worldwide voyages and introduced familiar livestock such as cattle (*Bos taurus*), domestic goats (*Capra hircus*), and sheep (*Ovis aries*) which soon became feral and proliferated in the absence of any predators or competitors (Tomich 1986). By 1822, "immense herds" of wild cattle protected by royal decree occupied the area around Mauna Kea (Ellis 1917), and cattle and other feral ungulates severely degraded the landscape by the 1850s (Baldwin and Fagerlund 1943).

The 'Āina Mauna Legacy Program (DHHL 2009) identifies several contemporary educational and cultural opportunities that the KBC may provide: ecosystem restoration in a culturally sensitive manner; sustainable resource gathering; cultural practices, and; seeing and understanding native forests. The area's proximity to Mauna Kea also makes it a valuable cultural resource. Native plants of the 'āina mauna provide food resources and habitat for wildlife, but also have a

variety of important historical and contemporary cultural uses (Medeiros et al. 1998, DHHL 2009):

- Koa (*Acacia koa*), a keystone species for native birds of montane forests, is also one of the most important timber species in Hawai'i, particularly for making traditional canoes. Currently and historically, the bark and leaves are important in various medicinal preparations.
- Māmane (*Sophora chrysophylla*) is also a keystone species for native birds of subalpine woodlands. Its flowers and seeds are used for *lei* making, flowers were medicinally used as an astringent, and the hard wood was used for posts, beams, *hōlua* sled runners, and tools.
- The fragrant heart wood of 'iliahi (*Santalum* spp.) was sometimes used by early Hawaiians for musical instruments, as a dye, or for scenting finished *kapa*, but became a major export commodity to China in the 19th century until it was widely depleted.
- The hard wood of naio (*Myoporum sandwicense*), another important woodland tree, was used as posts and frames for homebuilding, canoe parts, for net gauges, and fishing torches.
- Berries of pilo (*Coprosma montana*) were used and are still occasionally used today as a laxative. Berries of kūkaenēnē (*Coprosma ernodeoides*) were used for dyes. They are also important food resources for frugivorous birds.
- Berries of 'ōhelo (*Vaccinium reticulatum*) are used for food today as they have been used traditionally. Leaves, leaf buds, and fruit were also used traditionally for relief of abdominal pain, and new leaves, fruit, and flowers are used in contemporary *lei* making. They are also important food resources for frugivorous birds.
- Pūkiawe (*Leptecophylla tameiameiaae*) was burned and smoke was smudged on 'Ali'i who wished to mingle with commoners and sanctify the *Kapu* of the chiefs. It has one of the broadest elevational ranges of any Hawaiian plant.
- A'ali'i (*Dodonaea viscosa*) has many ethnobotanical uses, from medicinal to weaponry. Fruit may be used to make dye, and fruit and leaves are also popular in *lei* making.
- Young leaves and stems of 'aweoweo (*Chenopodium oahuense*) can be wrapped in ti leaves, steamed, and eaten in times of famine. Harder wood at the base of the plant can also be used for fish hooks.

Kanakaleonui Bird Corridor (KBC), which lies between 2,000 and 2,500 m asl on the east slope of Mauna Kea is intended to serve as a corridor for the movement of forest birds by providing a continuous link of native forest between subalpine woodlands of the Mauna Kea Forest Reserve and the mid-elevation mesic and wet forests (Figure 1). Restoring important fruiting plants such as 'iliahi, pilo, kūkaenēnē, 'ōhelo, pūkiawe, and naio may also attract the principal native frugivorous birds of the area, 'Ōma'o (*Myadestes obscurus*) and Nēnē (*Branta sandwicensis*), which may in turn further enhance the dispersal of these same plants. KBC is an ideal location to conduct such an experiment for four reasons:

- it is a culturally important area that is in need of restoration;

- it spans a 500 m elevation gradient;
- it is already protected from non-native ungulates which have degraded native forest ecosystems, and;
- the adjacent Mauna Kea Forest Reserve (>2,500 m asl) and Piha section of Hilo Forest Reserve (<2,000 m asl) contain appropriate high- and low-elevation sources for seeds of biologically and culturally important plant species.

Replicate outplanting locations were selected along a 500 m elevation gradient within KBC to minimize differences in extraneous abiotic factors such as substrates so that microclimate variables constituted the primary difference between sites. Rainfall ranged from 985 mm annually at the high-elevation boundary, to 2,085 mm annually at the low-elevation boundary (Giambelluca et al. 2013).

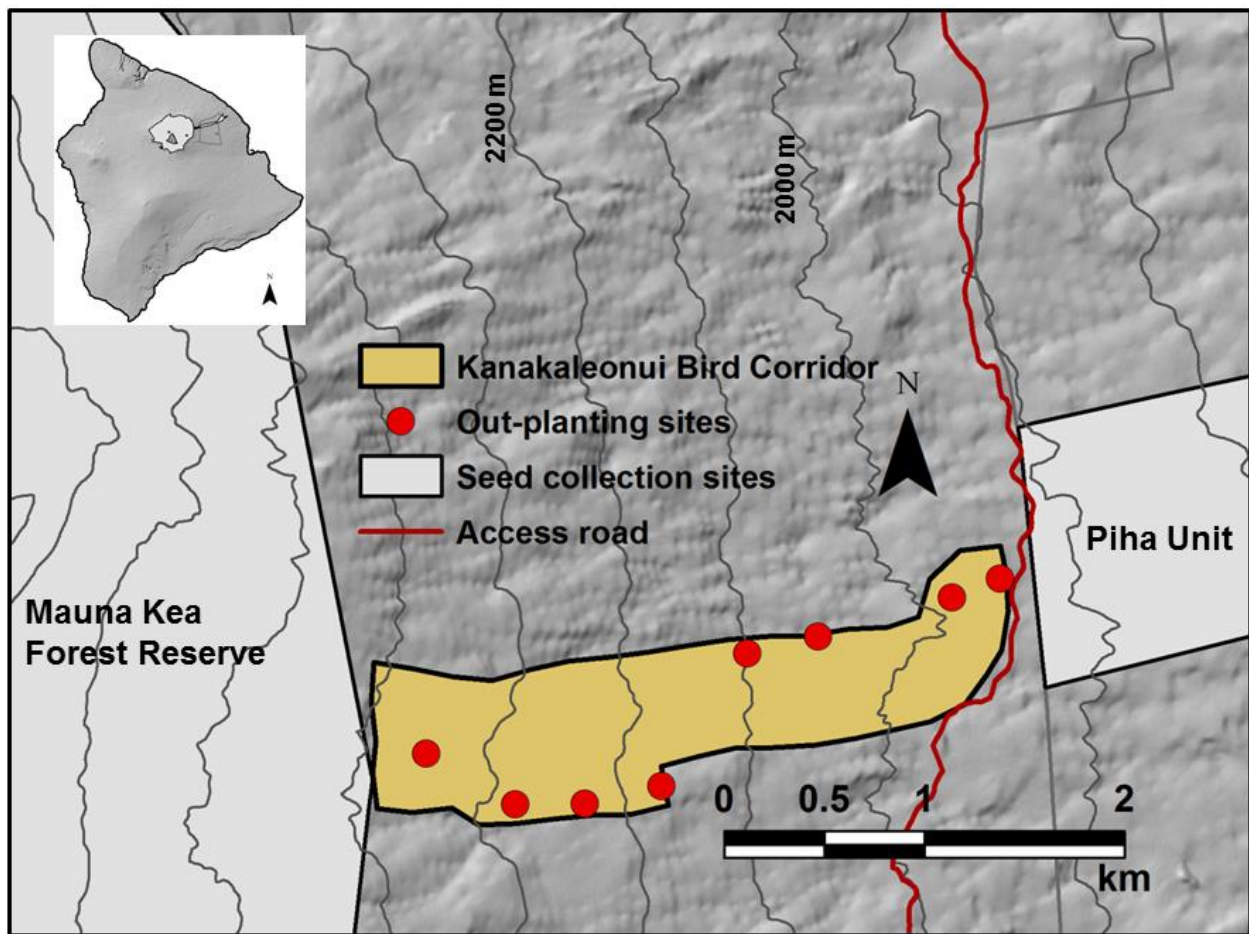


Figure 1. Kanakaleonui Bird Corridor (KBC) on Hawai'i Island. Microclimate data loggers were installed at 8 out-planting sites along an elevation gradient at approximately 60-m intervals throughout KBC.

Automated microclimate data loggers

Eight HOBO® micro station data loggers (H21-002) were installed at elevation intervals of approximately 60 m within KBC on 16 and 18 December 2014. Each data logger was equipped with two sensors to monitor: 1) temperature and relative humidity (S-TMB-M002), and 2) soil moisture (S-SMC-M005). Data loggers were programmed using HOBOWare supporting computer software to store average values at five-minute intervals to allow sufficient battery life and memory storage. Temperature, relative humidity, and soil moisture data were downloaded monthly and stations inspected for defects. Two stations were damaged by feral pigs in January 2015, and were repaired in March 2015. Fence enclosures were erected around all stations March–April 2015. A malfunctioning soil moisture sensor was replaced in April 2016, and another in August 2016 due to rat disturbance.

Seed collection

We collected seeds of seven native tree and plant species in the Mauna Kea Forest Reserve, and the Piha and Laupahoehoe Sections of the Hilo Forest Reserve (Figure 1). Seeds of seven native Hawaiian plant species were collected; however, high elevation sources for *Vaccinium reticulatum* and *Acacia koa* were not available. No seeds of *Santalum* spp. were available. (Table 1). Approximately 8,000 seeds were sent to Maui Native Nursery, LLC for storage and germination. Seed collection was completed in June 2015.

Plant propagation

Propagation of five species was attempted at the facilities of Maui Native Nursery, LLC. Species included *Chenopodium oahuense*, *Coprosma* spp., *Dodonaea viscosa*, *Myoporum sandwicense*, and *Sophora chrysophylla*. Only three species were successfully propagated: *C. oahuense*, *D. viscosa*, and *S. chrysophylla*. *Coprosma* spp. and *M. sandwicense* had negligible germination.

Site preparation and outplanting

Eight sites, all near microclimate stations, were identified as locations to plant seedlings. Sites were sprayed with imazapyr herbicide to kill invasive grasses in July–August 2015, and again with in January 2016. A total of 322 liters of herbicide was used for the first round of grass control, and a follow-up effort used another 116 liters. We received seedlings of three native plant species on October 12, 2015: 480 *C. oahuense*, 350 *D. viscosa*, and 115 *S. chrysophylla*. Nineteen *C. oahuense*, 22 *D. viscosa*, and 2 *S. chrysophylla* seedlings died before being outplanted. All seedlings were outplanted among the eight study sites February 29–March 2, 2016 to avoid freezing temperatures. Seedlings were thoroughly watered, coconut core substrate added when necessary, and amended with Nutricote 13-11-11 fertilizer according to standard protocols used by Mauna Kea Forest Watershed Alliance to ensure initial survival. Seedlings were measured to the nearest mm in the greenhouse prior to out-planting, and three times after out-planting during March, June and July 2016. March measurements were used as the initial height value in subsequent analyses. Weeds were removed throughout the 2016 growing period. Herbivory and seedling mortality was caused by non-native game birds at Plot 2, and data from that plot were eliminated from further analyses.

Analyses

We used linear mixed models to analyze factors associated with plant growth, and general linearized mixed models to analyze factors associated with survival. We created separate growth and survival models for each species to maintain comparability across model types, and because multi-species models did not converge. Separate models for each species also allowed model effects such as interactions to be more easily interpreted. Significant interactions might

mean that an origin effect differs based on temperature, which would suggest that origin of seed is an important consideration for restoration. An origin by elevation interaction effect, i.e., low origin seedlings do well in low but not high elevations and vice versa, might be indicative of origin matching elevation, as opposed to greater survival and growth in only low elevation origin plants.

Predictors for both the growth and survival models were the same: plot as a random effect, seed origin (high or low elevation), plot elevation, minimum temperature, maximum temperature, average temperature, temperature difference, relative humidity, and soil water content. Average temperature and relative humidity lacked variation between plots and were eliminated as model predictors. We used Pearson's correlation statistic to assess relationships between continuous predictors, and removed several to reduce collinearity. Minimum temperature was eliminated from consideration due to its strong negative correlation to elevation ($r=-0.77$) and moderate negative relationship to temperature difference ($r=-0.68$). Maximum temperature was eliminated as a factor for consideration due to a high correlation with temperature difference ($r=0.91$). There was a moderate negative correlation between elevation and soil water content ($r=-0.62$). Values for microclimate variables were individually assigned based on the time period each seedling was in the ground, i.e., plants that died between the June and July measurements were assigned an average of the variable using March–June data, while those surviving the duration of the experiment were assigned data from March–July.

Data for growth included an individual slope of growth per day for each seedling: growth (mm) in response to the number of days between measurements (growth per day = growth \sim days since initial height measurement). Data were weighted based on the number of days between measurements. Seedlings with measurements for March–July received a weight of 2, those with March–June 1.75, and those with June–July a weight of 1. All data analyses were conducted in R 3.3.1 (R Core Development Team 2015). Mixed effect models were used to account for variation due to microclimatic variables not captured by fixed effects. Plot was treated as a random effect. Additionally, despite perfect correlation between plot and elevation, elevation was included as a fixed effect to explain additional variation in models. Growth models were fitted using linear mixed effect models (Bates et al. 2015) and restricted maximum likelihood (REML) due to unbalanced samples. We analyzed seedling survival using logistic regression models (generalized linear mixed models with logit link function) due to the binary nature of the data. We used AICc reverse stepwise model selection for both growth and survival models (Mazerolle 2011). Fixed and random effects were evaluated using packages 'sjstats' and 'sjPlot' (Ludecke 2016a, Ludecke 2016b).

RESULTS

Microclimate

We summarized microclimate data and provided minimum, maximum, and average summaries by month (Figures 2, 3, and 4). There were two separate instances where soil water content data were not collected for a month; one occasion was due to a faulty sensor and another to disturbance by rodents.

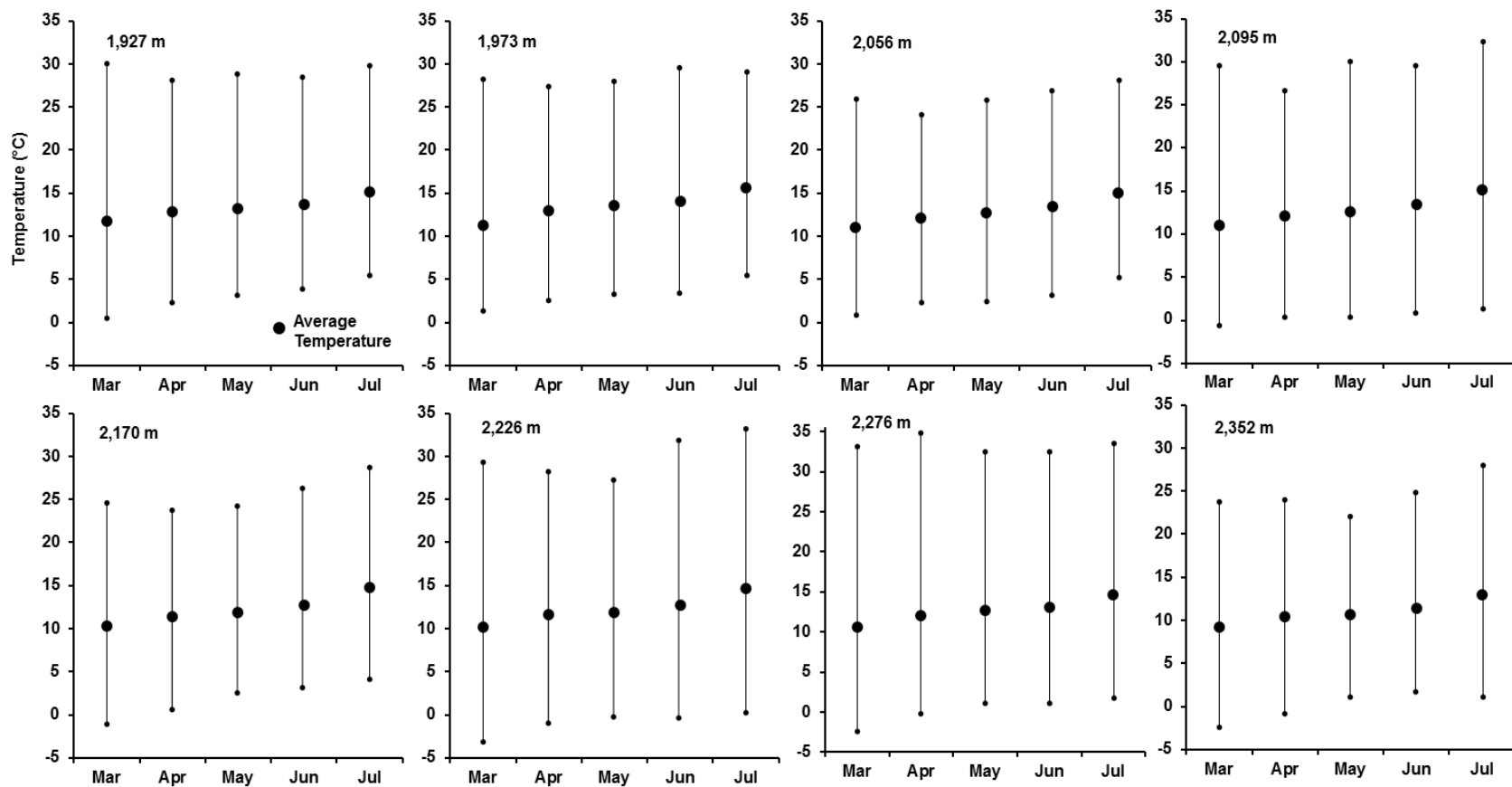


Figure 2. Monthly minimum, maximum, and average temperature (°C) by plot, March–July 2016. Data loggers recorded average values at five-minute intervals.

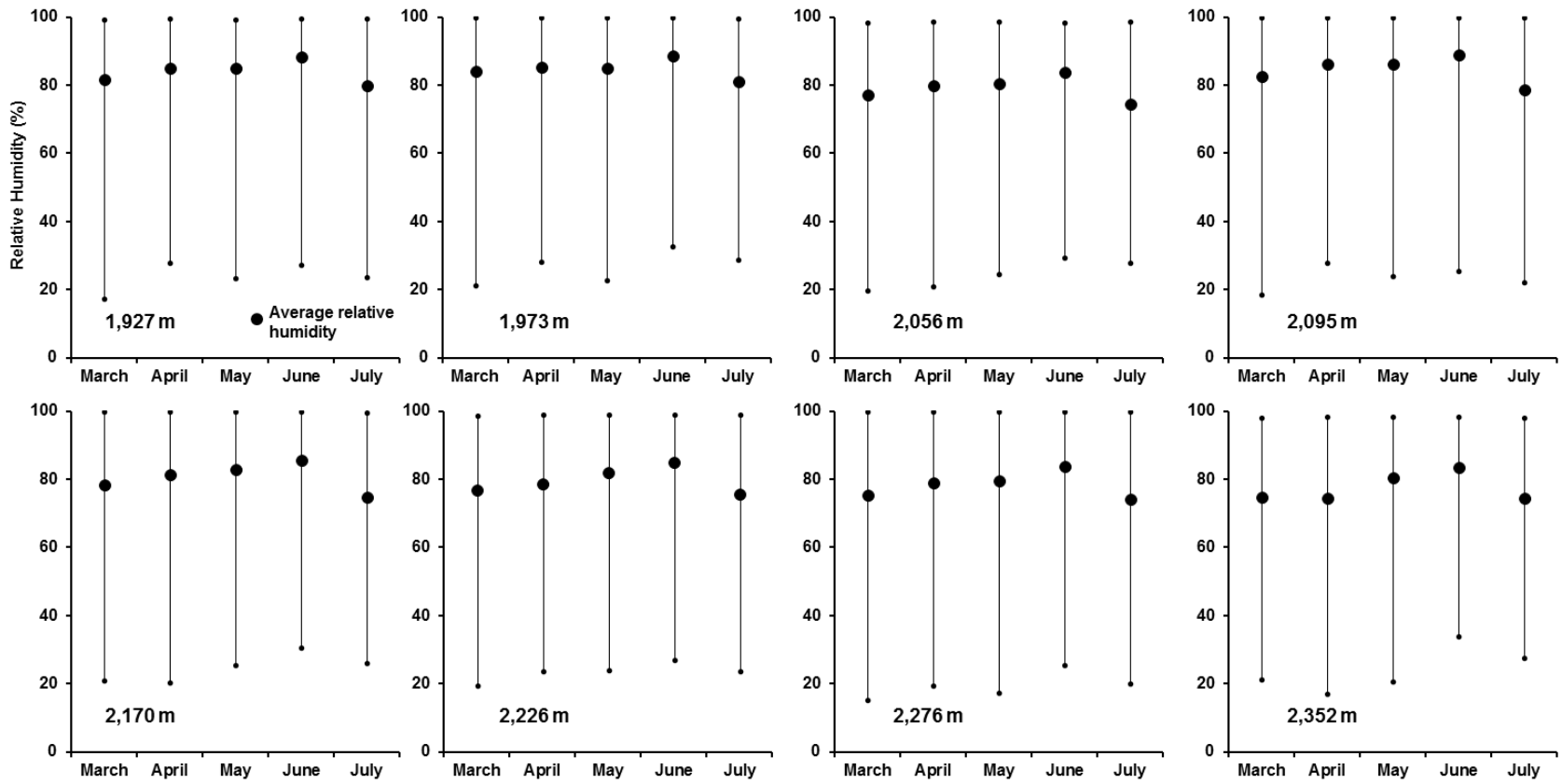


Figure 3. Monthly minimum, maximum, and average values of relative humidity (%) by plot, March–July 2016. Data loggers recorded average values at five-minute intervals.

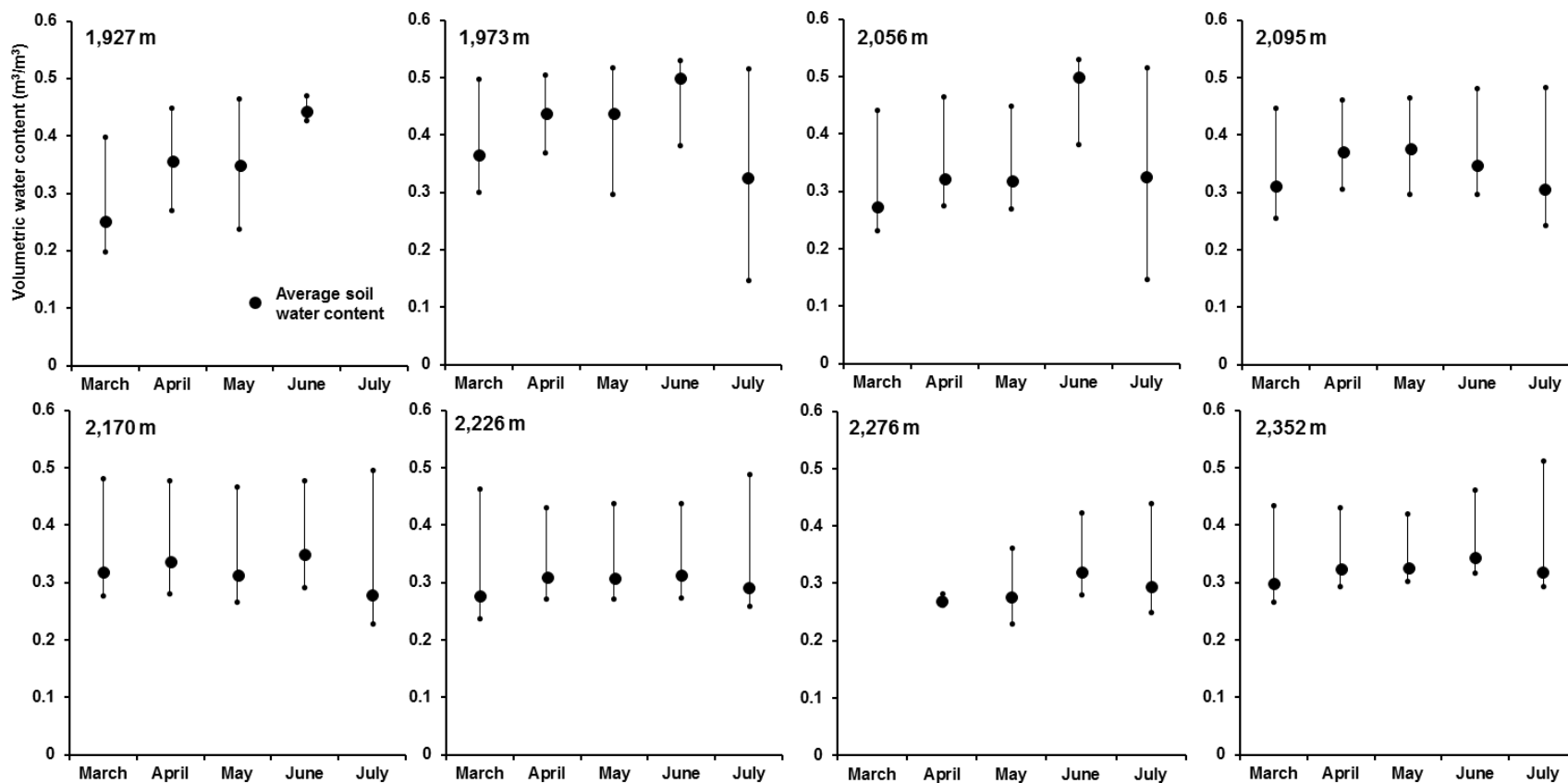


Figure 4. Monthly minimum, maximum, and average values of soil volumetric water content (m^3/m^3) by plot, February–July 2016. Data loggers recorded average values at five-minute intervals. Values are missing for the plot at 1,927 m for July and at 2,276 m for March, due to rat disturbance and a faulty sensor, respectively.

Survival

We compared overall seedling survival across and within each species, by origin (high or low-elevation) using chi-square tests. Plant survival was variable between plots (Figure 5), and generally high among all three plant species. High-elevation origin survival of *D. viscosa* (75.2%) was significantly greater than that of low-elevation origin (58.7%), but overall survival of other species did not differ between high- and low-elevation origins (Table 1).

Table 1. Chi-square tests of difference in survival between three species of seedlings grown from high and low-elevation sources at Kanakaleonui Bird Corridor, Hawai'i Island.

Species	χ^2	<i>P</i>
<i>C. oahuense</i>	0.009	0.924
<i>D. viscosa</i>	8.672	0.003
<i>S. chrysophylla</i>	1.900	0.168
All	0.963	0.326

In logistic regression mixed effect models, plant survival models varied across species (Table 2). Although survival of all three species was predicted by elevation and soil water content, the relationship was variable between species (Table 3). The random effect of plot did not explain variation in top models (ICC=0.00) for *D. viscosa* and *S. chrysophylla* (Table 4). However, plot was retained to demonstrate that micro-variation between plots was accounted for in the model, and to maintain model comparability across species.

C. oahuense survival probability was inversely related to soil water content, with approximately four times greater probability of survival in locations with low soil water content and elevation respectively (Table 4). Survival increased slightly with temperature range for all seedlings, and 163% for seedlings of low elevation origin.

Survival of *D. viscosa* was influenced by all microclimate variables and initial seedling height (Table 4). Seedlings of high-elevation origin had a 92% greater probability of survival overall. Soil water content and elevation were inversely related to seedling survival with seedlings at lower elevation having a 64% greater probability of survival, with an even lower survival probability of seedlings of low-elevation origin planted at high elevations. Initial height increased seedling survivorship probabilities by 95%, and increasing range of temperature by 66%. The random effect of plot did not explain additional variation in the model (ICC = 0.000).

Initial seedling height, elevation, and soil water content all positively influenced *S. chrysophylla* survival. The effect of origin was not informative in the top model alone or as an interaction term. Taller initial seedling heights increased survival probability by 292%, while seedlings at higher elevations and those with high soil water content increased survival probability by 174% and 169%, respectively.

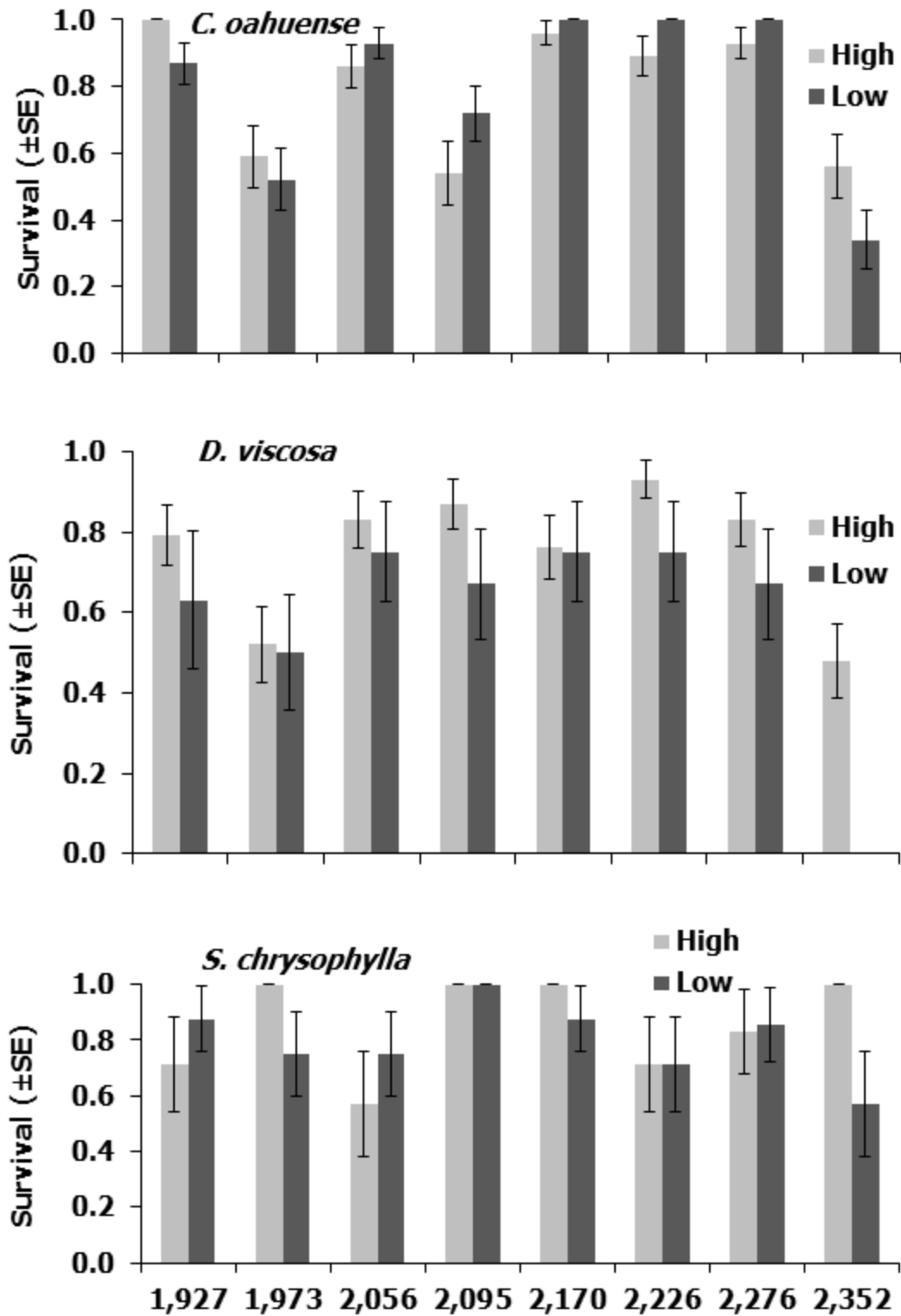


Figure 5. Survival of 896 seedlings planted along an elevation gradient across eight plots in 2016 at Kanakaleonui Bird Corridor, Mauna Kea, Hawai'i. The plot at 1,973 m elevation was removed from subsequent modeling due to heavy herbivory by non-native game birds.

Table 2. Summary of fixed effects of top models for each plant species, *Chenopodium oahuense*, *Dodonaea viscosa*, and *Sophora chrysophylla*. Plot was specified as a random effect in all models. Model predictors included initial seedling height (Initial height), seedling origin (Origin), plot elevation (Elev), temperature range (Temp), average soil water content (Water), and the interactions of Origin with Elev, Temp, and Water, respectively.

Model type	Model predictors
Survival model	
<i>C. oahuense</i>	Elev + Temp + Water + Origin + Temp*Origin + Plot
<i>D. viscosa</i>	Initial height + Elev + Temp + Water + Origin + Elev*Origin + Plot
<i>S. chrysophylla</i>	Initial height + Elev + Water + Plot
Growth model	
<i>C. oahuense</i>	Initial height + Temp+ Origin + Temp*Origin + Plot
<i>D. viscosa</i>	Plot
^A <i>S. chrysophylla</i>	Initial height + Plot; Plot

^A Indicates tie for top-ranked model

Table 3. Direction of effects on plant survival by species and origin of seed (reference category was high elevation origin). Initial seedling height, origin of seed (high or low elevation), plot elevation, temperature range, and average soil water content, as well as the interaction of origin with elevation, temperature, and origin, respectively, were fixed effect terms included in modeling. An ↑ indicates a positive influence on plant growth while a ↓ indicates a negative influence on plant growth. Dash indicates that the term was not a factor in the top linear mixed model. A double arrow indicates that origin influenced plant survival both as a stand-alone predictor, and in an interaction term.

Fixed effect	Plant Species					
	<i>C. oahuense</i>		<i>D. viscosa</i>		<i>S. chrysophylla</i>	
	High	Low	High	Low	High	Low
Initial height	–	–	↑	↑	↑	↑
Seed Origin	–	↑	–	↓	–	–
Elevation	↓	↓	↓	↓↓	↑	↑
Temperature	↑	↑↑	↑	↑	–	–
Soil Water	↓	↓	↓	↓	↑	↑

Table 4. Model output values, by species, for each best model predicting seedling survival. Initial seedling height, origin of seed (high or low elevation), plot elevation, temperature range, and average soil water content, as well as the interaction of origin with elevation, temperature, and origin, respectively, were fixed effect terms included in modeling. Odds ratio values (*OR*) indicate an increased probability of survival when values >1. A confidence interval (*CI*) and p-value (*p*) are presented for each fixed effect. Random effect interpretation includes: tau.00, Kendall's tau between-group variance of the random slope; and the intra-class correlation coefficient (*ICC*), the amount of overall variation that can be explained by the grouping of Plot (Ludecke 2016a).

	Plant Species								
	<i>C. oahuense</i>			<i>D. viscosa</i>			<i>S. chrysophylla</i>		
	<i>OR</i>	<i>CI</i>	<i>p</i>	<i>OR</i>	<i>CI</i>	<i>p</i>	<i>OR</i>	<i>CI</i>	<i>p</i>
<i>Fixed Effect</i>									
(Intercept)	8.75	4.16 – 18.40	<.001	5.05	3.39 – 7.50	<0.001	35.67	5.94 – 214.33	<0.001
Initial height				1.95	1.27 – 3.01	0.002	3.92	1.27 – 12.11	0.018
Seed origin (Low)	1.70	0.86 – 3.37	0.125	0.52	0.27 – 1.01	0.055			
Elevation	0.25	0.12 – 0.53	<0.001	0.61	0.41 – 0.91	0.015	2.74	1.10 – 6.80	0.030
Temperature	1.05	0.49 – 2.24	0.898	1.66	1.21 – 2.27	0.002			
Water	0.23	0.11 – 0.50	<0.001	0.66	0.46 – 0.95	0.025	2.69	1.03 – 7.07	0.044
Elevation*Origin				0.53	0.26 – 1.09	0.085			
Temperature*Origin	2.63	1.12 – 6.17	.027						
Water*Origin									
<i>Random Effect</i>									
T _{00, Plot}		0.459			0.000			0.000	
N _{Plot}		7			7			7	
ICC _{Plot}		0.122			0.000			0.000	
Observations		393			280			96	
Deviance		241.739			272.540			77.786	

Bold indicates statistical significance at the 0.05 level.

Growth

Plant growth within each species varied dramatically by plot (Figure 6). Predictors of plant growth in linear mixed models varied between species (Table 5), and for two species, the base model held the most weight (Appendices VI and VII). The model predicting growth per day for *C. oahuense* indicated that initial seedling height negatively influenced growth over time, and that as temperature range increased, growth rate increased for seedlings of low elevation origin (Table 5). The random effect of plot explained approximately 18% of the model variance (ICC= 0.184), and the fixed effect of elevation did not further explain variation in the model (Table 6).

Table 5. Direction of fixed effects on plant growth over time, by species and origin of seed. Initial seedling height, origin of seed (high or low elevation), plot elevation, average temperature, and average soil water content, as well as the interaction of origin with elevation, temperature, and origin, respectively, were fixed effect terms included in modeling. An ↑ indicates a positive influence on plant growth while a ↓ indicates a negative influence on plant growth. Dash indicates that the term was not a factor in the top linear mixed model.

Fixed Effect	Plant Species					
	<i>C. oahuense</i>		<i>D. viscosa</i>		<i>S. chrysophylla</i>	
	High	Low	High	Low	High	Low
Initial height	↓	↓	–	–	↓*	↓*
Seed Origin	–	↑	–	–	–	–
Elevation	–	–	–	–	–	–
Temperature	↓	↑	–	–	–	–
Water	–	–	–	–	–	–

* The model including the effect of initial seedling height was tied with the null model as a top model for *S. chrysophylla*, and is not necessarily a significant factor affecting seedling growth.

Table 6. Model output table, by species, for each best model predicting seedling growth over time. Initial seedling height, origin of seed (high or low elevation), plot elevation, temperature range, and average soil water content, as well as the interaction of origin with elevation, temperature, and origin, respectively, were fixed effect terms included in modeling. Slope (B) with a confidence interval (CI) and p-value (p) are presented for each fixed effect. Random effect interpretation includes: sigma-squared, the within-group variance; tau.00, Kendall's tau between-group variance of the random slope; and the intra-class correlation coefficient (ICC) is the amount of overall variation that can be explained by the grouping of Plot (Ludecke 2016a).

	Plant Species								
	<i>C. oahuense</i>			<i>D. viscosa</i> ^A			<i>S. chrysophylla</i> ^B		
	<i>B</i>	<i>CI</i>	<i>p</i>	<i>B</i>	<i>CI</i>	<i>p</i>	<i>B</i>	<i>CI</i>	<i>p</i>
<i>Fixed Effect</i>									
(Intercept)	0.29	-0.24 – 0.83	.303				-0.40	-0.54 – -0.26	<.001
Initial height	-0.41	-0.53 – -0.28	<.001				-0.13	-0.23 – -0.03	.010
Seed origin (Low)	0.37	0.14 – 0.59	.007						
Elevation									
Temperature	-0.06	-0.59 – 0.47	.826						
Water									
Elevation*Origin									
Temperature*Origin	0.31	0.09 – 0.52	.016						
Water*Origin									
<i>Random Effect</i>									
σ^2		2.125						0.159	
T _{00, Plot}		0.480						0.002	
N _{Plot}		7			7			7	
ICC _{Plot}		0.184			0.083			0.010	
Observations		345			234			82	
R ²		.332						.112	

Bold indicates statistically significant at the 0.05 level. ^ABase model was best for predicting seedling growth over time. ^BTop model tied with base model.

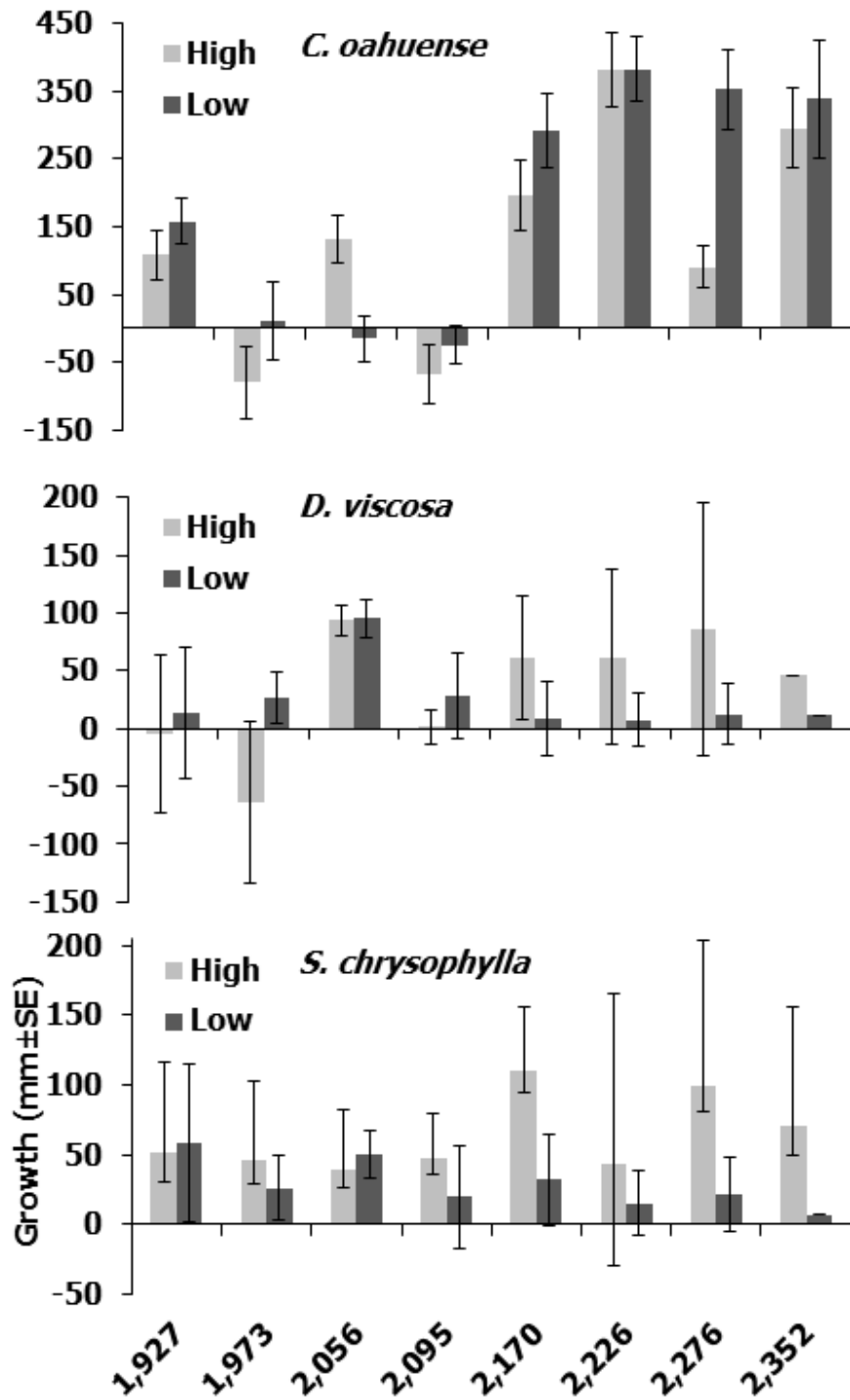


Figure 6. Growth per day of 744 seedlings planted along an elevation gradient across eight plots in 2016 at Kanakaleonui Bird Corridor, Mauna Kea, Hawai'i. Average growth and standard error are presented for each species, and categorized by high and low elevation seed origin. The plot at 1,973 m elevation was removed from statistical analyses due to heavy herbivory by non-native game birds.

The top model for *D. viscosa* was the base model, with a moderately strong model weight ($w_i = 0.52$). The second-ranking model contributed substantially to account for most of the remaining weight among those in the model suite ($w_i = 0.42$), which included the negative influence of water on seedling growth. The random effect of plot explained 8.3% of the variation in plant growth (ICC=0.083) in the base model (Table 8).

The base model and one including initial seedling height were tied as top models for predicting growth of *S. chrysophylla* seedlings, each holding nearly half of the model weight (Base $w_i = 0.45$, Height $w_i = 0.45$). The random effect of plot explained 2.4% of the variation in plant growth (ICC=0.024; Table 6), indicating that a mixed model may not have been more informative than a traditional linear model for predicting plant growth in this case. However, the random effect of plot was retained to demonstrate that micro-variation between plots was accounted for in the model, and to maintain model comparability across species.

DISCUSSION

Our findings did not support a clear common effect of seedling origin on plant survival or growth for three native montane species planted along an elevation gradient. The presence of distinct plant ecotypes was not supported in this experiment except for *D. viscosa*; survival did not differ between plants from lower-elevation closed canopy wet and mesic forests, and high-elevation subalpine woodland communities. Highest-ranked models of survival and growth had different combinations of predictors within and between species. Soil water content and elevation influenced survival of all species; however, these factors were not important predictors of growth. Moreover, there were no predictors for plant growth in common between species.

Plant growth was highly variable within and among species. *C. oahuense* plants frequently fell over and grew laterally, becoming bushy in many instances, causing them to lose absolute height, thus a meaningful measure of growth may not have been captured during the course of this experiment. Although height is a standard measurement in ecological experiments of plants, a better metric may have been total plant volume, which would have required destructive sampling. Initial seedling height for both *C. oahuense* and *S. chrysophylla* was negatively associated with subsequent growth; however, the negative association of initial height with growth in *S. chrysophylla* in the highest-ranked model was perhaps not informative given that it was not substantially better than the base model. *C. oahuense* of low-elevation origin were positively associated with growth, but those of high-elevation origin were not. No other model predictors significantly influenced *D. viscosa* or *S. chrysophylla* growth.

Overall survival of species did not differ by origin except for *D. viscosa*, which contrary to our hypothesis, had significantly greater survival in seedlings from high-elevation origin than those from low-elevation origin. When we controlled for potentially confounding factors in linearized mixed models, origin influenced patterns of survival in both *C. oahuense* and *D. viscosa*. Survival in *D. viscosa* decreased with plot elevation, especially in plants from low-elevation origin. Survival in *C. oahuense* was higher in plots with greater range in temperature, especially in plants from low-elevation origin. Taller initial plant heights were positively associated with survival of *D. viscosa* and *S. chrysophylla*, but not *C. oahuense*. *S. chrysophylla* survival was positively associated with soil water content.

Plots with lowest soil water content also had highest temperature ranges, and were somewhat correlated. It is possible that lower survival in *C. oahuense* and *D. viscosa* was associated with the correlation between these two predictors. Micro-topographic site variation was not explained by the random effect of plot. Most of this variation may have been captured by the measurements of temperature range and water content. Elevation was an important predictor in models of survival for all three species. It was positively associated with *S. chrysophylla* survival, but negatively associated with *C. oahuense* and *D. viscosa* survival, largely driven by poor survival of plants from low elevation origin. Larger-scale climate changes such as the trade wind inversion that limits upward movement of prevailing moisture-laden trade winds is an especially important influence of climate in montane environments of Hawai'i.

Weather variability, warming, and rainfall patterns are affected within the inversion layer (Cao et al. 2007). The inversion layer on Hawai'i Island has a diurnal base height range of 2,201–2,255 m, which included three of our study plots in the upper portion of KBC. Documented effects of increased number of trade wind inversion days, and their associated drier and warmer conditions have increased mortality and decreased recruitment of Haleakala silverswords (*Argyroxiphium sandwicense* subsp. *macrocephalum*), particularly near range limits, over the last decade (Krushelnycky et al. 2013). There is evidence that the inversion layer has been decreasing in elevation, and the lifting condensation level is increasing, which may result in reduced cloud thickness, rainfall, and overall size of the rain-belt on mountain slopes (Diaz et al. 2011). This shift could reduce the extent of wet and mesic forests at their upper-elevation limits, and perhaps favor drier mountain parkland communities. Restoration strategies may benefit from incorporating these future scenarios.

The scale of our experiment did not capture genetic differences that would be useful to exploit for restoration strategies. Although seed sources for *C. oahuense* and *S. chrysophylla* differed by 500 m in elevation, they were ≤ 4 km apart in distance. In contrast, the source for low-elevation *D. viscosa*, which had the lowest survival in our experiment, was approximately 30 km from KBC on the southwestern slope of Mauna Kea. Survival models for *C. oahuense* and *D. viscosa* indicated that microclimate conditions at high elevation locations may have been unfavorable. However, survival increased with elevation for *S. chrysophylla*, the dominant subalpine tree species. Thus, local seed sources may confer greater short-term survival, but not contribute to substantial genetic enrichment.

The short-term nature of our experiment precluded meaningful findings about enhancing genetic enrichment to build resiliency in restoration strategies; however, limited as it was, it represents one of the few attempts to examine the effects of local adaptation to prospective climate scenarios within species' current ranges. Other studies have examined upper-elevation extension of species ranges by observation (Beckage et al. 2008, Feeley et al. 2011, Pauli et al. 2012) or manipulation (Mathiasen and Premoli 2016, Rehm and Feeley 2016, Van der Veken et al. 2012), but have not addressed continued persistence within existing species' ranges, which will be essential for understanding responses of broadly distributed species. Moreover, these studies also examined relatively intact ecosystems in contrast to the degraded mountain parkland in our study (Cuddihy 1984, Tunison et al. 1995). Although factors such as ungulates had been eliminated, competition with a suite of aggressive invasive plants such as matt-forming grasses and bull thistle (*Cirsium vulgare*), and herbivory by non-native birds presented formidable obstacles to conducting our experiment at KBC. Herbivory by birds caused us to discard >10% of our data in model analyses. Introduced pasture grasses present perhaps the most pervasive obstacle to restoration of many native ecosystems in Hawai'i, reinforcing a

trajectory of conversion away from forested environments (Alexander et al. 2015, Leopold and Hess 2016). Although we treated grass in all plots with herbicide prior to planting, grasses quickly re-grew despite our repeated manual control attempts. Quantifying invasive grass regrowth would have been a better approach to model its competitive effects on survival and growth.

The case for understanding future restoration strategies for highly degraded Hawaiian ecosystems is more complicated than predicting native species responses to forecasted climate scenarios (Fortini et al. 2013), because they must also predict and address the interactive responses of invasive species (Walther et al. 2009). Further experimentation on larger spatial and temporal scales is necessary to determine the empirical responses of species and communities to changing climate in the full context of these biological complexities.

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APPENDIX I

Appendix I. Number of each species that survived by origin and plot at Kanakaleonui Bird Corridor, Hawai'i Island. Proportion survived is indicated in parentheses.

Plot (m)	Species					
	<i>C. oahuense</i>		<i>D. viscosa</i>		<i>S. chrysophylla</i>	
	High	Low	High	Low	High	Low
1,927	28/28 (1.00)	26/30 (0.87)	23/29 (0.79)	5/8 (0.63)	5/7 (0.71)	7/8 (0.88)
1,973	16/27 (0.59)	15/29 (0.52)	15/29 (0.52)	6/12 (0.50)	7/7 (1.00)	6/8 (0.75)
2,056	25/29 (0.86)	26/28 (0.93)	24/29 (0.83)	9/12 (0.75)	4/7 (0.57)	6/8 (0.75)
2,095	15/28 (0.54)	21/29 (0.72)	26/30 (0.87)	8/12 (0.67)	6/6 (1.00)	7/7 (1.00)
2,170	27/28 (0.96)	29/29 (1.00)	22/29 (0.76)	9/12 (0.75)	6/6 (1.00)	7/8 (0.88)
2,226	25/28 (0.89)	30/30 (1.00)	27/29 (0.93)	9/12 (0.75)	5/7 (0.71)	5/7 (0.71)
2,276	27/29 (0.93)	29/29 (1.00)	25/30 (0.83)	8/12 (0.67)	5/6 (0.83)	6/7 (0.86)
2,352	15/27 (0.56)	10/29 (0.34)	14/29 (0.48)	0/12 (0.00)	7/7 (1.00)	4/7 (0.57)
Overall	178/224 (0.80)	186/233 (0.80)	176/234 (0.75)	54/92 (0.59)	51/53 (0.96)	60/67 (0.90)

APPENDIX II

Appendix II. All logistic regression models tested using 'drop1' function in R 3.3.1 to determine factors influencing survival of *Chenopodium oahuense* seedlings. Model terms included initial seedling height (Initial height), origin of seed (Origin), elevation at which seedling was planted (Elev), temperature range (Temp), soil water content (Water), and the interaction of Origin with each climate variable: Elev, Temp and Water.

Models	<i>K</i>	AIC _c	Δ AIC _c	<i>w_i</i>
Origin + Elev + Temp + Water + Temp*Origin + (1 Plot)	7	268	0.00	0.31
Origin + Elev + Temp + Water + Elev*Origin + Temp*Origin + Water*Origin + (1 Plot)	9	268	0.36	0.26
Origin + Elev + Temp + Water + Temp*Origin + Water*Origin + (1 Plot)	8	269	0.96	0.19
^A Initial height + Origin + Elev + Temp + Water + Elev*Origin + Temp*Origin + Water*Origin + (1 Plot)	10	269	1.54	0.14
Origin + Elev + Temp + Water + (1 Plot)	6	271	3.18	0.06
(1 Plot)	2	272	4.28	0.04

K indicates Degrees of freedom. ^AIndicates full model.

APPENDIX III

Appendix III. All logistic regression models tested using 'drop1' function in R 3.3.1 to determine factors influencing survival of *Dodonaea viscosa* seedlings. Model terms included initial seedling height (Initial height), origin of seed (Origin), elevation at which seedling was planted (Elev), temperature range (Temp), soil water content (Water), and the interaction of Origin with each climate variable: Elev, Temp, and Water.

Models	K	AIC_c	ΔAIC_c	w_i
Initial height + Origin + Elev + Temp + Water + Origin:Elev + (1 Plot)	8	289	0.00	0.37
Initial height + Origin + Elev + Temp + Water + (1 Plot)	7	290	1.03	0.22
Initial height + Origin + Elev + Temp + Water + Elev*Origin + Water*Origin + (1 Plot)	9	290	1.29	0.19
Initial height + Origin + Elev + Temp + (1 Plot)	6	291	2.41	0.11
^A Initial height + Origin + Elev + Temp + Water + Elev*Origin + Temp*Origin + Water*Origin + (1 Plot)	10	292	3.42	0.07
Initial height + Temp + Origin + (1 Plot)	5	293	4.28	0.04
(1 Plot)	2	308	19.94	0.00

K indicates Degrees of freedom. ^AIndicates full model.

APPENDIX IV

Appendix IV. All logistic regression models tested using 'drop1' function in R 3.3.1 to determine factors influencing survival of *Sophora chrysophylla* seedlings. Model terms included initial seedling height (Initial height), origin of seed (Origin), elevation at which seedling was planted (Elev), temperature range (Temp), soil water content (Water), and the interaction of Origin with each climate variable: Elev, Temp, and Water.

Models	<i>K</i>	AIC _c	Δ AIC _c	<i>w_i</i>
Initial height + Elev + Water + (1 Plot)	5	88.5	0.00	0.32
Initial height + Origin + Elev + Water + Elev*Origin + (1 Plot)	7	89.3	0.88	0.21
Initial height + Origin + Elev + Water + Elev*Origin + Water*Origin + (1 Plot)	8	89.7	1.22	0.17
Initial height + Origin + Elev + Water + (1 Plot)	6	90.7	2.2	0.11
Initial height + Elev + (1 Plot)	4	91.1	2.67	0.08
Initial height + Elev + Temp + Water + Origin + Elev*Origin + Water*Origin + (1 Plot)	9	92.0	3.56	0.05
^A Initial height + Origin + Elev + Temp + Water + Elev*Origin + Temp*Origin + Water*Origin + (1 Plot)	10	93.2	4.72	0.03
(1 Plot)	2	93.7	5.27	0.02

K indicates Degrees of freedom. ^AIndicates full model.

APPENDIX V

Appendix V. All linear mixed models tested using 'drop1' function in R 3.3.1 to determine predictors of *Chenopodium oahuense* seedling growth. Model terms included initial seedling height (Initial height), origin of seed (Origin), elevation at which seedling was planted (Elev), temperature range (Temp), soil water content (Water), and the interaction of Origin with each climate variable: Elev, Temp, and Water.

Models	K	AIC_c	ΔAIC_c	w_i
Initial height + Temp + Origin + Temp*Origin (1 Plot)	7	1044	0	0.73
Initial height + Water + Temp + Origin + Temp*Origin + (1 Plot)	8	1046	2.22	0.24
Initial height + Temp + Water. + Origin + Water*Origin + Temp*Origin + (1 Plot)	9	1050	6.38	0.03
Initial height + Elev + Temp + Water. + Origin + Temp*Origin + Water*Origin + (1 Plot)	10	1052	8.16	0.01
^A Initial height + Elev + Temp + Water + Origin + Elev*Origin + Temp*Origin + Water*Origin + (1 Plot)	11	1056	12.23	0.00
(1 Plot)	3	1074	30.33	0.00

K indicates Degrees of freedom. ^AIndicates full model.

APPENDIX VI

Appendix VI. All linear mixed models tested using 'drop1' function in R 3.3.1 to determine predictors of *Dodonaea viscosa* seedling growth. Model terms included initial seedling height (Initial height), origin of seed (Origin), elevation at which seedling was planted (Elev), temperature range (Temp), soil water content (Water), and the interaction of Origin with each climate variable: Elev, Temp, and Water.

Models	<i>K</i>	<i>AIC_c</i>	ΔAIC_c	<i>w_i</i>
(1 Plot)	3	216	0.00	0.52
Water + (1 Plot)	4	216	0.42	0.42
Initial height + Water + (1 Plot)	5	220	4.56	0.05
Initial height + Elev + Water + (1 Plot)	6	225	9.74	0.00
Initial height + Elev + Temp + Water + (1 Plot)	7	231	15.49	0.00
Initial height + Elev + Temp + Water + Origin + (1 Plot)	8	237	21.28	0.00
Initial height + Origin + Elev + Temp + Water + Temp* Origin + (1 Plot)	9	242	26.43	0.00
Initial height + Origin + Elev + Temp + Water + Elev*Origin + Temp* Origin + (1 Plot)	10	247	31.11	0.00
^A Initial height + Origin + Elev + Temp + Water + Elev* Origin + Temp*Origin + Water*Origin + (1 Plot)	11	251	35.41	0.00

K indicates Degrees of freedom. ^AIndicates full model.

APPENDIX VII

Appendix VII. All linear mixed models tested using 'drop1' function in R 3.3.1 to determine predictors of *Sophora chrysophylla* seedling growth. Model terms included initial seedling height (Initial height), origin of seed (Origin), elevation at which seedling was planted (Elev), temperature range (Temp), soil water content (Water), and the interaction of Origin with each climate variable: Elev, Temp, and Water.

Models	K	AIC_c	ΔAIC_c	w_i
Initial height + (1 Plot)	4	42.7	0	0.45
(1 Plot)	3	42.7	0.02	0.45
Initial height + Water + (1 Plot)	5	45.8	3.11	0.10
Initial height + Temp + Water + (1 Plot)	6	52.7	10.00	0.00
Initial height + Origin + Temp + Water + (1 Plot)	7	58.7	16.02	0.00
Initial height + Origin + Elev + Temp + Water + Temp*Origin + (1 Plot)	8	62.6	19.85	0.00
Initial height + Origin + Elev + Temp + Water + Temp*Origin + Water*Origin + (1 Plot)	9	68.4	25.71	0.00
Initial height + Origin + Elev + Temp + Water + Temp*Origin + Water*Origin + (1 Plot)	10	75.6	32.91	0.00
^A Initial height + Origin + Elev + Temp + Water + Elev*Origin + Temp*Origin + Water*Origin + (1 Plot)	11	81.3	38.61	0.00

K indicates Degrees of freedom. ^AIndicates full model.