

## Effects of Extreme Drought on Vegetation of a Lava Flow on Mauna Loa, Hawai'i<sup>1</sup>

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**ABSTRACT:** Effects of an extreme drought were examined along an elevational gradient on Mauna Loa Volcano, Hawai'i. The composition, vigor, and survivorship of plants were examined on a 2400-yr-old *pāhoehoe* lava flow at three elevations: 1755, 2000, and 2195 m above sea level. Three plant species, *Coprosma ernodeoides* A. Gray, *Styphelia tameiameia* (Cham. & Schlechtend.) F. v. Muell., and *Vaccinium reticulatum* Sm., were encountered most frequently at the three sites. Greatest mortality occurred at the site at 2000 m elevation, where the drought caused a shift from a slight excess of precipitation over evaporation to a large excess of evaporation. Occasional severe droughts may play an important part in shaping primary succession in this region.

MAUNA LOA VOLCANO on the island of Hawai'i is a valuable resource for studies of primary succession/ecosystem development because it supports a large number of well-mapped, well-dated lava flows that span a wide range of ages and because climate also varies markedly, but predictably, with elevation and aspect on the mountain. Mauna Loa has been utilized in a number of vegetation studies (Jacobi et al. 1983, Drake and Mueller-Dombois 1993, Aplet and Vitousek 1994, Karpa and Vitousek 1994). Implicit or explicit in most of these studies is the assumption that the current vegetation and/or soils of each site reflect ecosystem development under more or less constant conditions; directional change (other than with age) and rare episodic events are assumed to be absent or relatively unimportant in shaping primary succession.

Mauna Loa lies within the trade wind zone, and, under normal conditions, the windward

east slope of Mauna Loa receives a surplus of precipitation that extends up to the trade wind inversion near an elevation of 2000 m (Juvik et al. 1978, Vitousek et al. 1992). Between January and May 1992, Hawai'i experienced a severe drought associated with an El Niño Southern Oscillation (ENSO) event. During that time period, rainfall in the coastal city of Hilo on the east side of Mauna Loa was the lowest recorded in more than 100 yr of observations. Moreover, the severity of the drought increased with increasing elevation on Mauna Loa.

In this paper, we describe our study of the effects of this drought on vegetation across a range of elevations on a single lava flow on Mauna Loa to ascertain whether occasional droughts could influence the survivorship of plants and thereby affect the course of primary succession. To this end, we determined how plant vigor varied with plant size, vegetation cover, topographic position, and soil depth.

### Study Site

The study was conducted on a *pāhoehoe* lava flow (smooth, ropy surface texture) on the windward east flank of Mauna Loa, Hawai'i, in July and August 1992. The location and age of the 2400 ± 150-yr-old flow were determined from unpublished open-file maps obtained from J. Lockwood, U.S. Geo-

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logical Survey (see also Lockwood et al. 1988). Three study sites were established, at 1755, 2000, and 2195 m elevation, to examine the effects of the drought across an elevation range; field observations suggested that the greatest effects of the drought occurred within that range. The two higher sites were undisturbed, native-dominated shrub communities; the lowest-elevation site had been grazed by sheep from the late nineteenth century until 1935 (N. Santos, pers. comm.), and alien grasses were an important component of its flora.

#### MATERIALS AND METHODS

The water available to plant roots is a function of moisture inputs (rainfall, fog catch, dew), evaporative demand by the atmosphere, infiltration, water retention in the soil, and root distribution. Although a complete water balance incorporating all of these elements seldom is practicable, a simple procedure comparing the principal input (rainfall) and the principal loss (evaporative demand) provides a useful index of moisture availability. In this study, we calculated rainfall minus atmospheric evaporative demand (potential evaporation [PET], henceforth called simply evaporation) to approximate the surplus or deficit of water available to plants.

Drought-period rainfall was compiled from NOAA records for Hilo Airport (11 m), Kūlani Camp (1576 m), Kūlani School Site (1748 m), Kūlani Mauka (2530 m), and Mauna Loa Observatory (3400 m). Rainfall data for three sites, at 710, 1130, and 1640 m, were available through a companion project (Juvik and Nullet 1994). These data were averaged over the 5-month drought period, January through May 1992.

Normal rainfall data for January through May were interpolated from the recent atlas by Giambelluca et al. (1986). Evaporation data are from Bean et al. (1994). Bean measured evaporation between sea level and 3400 m, including many of the same sites used in our study. Her Mauna Loa 2 transect (14 February through 6 July 1987) closely approximates the months we used (although for

a different year), and these data, along with sea level measurements from her Mauna Loa 1 transect, were used in our study. Because the year-to-year variability for monthly evaporation in Hawai'i is low (Chang and Ekern 1985), Bean's data can be used for both the normal and drought-period water balance indices.

#### *Vegetation Survey*

In July 1992, after the drought had ended, transects were established to evaluate plant vigor. Five 100-m transects were placed randomly within each site except at the upper-elevation site at 2195 m, where only four transects were established because of the lack of *pāhoehoe* substrate at the origin of the flow. No measurements of vigor had been made before the drought. However, vegetation on this and nearby flows had been analyzed extensively (Aplet and Vitousek 1994, Karpa and Vitousek 1994), and dead or dying plants rarely were observed along this gradient.

Species and cover along the line were measured using line intercept sampling procedures at 1-m increments along the transect. If no plant occurred along that 1-m increment, nothing present (NP) was recorded. Grasses were not sampled because of the difficulty in differentiating individuals.

Six parameters were recorded for each plant surveyed at each meter mark. These included two diameter measurements and a height measurement to the nearest centimeter (Mueller-Dombois and Ellenberg 1974). Each individual was also classified into one of five vigor classes: 1, <5% dead; 2, 5 to 25% dead; 3, 25 to 50% dead; 4, 50 to 99% dead; and 5, 100% dead, with the percentage estimated visually from the dead leaf material present. The microtopographic position (pit, mound, or slope) of the plant was recorded, and the soil cover at the base of the plant was measured by inserting a metal rod down to the lava substrate and recorded to the nearest centimeter. Every 10 m along the belt transect, a circle 1 m in diameter was placed on the center of the target plant, and the cover of the neighboring plants was estimated visually within the circle. This esti-

mate was used to evaluate the effects of neighboring plant cover on the vigor of the corresponding target plant; grasses were included in this measurement of cover.

Of the three most common species (*Styphelia tameiameia* [Cham. & Schlechtend.] F. v. Muell. [Epacridaceae], *Coprosma ernodeoides* A. Gray [Rubiaceae], and *Vaccinium reticulatum* Sm. [Ericaceae]), *S. tameiameia* was encountered infrequently along the transects at the lowest-elevation site. We sampled a 20 by 50 m plot for *S. tameiameia* to allow comparisons across elevations for this species. All six parameters were recorded for each plant in the plot as in the belt transects. For *C. ernodeoides*, a prostrate shrub, the ramet crossing the transect was measured for cover along the line and for its length, and the length was treated as an estimate of size.

Twenty-five of the class 5 (apparently dead) individuals of *C. ernodeoides*, *V. retic-*

*ulatum*, and *S. tameiameia* were permanently marked at the 2000-m site to determine possible recovery from the drought. Six months after the survey was performed, these plants were assessed for changes in vitality or for recovery. Any individual plant that had not changed in condition was assumed to have died.

## RESULTS

### *Water Balance along the Elevational Gradient*

Figure 1 illustrates the relationship between rainfall and evaporation under normal and 1992 drought conditions. The evaporation rate decreased from sea level to a minimum near 1000 m and then increased with height through and above the inversion layer to >180 mm/month at 3400 m. Although

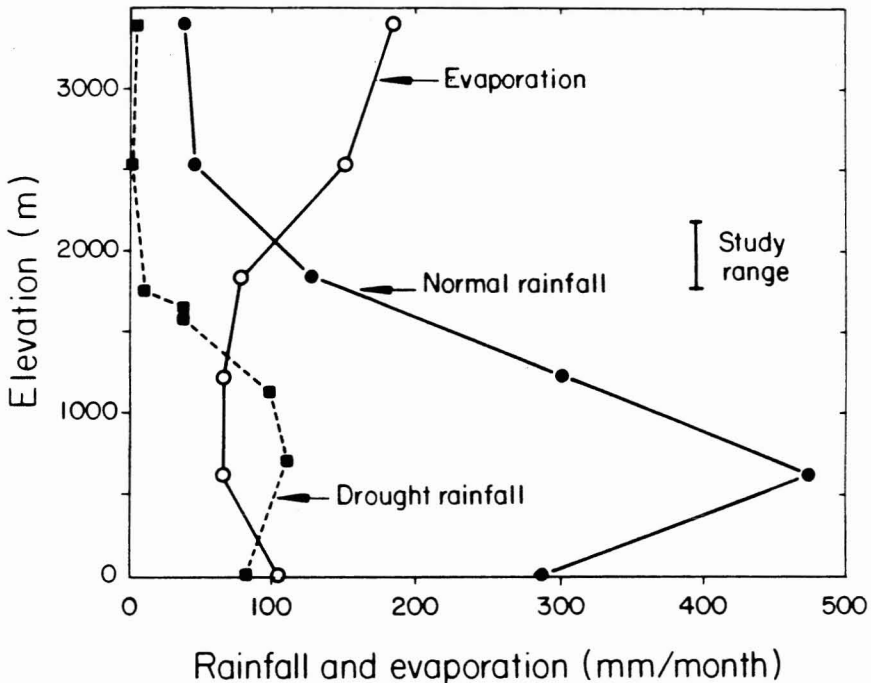


FIGURE 1. A comparison of normal and drought-period (January through May 1992) water balance parameters between sea level and 3400 m for windward Mauna Loa, Hawai'i. Evaporation rates were taken from Bean et al. (1994), normal rainfall was interpolated from Giambelluca et al. (1986), and drought-year precipitation was measured at the stations described in the text.

the magnitude of rainfall was 70–95% below normal during the drought period, the shape of the rainfall profile was identical over the transect during both normal and drought conditions, with maxima near 700 m. During normal conditions, the transition from water surplus to water deficit occurs at or above the inversion layer near 2100 m. During the drought period, however, this crossing point dropped below the inversion level to about 1350 m, resulting in a change from moisture surplus to moisture deficit over most of the study area (1755 to 2195 m). Moreover, our moisture index may underestimate the impact of drought; soil moisture storage is low in porous lava substrates, and the infiltration rate is high, causing much of the rainwater to be lost below the root zone by rapid percolation.

#### *Vegetation Composition along the Elevational Gradient*

A total of nine species, including five shrubs, three ferns, and one tree, was encountered along the transects at the three sites. Others were observed but not encountered along the transects, including *Dubautia ciliaris* and *Dubautia scabra* (DC) D. Keck (Asteraceae). Three shrubs, *Coprosma ernodeoides*, *Vaccinium reticulatum*, and *Styphelia tameiameia*, were frequent at all the sites (Table 1). *Dodonaea viscosa* Jacq. (Sapindaceae) was first recorded at the highest-elevation site, where it had a high relative frequency compared with the three dominant species. Mean plant cover, estimated by the measurements in 1-m-diameter circles, decreased with increasing elevation (Table 1). Plant size was estimated by multiplying the two recorded diameter measurements and corresponding height measurement ( $d^2h$ ). The mean size of *S. tameiameia* and *C. ernodeoides* decreased with increasing elevation (Table 2). For the most part, all three dominants were observed more frequently on mounds and slopes than in pits.

#### *Vigor along the Elevational Gradient*

Recently killed individuals were readily identifiable, and, from earlier sampling in

TABLE 1  
RELATIVE FREQUENCIES OF PLANT SPECIES ON  
A 2,400-YR-OLD *pāhoehoe* LAVA FLOW AT THREE  
DIFFERENT ELEVATION SITES

SPECIES	RELATIVE FREQUENCY (%)		
	1,755 m	2,000 m	2,195 m
<i>Coprosma ernodeoides</i> (Rubiaceae)	42	30	9.6
<i>Coprosma montana</i> Hillebr. (Rubiaceae)	0	0.9	0
<i>Cibotium glaucum</i> (Sm.) Hook. & Arnott (Dicksoniaceae)	1	0	0
<i>Dodonaea viscosa</i> (Sapindaceae)	0	0	22
<i>Dryopteris wallichiana</i> (Spreng.) Hyl. (Woodsiaceae)	0.3	0	0
<i>Metrosideros polymorpha</i> Gaud. (Myrta- ceae)	0.8	0.5	0
<i>Pellaea ternifolia</i> (Cav.) Link (Adiantaceae)	0	0.2	3
<i>Styphelia tameiameia</i> (Epacridaceae)	7.7	42	43
<i>Vaccinium reticulatum</i> (Ericaceae)	48	26	23
Plant cover (%)	64	62	42

NOTE: Plant cover was estimated from the average of measurements of cover every 10 m along the transect at each site.

and near these sites, we knew that most recorded class 5 plants represented drought-induced mortality. However, because variation in plant vigor had not been measured on this flow before the drought, it could not be safely assumed that vigor classes other than class 5 reflected the effects of the drought. Class 1 through class 4 were therefore lumped into a single live class, and the proportion of dead (class 5) to live plants (sum of class 1 through class 4) for each of the three dominant species was compared among pairs of sites using a chi-square 2 by 2 contingency table (Snedecor and Cochran 1989: 125–126). Plant vigor differed significantly with elevation (Table 3, Figure 2), and the probability of drought-induced mortality in plants peaked at the middle-elevation site (Figure 3).

At the middle-elevation site, where mortality was the greatest, the vigor of *S. tameia-*

TABLE 2  
DISTRIBUTION OF SIZE OF THREE DOMINANT PLANT SPECIES OVER ELEVATION

SPECIES	SAMPLE SIZE	ELEVATION (m)	MEAN SIZE (m <sup>3</sup> )	STANDARD DEVIATION
<i>Styphelia tameiameia</i>	85	1,755	1.58	2.4
	181	2,000	0.3	0.39
	58	2,195	0.23	0.23
<i>Vaccinium reticulatum</i>	174	1,755	0.07	0.23
	114	2,000	0.05	0.11
	31	2,195	0.08	0.15
<i>Coprosma ernodeoides</i>	158	1,755	0.46	0.39
	32	2,000	0.57	0.37
	13	2,195	0.11	0.10

NOTE:  $d^2h$  was used as an estimate of size for *Styphelia tameiameia* and *Vaccinium reticulatum* along the Mauna Loa transect. The length of the ramet that crossed the belt transect was used as an estimate of size for *Coprosma ernodeoides*.

TABLE 3  
CHI-SQUARE COMPARISON OF FREQUENCY OF VIGOR CLASSES BETWEEN ELEVATIONS FOR *Styphelia tameiameia*, *Vaccinium reticulatum*, AND *Coprosma ernodeoides*

SPECIES	$\chi$	1,755 m	2,000 m
<i>Coprosma ernodeoides</i>	2,000 m	11.25***	
	2,195 m	11.91***	36.78***
<i>Styphelia tameiameia</i>	2,000 m	20.59***	
	2,195 m	6.27*	4.41**
<i>Vaccinium reticulatum</i>	2,000 m	20.59***	
	2,195 m	5.12*	0.871NS

NOTE: Proportion of dead (class 5) to live (sum of classes 1 through 4) plants at two different elevation sites was compared by constructing a chi-square 2 by 2 contingency table to test the null hypothesis that the proportion of dead to live plants was independent of elevation, where  $p_{1755} = p_{2000}$ ,  $p_{2000} = p_{2195}$ , and  $p_{1755} = p_{2195}$ . The  $\chi^2$  values are given.

\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.005$ ; NS, not significant.

*meia* and *V. reticulatum* varied with plant size. The results of a logistic regression analysis showed that the probability of mortality was marginally significantly correlated with decreasing plant size at the 2000-m site for *S. tameiameia* ( $\chi^2 = 9.37$ ,  $n = 181$ ,  $P = 0.052$ ) and *V. reticulatum* ( $\chi^2 = 9.16$ ,  $n = 114$ ,  $P = 0.057$ ). At 2195 m above sea level (asl), *V. reticulatum* ( $\chi^2 = 15.1$ ,  $n = 31$ ,  $P = 0.01$ ) was found to follow the opposite trend, with the probability that a plant was a class 1 plant significantly correlated with small plant size. At the lowest-elevation site, vigor was independent of size for all three species. For

all three dominants at the three different sites, the probability of finding a class 5 plant was not correlated with the neighboring plant cover, with soil depth, or with its topographic position.

Of the 75 marked class 5 plants at 2000 m, 88% of the marked plants showed no sign of recovery after 6 months. Resprouting was observed in four of the 25 *S. tameiameia* plants, and one plant had a small number of live leaves that appeared to have been present at the time of marking. For *V. reticulatum*, it was difficult to differentiate new seedlings from basal sprouts, but we believed that only four plants were resprouting.

#### DISCUSSION

Changes in plant vigor were correlated with the changes in water balance with elevation. The water balance diagram in Figure 1 suggests a relatively small water deficit at the lowest site, and mortality there was negligible except for *C. ernodeoides* (Figure 2). Moreover, logistic regression indicated that vigor for all three species was independent of size, topographic position, and neighboring plant density at this elevation.

The response of *C. ernodeoides* at this site, and its even higher mortality rate at 2000 m, might be explained by a difference in root system architecture between these plants. Excavation studies showed *C. ernodeoides* to

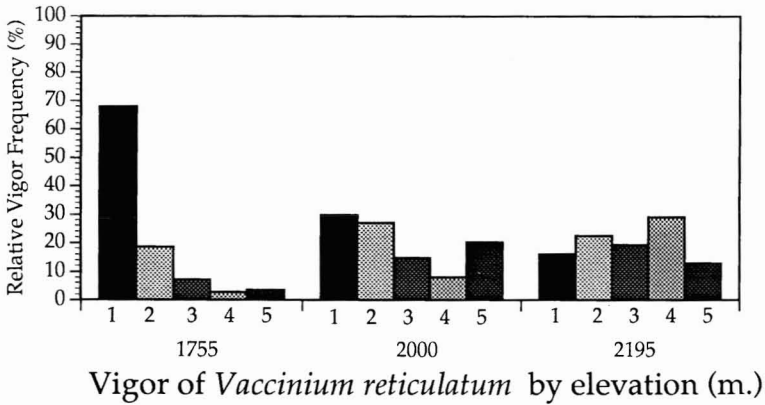
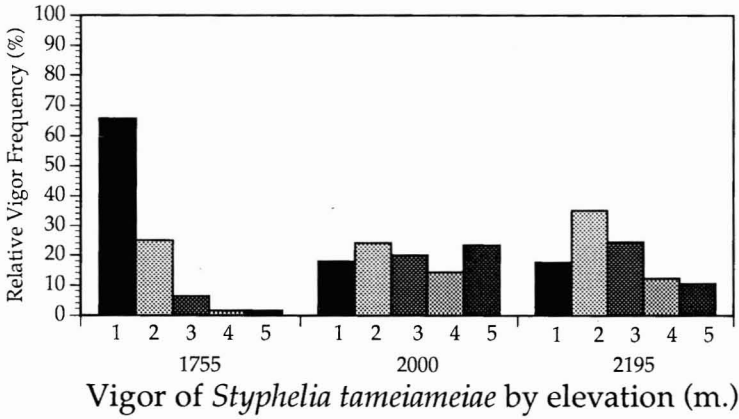
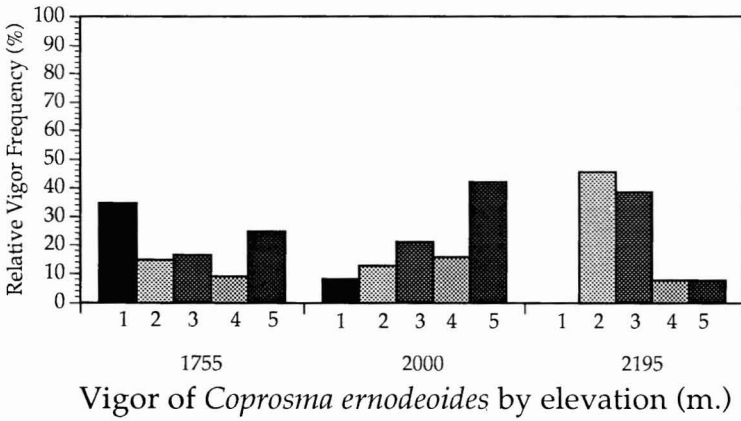


FIGURE 2. Relative frequency of individuals in the five vigor classes for *Styphelia tameiameia*, *Coprosma ernodeoides*, and *Vaccinium reticulatum* at 1755, 2000, and 2195 m. The numbers (1–5) represent the vigor classes, which were defined as follows: 1, <5% dead; 2, 5 to 25% dead; 3, 25 to 50% dead; 4, 50 to 75% dead; 5, 100% dead, with the percentage estimated visually from dead leaf material present.

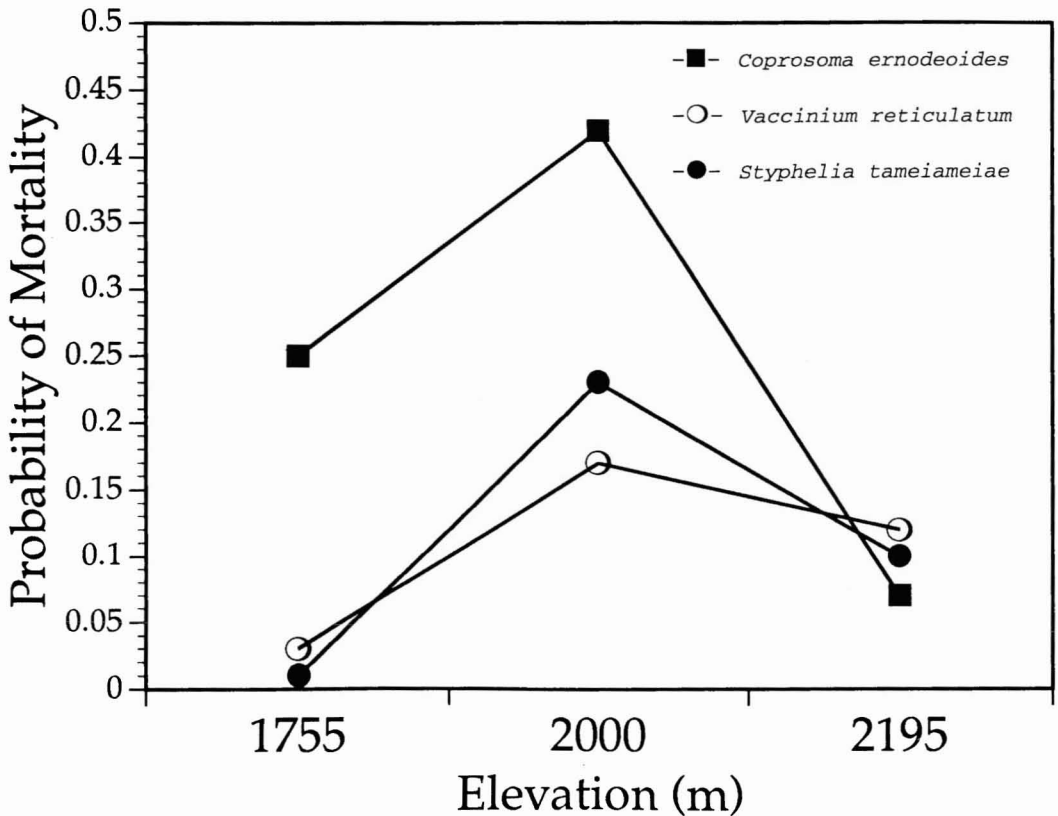


FIGURE 3. The proportion of observed class 5 (dead) individuals to live classes 1–4 individuals as an estimate of probability of mortality at the three different sites.

be shallowly rooted (unpubl. data). Because the largest changes in water availability occur at the soil surface (Caldwell et al. 1977, Fowler 1986, Frazer and Davis 1988), *C. ernodeoides* might have been more susceptible to changes in water availability. In addition, *V. reticulatum* was observed to reduce its leaf area through leaf shedding and *S. tameiameia* to increase its leaf angle to a nearly vertical position, but *C. ernodeoides* did not respond obviously to water stress.

Plants at both upper sites experienced a more substantial water deficit, with the larger departure from normal conditions taking place at the 2000-m site, where a greater rate of mortality was observed (Figure 3). Logistic regression analysis showed that the probability of observing a dead (class 5) plant at the 2000-m site was associated with small

plant size, suggesting that larger plants may have larger root systems that can capture more water and survive better under water stress. Donovan and Ehleringer (1992) indicated that larger plants in semiarid environments may have a greater ability to store water in their stems and leaves and therefore survive better under stress than smaller plants. They also suggested that smaller plants may be intrinsically different from larger plants in their responses to water availability. In other sites under drought conditions, higher mortality was observed in small seedlings relative to established adults (Schlesinger et al. 1982). The highest-elevation site normally experienced a water deficit in the summer (Juvik et al. 1978), so the 1992 drought period might not have represented as large a perturbation as it did at 2000 m.

The effects of the El Niño drought on the vegetation of this lava flow suggest that drought can have a substantial influence on patterns of survivorship and thereby affect the dynamics of primary succession. A recent study by Karpa and Vitousek (1994) suggested that montane grasslands develop successionaly from woody-dominated vegetation on older *pāhoehoe* flows (>3000 yr) at this elevation range on Mauna Loa. Our results suggest that a severe drought could serve as a possible mechanism causing or reinforcing a shift from dominance by woody species to dominance by herbaceous species; several studies in temperate grasslands have suggested a similar mechanism whereby occasional severe droughts may restrict the establishment of woody species in grasslands (Tannehill 1947, Borchert 1950, Coupland 1979, Cook and Irwin 1992).

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#### LITERATURE CITED

- APLET, G., and P. M. VITOUSEK. 1994. An age-elevation matrix analysis of Hawaiian rainforest succession. *J. Ecol.* 82:137–147.
- BEAN, C., J. O. JUVIK, and D. NULLET. 1994. Mountain evaporation profiles on the island of Hawaii. *J. Hydrol.* 156:181–192.
- BORCHERT, J. R. 1950. The climate of the North American grassland. *Ann. Assoc. Am. Geogr.* 40:1–30.
- CALDWELL, M. M., R. S. WHITE, R. T. MOORE, and L. B. CAMP. 1977. Carbon balance, productivity, and water use of cold winter desert scrub communities dominated by  $C_3$  and  $C_4$  species. *Oecologia (Berl.)* 29:275–300.
- CHANG, J.-H., and P. C. EKERN. 1985. Pan evaporation in the state of Hawai'i, 1894–1983. Department of Land and Natural Resources Report R74, State of Hawai'i, Honolulu, Hawai'i.
- COOK, J., and L. IRWIN. 1992. Climate-vegetation relationships between the Great Plains and Great Basin. *Am. Midl. Nat.* 127:316–326.
- COUPLAND, R. T. 1979. The nature of grassland. Pages 23–29 in R. T. Coupland, ed. *Grassland ecosystems of the world: Analysis of grasslands and their uses*. Cambridge University Press, Cambridge.
- DONOVAN, L. A., and J. R. EHLERINGER. 1992. Contrasting water-use patterns among size and life-history classes of a semi-arid shrub. *Funct. Ecol.* 6:482–488.
- DRAKE, D. R., and D. MUELLER-DOMBOIS. 1993. Population development of rain forest trees on a chronosequence of Hawaiian lava flows. *Ecology* 74:1012–1019.
- FOWLER, N. L. 1986. The role of competition in plant communities in arid and semi-arid regions. *Annu. Rev. Ecol. Syst.* 17:89–110.
- FRAZER, J. M., and S. D. DAVIS. 1988. Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia (Berl.)* 76:215–221.
- GIAMBELLUCA, T. W., M. A. NULLET, and T. A. SCHROEDER. 1986. Rainfall atlas of Hawai'i. Department of Land and Natural Resources Report R76, State of Hawai'i, Honolulu, Hawai'i.
- JACOBI, J. D., G. GERRISH, and D. MUELLER-DOMBOIS. 1983. Ohi'a dieback in Hawai'i: Vegetation changes in permanent plots. *Pac. Sci.* 37:327–337.
- JUVIK, J. O., and D. NULLET. 1994. A climate transect through tropical montane rainforest in Hawaii. *J. Appl. Meteorol.* 33:1304–1312.
- JUVIK, J. O., C. SINGLETON, and G. G. CLARKE. 1978. Climate and water balance on the Island of Hawaii. Pages 129–139 in *Mauna Loa Observatory 20th Anniversary report*. National Oceanic and Atmospheric Administration, Silver Spring, Maryland.
- KARPA, D., and P. M. VITOUSEK. 1994. Successional development of Hawaiian montane grassland. *Biotropica* 26:2–11.



- LOCKWOOD, J. P., P. W. LIPMAN, L. D. PETERSON, and F. R. WARSHAUER. 1988. Generalized ages of surface lava flows of Mauna Loa Volcano, Hawaii. U.S. Geological Survey Miscellaneous Publications Map I-1908, U.S. Government Printing Office, Washington, D.C.
- MUELLER-DOMBOIS, D., and H. ELLENBERG. 1974. Aims and methods of vegetation ecology. Wiley & Sons, New York.
- SCHLESINGER, W. H., J. T. GRAY, D. S. GILL, and B. E. MAHALL. 1982. *Ceanothus megacarpus* chaparral: A synthesis of ecosystem process during development and annual growth. *Bot. Rev.* 48:71-117.
- SNEDECOR, G., and W. COCHRAN. 1989. Statistical methods. Iowa State University Press, Ames.
- TANNEHILL, I. R. 1947. Drought, its cause and effects. Princeton University Press, Princeton, N.J.
- VITOUSEK, P. M., G. APLET, D. TURNER, and J. LOCKWOOD. 1992. The Mauna Loa environmental matrix: Foliar and soil nutrients. *Oecologia (Berl.)* 89:372-382.