Population Dynamics of *Marsilea villosa* (Marsileaceae) on O'ahu, Hawai'i[1]

Lyndon Wester,[2,4] *John Delay,*[2,4] *Lam Hoang,*[2,4] *Byron Iida,*[2,4] *Nicholas Kalodimos,*[2,4] *and Tamara Wong*[3,4]

Abstract: *Marsilea villosa* Kaulfuss is an endemic Hawaiian fern with a very small, fragmented natural range and an ephemeral habit that makes it difficult to assess population health. Its sporocarps are presumed to remain viable for many years, allowing it to survive periods of drought and then sexually reproduce when there is sufficient precipitation to cause them to be submerged in standing water. Surveys of plant cover at 'Ihi'ihilauākea Crater, where the largest and best-protected stand was located, have shown that vigorous growth of the species occurs after the crater floor is flooded. This study documents dramatic decline over the last 8 yr, during which growth has been largely vegetative. Analyses of rainfall records suggest that events producing long-duration floods occur on average every 6.5 yr, yet 13 yr have elapsed since the last one. Although this may in part explain the poor condition of the population, other ecological changes have occurred including decline of the dominant trees and invasion of alien grasses that may influence flooding frequency. *Marsilea villosa* may be able to avoid extinction because flooding caused by rare climatic events will kill off the competitors that have encroached on its former ecological space. However, it is predicted to be a less-conspicuous part of the ecosystem most of the time unless management can effectively suppress invaders.

Ephemeral species, with growth patterns dependent on environmental conditions that vary greatly from year to year, present special problems for conservation. Their lack of vigor, rarity, or even disappearance from sites may only mean that conditions are temporarily unsuitable. Long-term monitoring, and a clear understanding of their ecological constraints, can help to assess whether they are in danger of extinction or just responding to natural perturbations.

Marsilea villosa Kaulfuss or 'ihi lā'au, a fern endemic to Hawai'i, represents such a case and is of particular interest because wild populations are few (Pukui and Elbert 1986, Palmer 2003). The total areal cover of the species is currently no more than 1 ha, scattered at five sites on two islands (U.S. Fish and Wildlife Service 1993). These populations all lie in dry lowlands that experience highly variable rainfall and have suffered the most severe environmental degradation of all the habitats. The population in the 'Ihi'ihilauākea Crater of Koko Head on O'ahu has been generally regarded as the most secure because it is located in a nature preserve created to protect the plant and is surrounded by public land designated and managed for conservation. In spite of the protection, monitoring, and weed management, the total cover of *M. villosa* in 2004 had contracted to less than 1% of its extent a decade before. In this paper we document changes in plant populations at 'Ihi'ihilauākea Crater between 1988 and 2004 with particular reference to rainfall variation and events that produce flooding.

[1] Manuscript accepted 3 August 2005.

[2] Department of Geography.

[3] Department of Botany.

[4] University of Hawai'i at Mānoa, Honolulu, Hawai'i 96822.

Pacific Science (2006), vol. 60, no. 3:385–402

Habitat and Growth Pattern

Marsilea villosa is closely related to *M. vestita* of the western United States (Johnson 1986) and shares that congener's phenology and habitat preferences for growing in seasonally wet depressions with clay or calcareous soils (Johnson 1986) that may be regarded as ephemeral pool habitats (Zedler 1987).

In addition to the population of *M. villosa* at 'Ihi'ihilauākea Crater, other small patches exist on O'ahu at Makapu'u and in Lualualei Valley, where there are four subpopulations within about 0.5 km of each other (Figure 1). Three are found in shallow depressions. The Makapu'u sites are within a few meters of each other. One site appears to be a seep in a natural depression and the other is an artificial ditch alongside a rough dirt track. The population is reported to have been planted (U.S. Fish and Wildlife Service 1993), but specimens were collected in the general area by Degener in 1925 and Kaneshiro in 1968 (Bruegmann 1986) and so the stand may be natural (Figure 2*C*,*D*). The Makapu'u site and one of the Lualualei sites were burned by separate wildfires in the summer of 2005.

Two additional sites on Moloka'i at Kamāka'ipō and Mokio (U.S. Fish and Wildlife Service 1993) account for the entire known range of the species. In the 1920s the fern was also known from O'ahu in Kaimukī (Forbes 1920) and 'Ewa. Both localities are now urbanized and so the populations are almost certainly extinct (Bruegmann 1986). The species was also collected once on Ni'ihau in 1949 but has not been recorded since. Although it grows satisfactorily in cultivation,

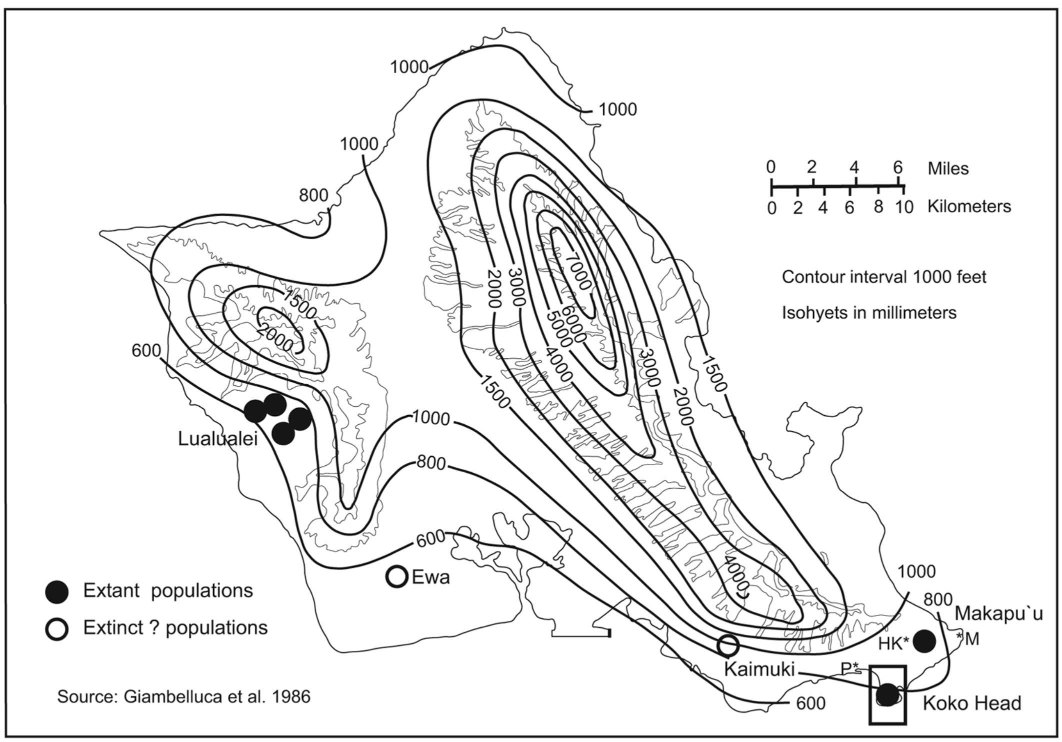

FIGURE 1. Location of sites where *Marsilea villosa* has been collected on O'ahu. The study site of 'Ihi'ihilauākea Crater in Koko Head is indicated with a rectangle. Rain gauges are indicated with asterisks. P, Paikō Drive; HK, Hawai'i Kai Golf Course; M, Makapu'u.

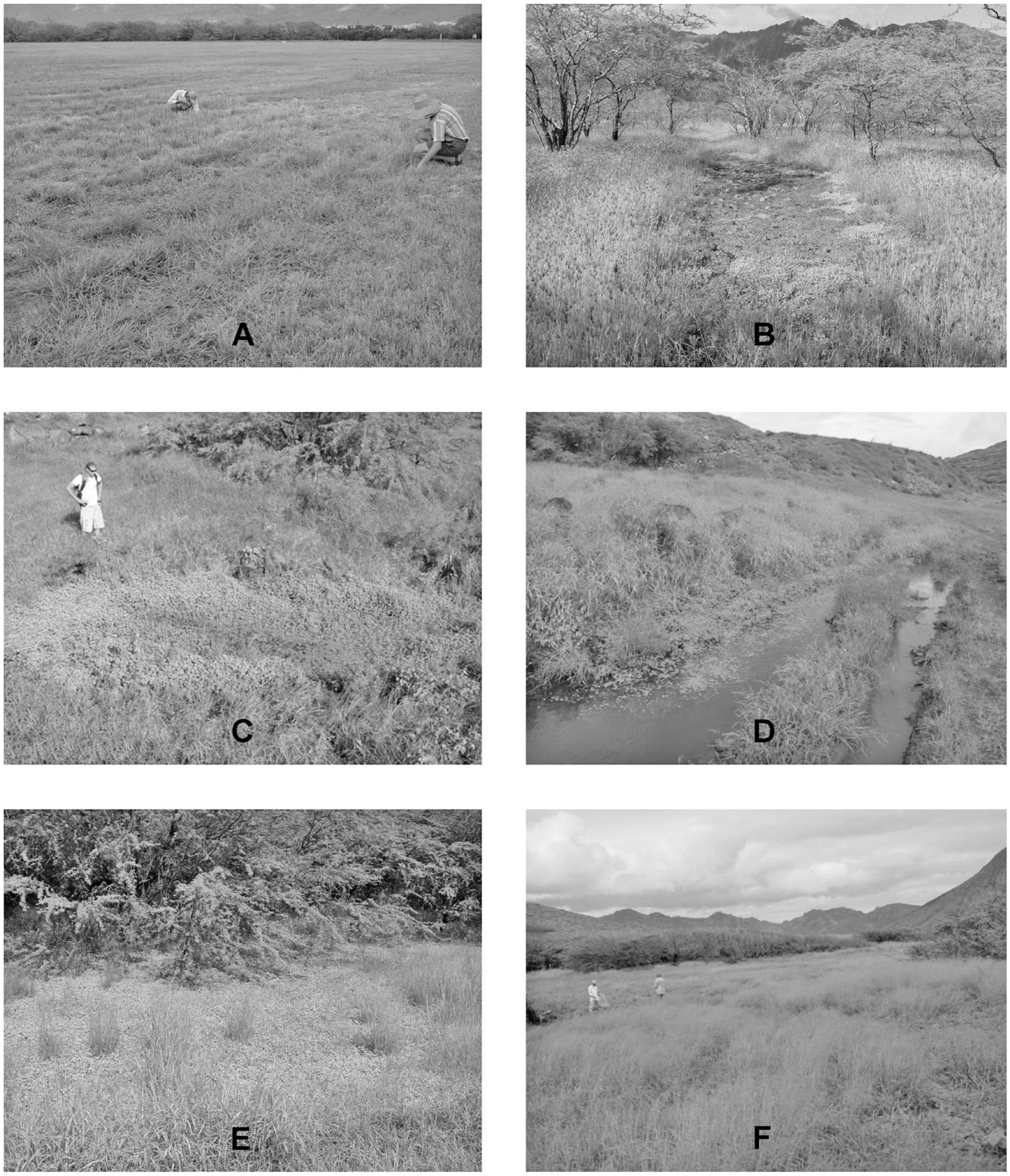

FIGURE 2. Habitats that *Marsilea villosa* occupies on O'ahu. *A*, Depression in mowed field at Lualualei; *B*, ephemeral pool in a poorly defined drainage line at Lualualei; *C*, rock pool in ephemeral stream at Makapu'u; *D*, roadside ditch at Makapu'u; *E*, vigorous *M. villosa* patches in an area where the construction of a road has impeded drainage in Lualualei; *F*, floor of 'Ihi'ihilauākea Crater, densely invaded by grasses and where dead stems of *Prosopis pallida* ring the depression.

the extremely limited extent of its wild populations led to its listing as a federally endangered species in 1992 (U.S. Fish and Wildlife Service 1993).

All wild *M. villosa* populations lie in areas that are typified by hot, dry summers and a wetter, cooler winter season and where the rainfall regime is dominated by infrequent but intense winter storms. The fern is tolerant of drought conditions, at which time all vegetative growth stops, leaves die back, and the rhizome becomes dormant and dry, but growth returns quickly with adequate moisture. An adaptation of this genus to seasonally dry habitats is the production of hard sporocarps at the base of the plant as the soil moisture decreases and the plants undergo water stress (Tryon and Tryon 1982). These are extremely resistant to desiccation and can remain viable for many years. Allsop (1952) was able to successfully germinate *M. fournieri* and *M. vestita* sporocarps more than 60 yr old, and Johnson (1985) reported germinating *M. crenata* sporocarps more than 100 yr old. The sporocarps open only when submerged in standing water (U.S. Fish and Wildlife Service 1993), and thus sexual reproduction is dependent upon rain events that flood the site. In seasons or in places where no flooding occurs, *M. villosa* populations maintain themselves by vegetative reproduction. It can form dense monospecific stands but may also be found growing in small patches under partial shade and mixed with other species.

Factors that restrict the range of *M. villosa* are related primarily to its narrow habitat requirements and human modification of these sites that includes competition from some of the world's most aggressive grasses imported to the Islands in the last 200 yr. Weeding experiments showed that *M. villosa* responded positively when competing species were removed by hand, but the effect lasted only a few months (Wester 1994). At two sites in Lualualei that are subject to regular mowing (Figure 2*A*), populations of *M. villosa* have been able to maintain themselves and appear to benefit from the cutting of taller-growing competitors.

Past threats from off-road vehicles, as well as trampling and grazing by cattle, have also been named as disturbing factors (U.S. Fish and Wildlife Service 1993). The ecological relationship between cattle and *M. villosa* is a matter of some disagreement. Zedler (1987) did not consider them a substantial threat, yet Hodder and Low (1978) noted that the Australian species was readily grazed upon and concluded that cattle had a negative effect. However, the Mā'ili'ili subpopulation at Lualualei did poorly when cattle were removed from the site but thrived after the cattle were returned (U.S. Fish and Wildlife Service 1993). The cattle appeared to eat the grasses but not the *M. villosa* (M. M. Bruegmann, pers. comm., 2005). *Marsilea villosa* may benefit more from the reduction in competition as the taller-growing grasses are grazed than it suffers from being grazed upon.

In general, ferns in the genus *Marsilea* have a competitive advantage in areas that flood regularly, and Holland (1976) stated that ephemeral pools resist the invasion of exotic plants better than many other habitats. However, in contrast to the relatively consistent seasonal rainfall observed by Holland in North America, the highly irregular occurrence of flooding rains on the dry lowlands of the Hawaiian Islands means that *M. villosa* only rarely has this major ecological advantage over its competitors.

Flooding events that last several weeks at 'Ihi'ihilauākea Crater have been observed to eliminate virtually all of the competitive vascular plants and encourage *M. villosa* to reproduce both sexually and vegetatively. As long as viable sporocarps are present, it might be assumed that the species could reestablish itself during similar future events. *Marsilea villosa* produces long-stemmed, floating leaves where it grows in pools and will also form a dense mat of free-standing leaves and stems at the edge of water bodies as they contract. Once this mat is established in a saturated or moist substrate, it has been observed that seedlings of competing species initially do not seem to be able to insinuate themselves into the sward. Indeed, very dense mats of leaves and stems formed one year seem to persist over the dry season and resist the invasion of competing species the following year.

However, if conditions for vigorous growth do not continue, the mat becomes abraded and other species are able to intrude. Alien grass species seem to be particularly effective in shading and suppressing the growth of *M. villosa* and are probably more aggressive competitors than the native Hawaiian species they replaced. The decline of *M. villosa* and increase of invasive grasses in recent years when there have been no floods has been the subject of concern and the justification for periodic weed management by cutting and herbicide application.

MATERIALS AND METHODS

The *M. villosa* population at 'Ihi'ihilauākea Crater was surveyed during the 2003–2004 growing season using a grid of 10 by 10 m quadrats that had been created in 1988 (Figure 3). The goal was to replicate the methods and procedures used in past studies as much as possible to ensure that the data sets were comparable (Wester 1994). Cover of all species in each quadrat was estimated on 7 December 2003, soon after the first rains, and again on 18 January 2004, after heavy precipitation had fallen at the beginning of the month.

A series of aerial photographs from 1939 to 1941 (date uncertain), 1952, 1963, 1968, 1978, 1993, and 2000 was analyzed to determine the condition of the tree canopy of *Prosopis pallida*, which extends over much of the crater floor, as well as the area and shape of the open treeless site in the deepest part of the crater where the *M. villosa* occurs. The photographs were also searched for other habitat modification, such as conspicuous erosion, that would suggest hydrological changes of the site.

The crater floor was mapped using a Total Station survey instrument to produce a map with a 20-cm contour interval. Soil analysis was performed on 20 soil cores taken at regular intervals along a transect across the crater floor to establish baseline data and for comparison with growing conditions elsewhere (Figure 3). The fraction of organic matter was determined following procedures described by Rhodes et al. (1981) and Ben-Dor (1989). Measures of pH, nitrogen, potassium, and phosphorus were performed at the University of Hawai'i at Mānoa, College of Tropical Agriculture and Human Resources, Agricultural Diagnostic Service Center.

Because long-duration flooding appeared to be important to eliminate competitors of *M. villosa*, on the basis of three known events, we attempted to determine how often similar floods may have occurred in the past 90 yr for which data were available. Surface runoff is determined not only by the intensity of a rainfall event but also by the moisture condition of the soil before the rain, so we examined annual rainfall, monthly rainfall, and 24-hr extremes for conditions that exceeded those experienced in 1988, the lowest precipitation associated with a known long-duration flood. No rain gauges exist at 'Ihi'ihilauākea Crater so data from the closest and most comparable stations were selected. The orographic effect induced by the Ko'olau Mountain Range produces large variation over quite small distances, but stations at Makupu'u for the period 1911–1973 and at Paikō from 1976 to 2001 were considered comparable. Even with these two stations, there is a gap in the data for the 1974–1975 period (U.S. Department of Agriculture 1922, 1960, Giambelluca et al. 1986). The most comparable station operating during this period was Waikīkī at the Honolulu Zoo, which had the same 10-yr, 24-hr intensity (<178 mm) as the stations closer to Koko Head and did not experience 24-hr totals exceeding those of January 1988 (Giambelluca et al. 1986).

RESULTS

The dominant woody plant in 'Ihi'ihilauākea Crater is *Prosopis pallida*, which takes on a tree or shrub form depending on exposure to wind. The tree canopy is more than 3 m high over much of the crater floor, but the lowest part, where the water was observed to fill to a depth of approximately 1 m, has not been colonized by the trees (Figure 4). Indeed the total extent of the tree cover remained remarkably constant, and individual trees or tree clusters can be traced through the whole time period from 1941 to 2000. What is ap-

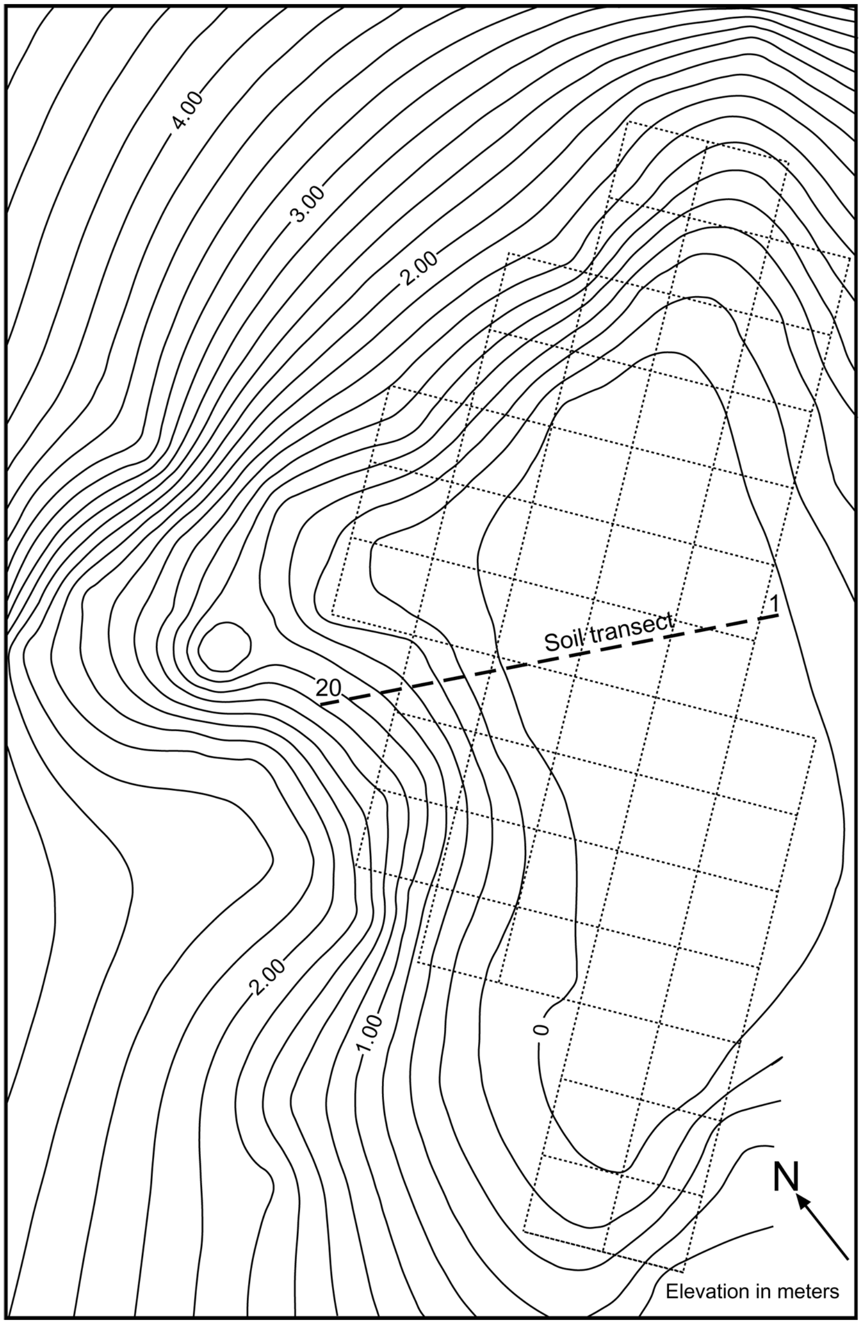

Figure 3. Relief map at 20-cm contour interval showing configuration of the ʻĪhiʻihilauākea Crater floor. The grid used for cover estimates is shown and also illustrates the approximate extent of *Marsilea villosa* at the site. The location of the soil transect and samples from 1 to 20 is indicated.

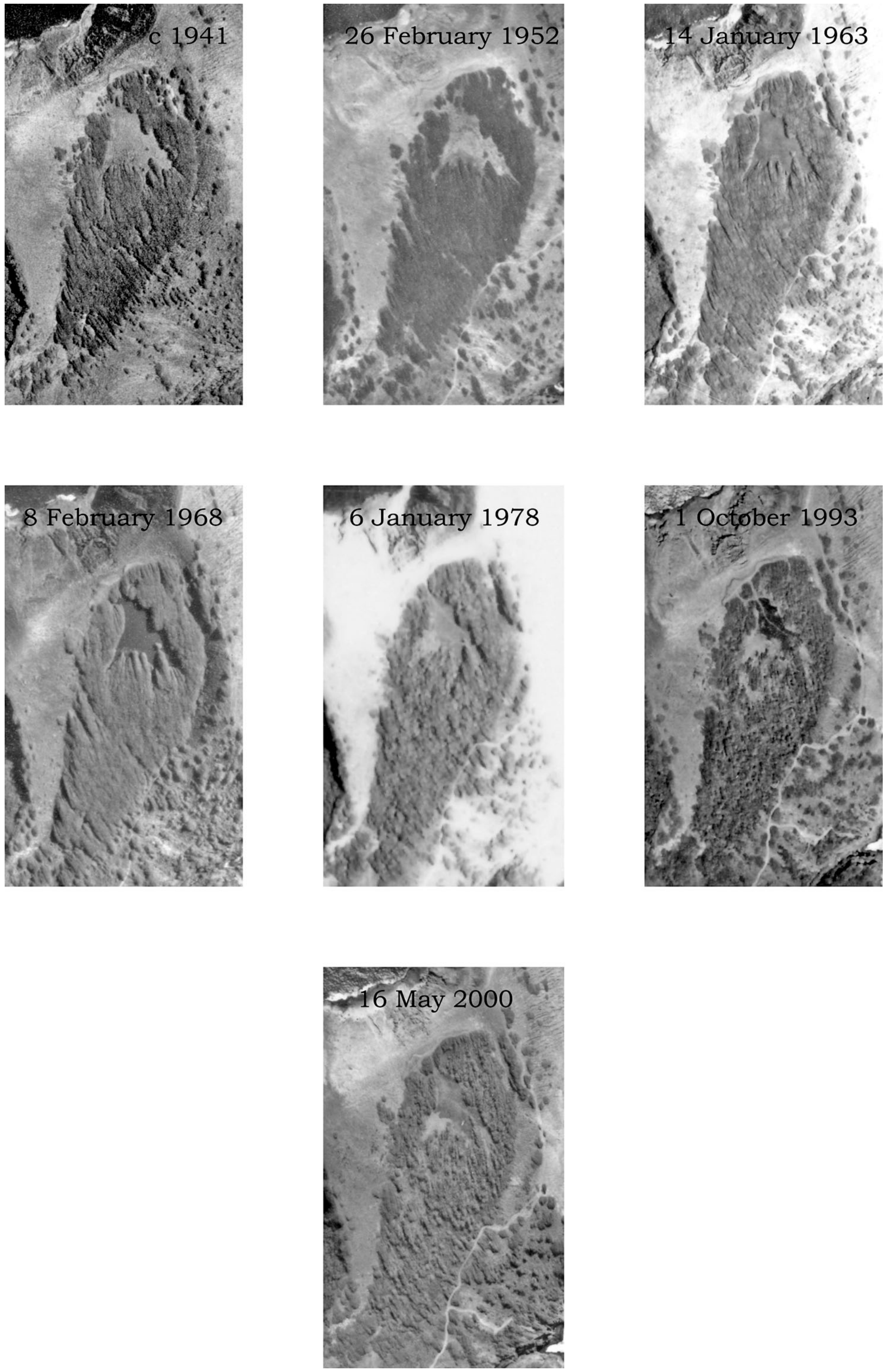

FIGURE 4. Sequence of aerial photographs from 1941 to 2000 showing the floor of ʻIhiʻihilauākea Crater and the vegetation cover therein.

parent however is that the *P. pallida* canopy has become more open. The continuous, closed canopy seen in the 1941 aerial photograph became fragmented into wind-shaped rows with much open space between after 1968 (Figure 4). For many decades of the nineteenth and early twentieth centuries the Koko Head region was used as rangeland for neighboring cattle ranches (Egler 1947). The removal of cattle may have inhibited *P. pallida* regeneration because no seedlings were evident in surveys. The thinning of the canopy and many dead stems and branches are perhaps evidence of a senescent stand.

The percentage cover was estimated for all species in 10 by 10 m quadrats on the floor of ʻIhiʻihilauākea Crater in the years 1988, 1990, 1991, 2003, and 2004. The total number of species recorded at the site varied from a minimum of 21 in 1991 to 33 in January 2004 (Figure 5, Appendix). Notable in the survey of 1991, which immediately followed a flooding event, was the absence, or dramatic reduction in cover, of perennial species such as *Sida fallax*, *Waltheria americana*, *Leucaena leucocephala*, *Asystasia gangetica*, and *Lantana camara*, which were observed to be killed or suppressed by immersion but to reestablish in subsequent years. The species composition varies during the course of the growing season as is evident by comparing data from 7 December 2003, soon after the first rains of the season, and 18 January 2004, about the peak of the growing season when seven additional species were observed.

The majority of the species with the highest cover values have long-established populations in the area and were noted by Fosberg (1961). However, two species with high cover values appear to be relatively new to the site. Fosberg made no mention of *Panicum maximum* in his description of the site in 1961, yet it is clearly visible in an aerial photograph taken in 1984, when it can be seen forming a high, dense border at the edge of the crater floor (Wester 1994), and was recorded by Brugemann in 1986. There now appears to be two distinct varieties of *P. maximum* at the site (and elsewhere on Oʻahu) without intermediate forms, which may be explained by the fact that the taxon is reported to have numerous polyploids (Wagner et al. 1999). The taller of the two varieties has become less common and in 2004 was restricted to a few patches around the fringes of the clearing and under the *P. pallida* canopy.

Another perennial bunchgrass, *Cenchrus ciliaris*, is a still more recent arrival that was first recorded in 1990. Although purposefully removed as a part of the weed management program, it reappeared in subsequent years and by 2004 had become the codominant with *Panicum maximum*. *Cenchrus ciliaris* is widely used for erosion control and has recently spread through other parts of arid Oʻahu and has become the dominant species in many dry habitats including remote Molokini Island (Smith 2004).

A third grass, which is ecologically important at the site, is the low-growing, deep-rooted *Cynodon dactylon*. Fosberg recorded it in 1961 and it has increased slightly at the site over the period of the surveys (1988–2004) (Figure 5, Appendix). In the early surveys it was regarded as a minor and localized threat to the health of the *M. villosa* population because where it occurred the *M. villosa* cover was relatively low (Wester and Ikagawa 1988). At sites where *M. villosa* and *Cynodon dactylon* coexisted in 2004, the cover of *M. villosa* was not much changed from previous years but now represented some of the most extensive growth of *M. villosa* (Wester 1994). In contrast, where *M. villosa* once grew more densely, in 2004 these sites were occupied by *P. maximum* and *Cenchrus ciliaris* to the exclusion of *M. villosa*. It is to be noted that *Cynodon dactylon* cover was slightly suppressed by flooding but it appeared not be drowned like the other perennial grasses and recovered by regeneration from its deep stoloniferous roots. Furthermore, sites where it has been long established are not much invaded by *P. maximum* and *Cenchrus ciliaris.*

Certain other grass species were observed to decrease during the survey period. *Digitaria insularis* was one of the main components of the ecosystem in 1990 and 1991, but now it has almost completely disappeared. *Echinochloa colona* (barnyard rice grass) has a low spreading habit, which may place it at a disadvantage in competition with the taller *P. max-*

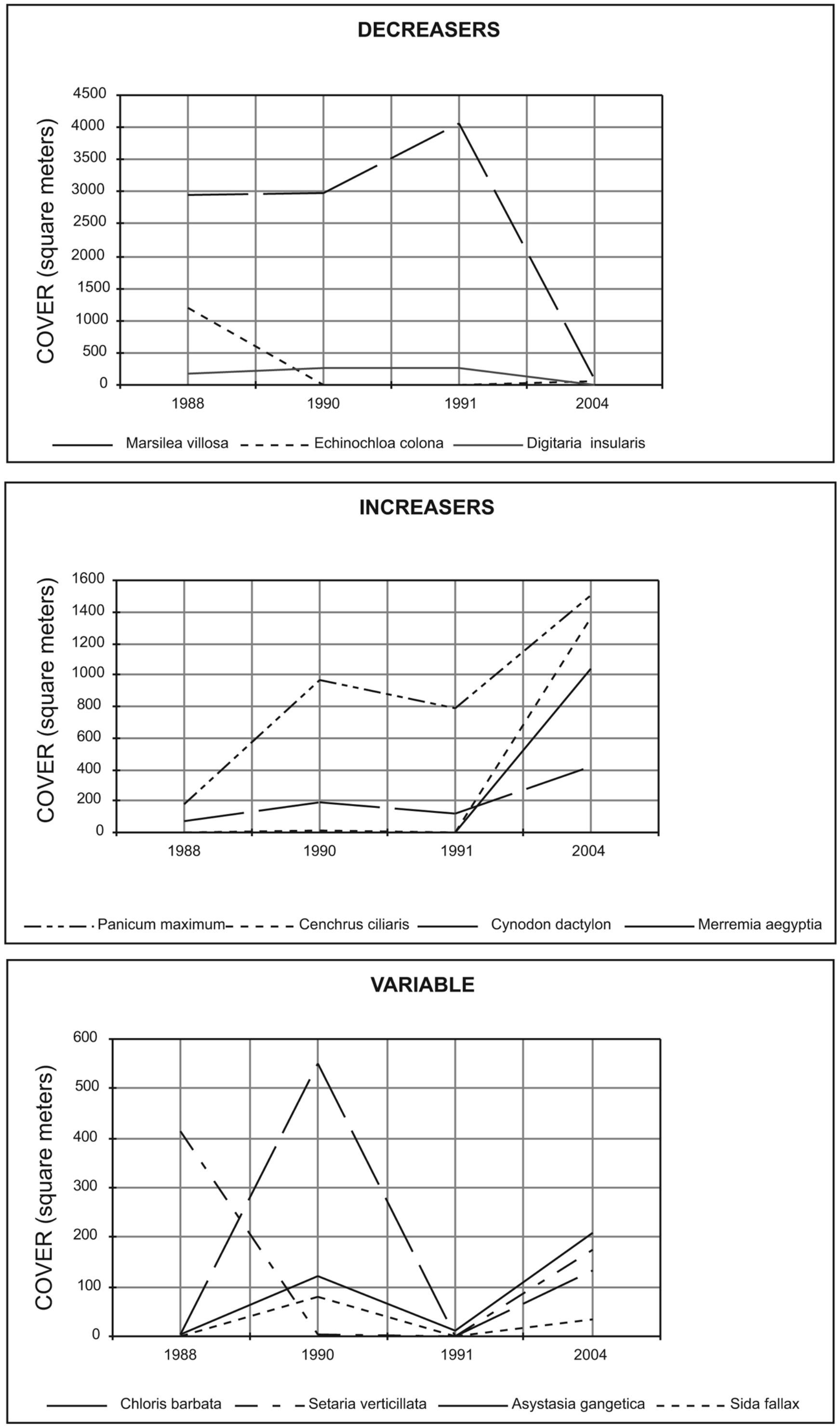

Figure 5. Change in cover of the dominant species that act as competitors of *Marsilea villosa* at ʻIhiʻihilauākea Crater.

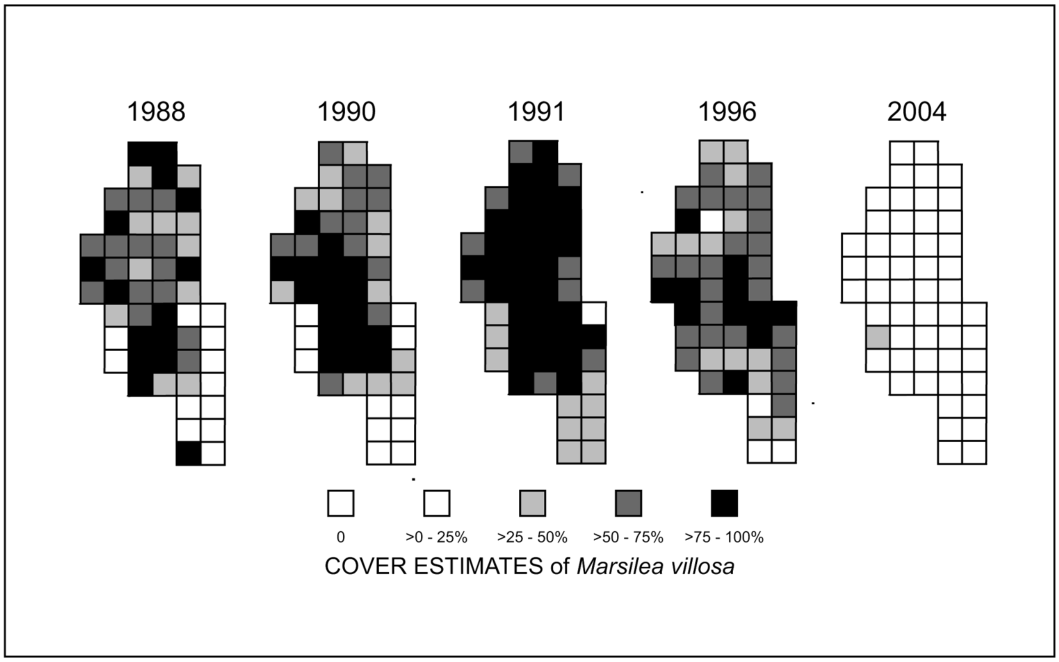

FIGURE 6. Cover estimates of *Marsilea villosa* in 10 by 10 m quadrats at ʻIhiʻihilauākea Crater from 1988 to 2004. The 1996 survey was done by Wilkinson (1997).

imum and *Cenchrus ciliaris*. After the flooding of 1988 it responded faster than the other grasses and became the dominant grass for a while and the main competitor with *M. villosa*. Two annual grasses, *Chloris barbata* and *Setaria verticillata*, have also shown marked variation in cover from one season to another, as did the creeper *Merremia aegyptia*.

Of special interest is the variation of the cover of *M. villosa* over time. A survey in 1996 by Wilkinson (1997) has been included for comparison because she duplicated the methods used in earlier research (Figure 6). The first survey in 1988, done immediately after a long-duration flood, showed that *M. villosa* grew densely and the mat maintained itself through years of average rainfall to 1990 without flooding events of any great depth or long duration. The 1991 long-duration flood resulted in the most extensive cover of *M. villosa* ever surveyed, although this still was not equal to the densities observed by Lamoureux in 1978 and Bruegmann in the early 1980s (M. M. Bruegmann, pers. comm., 2005). Some decline was observable by 1996, and this trend continued to 2004 when dense patches of *M. villosa* were small and extended over only a few square meters. Some lower-density stands were found in association with *Cynodon dactylon*. The total cover values of *M. villosa* in 2004 were low in spite of an unusually wet season that produced short-term flooding. The decline occurred despite protection afforded by the creation of a nature reserve, continued surveillance, and management in the form of infrequent mowing and herbicide treatment of competing grasses.

Exposed soil horizons, and bare roots around the fringes of the *P. pallida* stand, suggest that substantial soil erosion has occurred, although only a small amount of erosion in recent decades can be detected from the aerial photographs. Bare, chemically weathered bedrock extends over most of the steeper slopes that ring the flat crater floor. This indicates that soils once blanketed the slopes and probably supported substantially more vegetation cover than currently. The degradation that removed most of the native vegetation, and caused the subsequent soil erosion, appears to have occurred before 1941.

The soils in the crater floor, classified as Koko silt loam (KsB), are well-drained soils formed of alluvium washed from volcanic ash, cinders, and tuff deposits on fans and volcanic spurs near Koko Head, Koko Crater, and Diamond Head (Foote et al. 1972). Analysis of soil samples collected on site showed that the organic matter content displayed the greatest variation, with samples 14 to 19 having a much higher percentage than the others (Figure 7). Predictably, the NPK (nitrogen, phosphorus, potassium) content was positively correlated with the fluctuation in organic matter percentages. Mahlberg and Yarus (1977) reported that the optimum pH range for *Marsilea* germination is pH 7–8, and pH 7 for sporophyte development. Our soil sampling showed a pH range of 5.7 to 6.6.

Climatological records suggest that, on leeward Oʻahu, high-intensity rainfall events that, on the average, occur only once in 7 yr (the 7-yr return rate) are most likely to fall in the period from September to April. Furthermore, the month of February has the greatest chance of receiving rainfall of this intensity (Giambelluca et al. 1986). Annual totals are largely the product of a few high-intensity events. Three long-duration floods at ʻIhiʻihilauākea Crater can be fixed from personal accounts and photographs (Table 1) and related to particular high-intensity rainfall events. L.W. observed deep flooding in January 1988 and March 1991. At those times water remained in the crater for several weeks and long enough for nonaquatic species to be killed. After the 1988 flood, sporocarp germination and sporophyte establishment was observed (M. M. Bruegmann, pers. comm., 2005). *Marsilea villosa* grew vigorously after each of these episodes and established a dense mat of leaves and stems in every quadrat of the study site (Wester and Ikagawa 1988, Wester 1989, 1994).

An aerial photograph taken in February 1968 (Figure 4) provides evidence of a third long-duration flood. The winter of 1967–1968 was an unusually wet one. The month of December 1967 received 439 mm of rainfall, and over half of this (245 mm) fell on 18 December. The following month received an additional 188 mm, with 80 mm falling in one 24-hr event on 17 January 1968 (Table 1). No accounts of the condition of the *M. villosa* population in the months immediately after this flood have been found, although reports were made the following winter, which also appears to have been wetter than average but did not quite meet our criteria for producing a long-duration flooding event (Table 1). In May 1969, late in the growing season, Herbst described *M. villosa* as "completely and densely carpeting the entire bottom of ʻIhiʻihilauākea Crater" (BISH 457520), suggesting that, even if no long-duration flooding occurred that winter, higher than average rainfall kept the *M. villosa* in a very vigorous condition after the flood of the previous season.

The winter of 2003–2004 was also an unusually wet one but did not cause a long-duration flood. However it did provide a basis to test our criteria by which to identify rainfall events that do produce them under current conditions. The nearby Hawaiʻi Kai Golf Course rain station received more than 200% of the normal precipitation for the region. A short-duration flood was witnessed in the crater by N.K. after 25 mm of rainfall on 1 January 2004, followed by 149 mm on 2 January. At times the rainfall intensity exceeded 20 mm/hr. It produced ponding of a few centimeters and stimulated opening of some sporocarps, but the duration of the standing water was not sufficient to kill the dominant nonaquatic species. Grasses already released from dormancy, or generating from seeds after earlier rains, then grew extremely vigorously. A further rainfall event, almost as intense as the one in January, occurred in August 2004 after the substrate had time to dry out. Although 115 mm fell in 6 hr, it produced no flooding (C. Leavitt, pers. comm., 2004).

Having identified the three rainfall events that caused verifiable long-duration floods

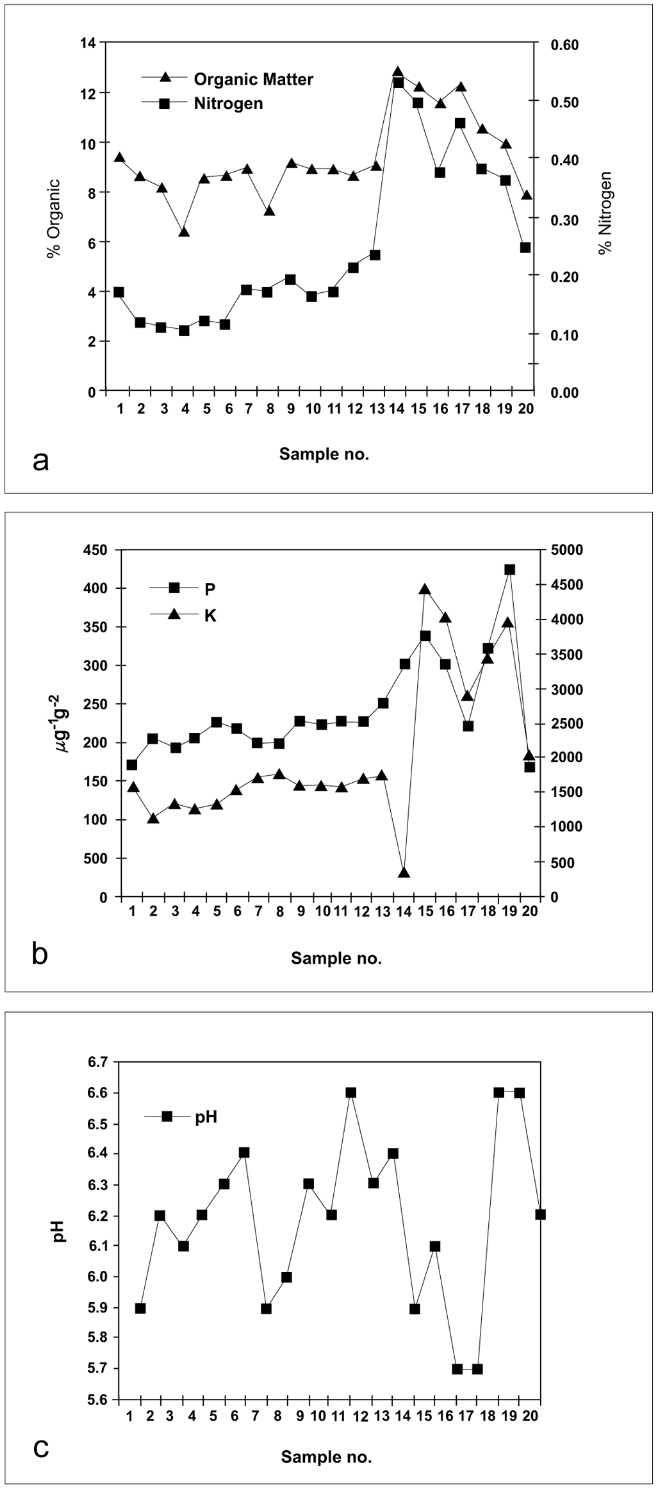

FIGURE 7. Variation in soil characteristics across ʻIhiʻihilauākea Crater: *a*, organic matter and nitrogen; *b*, phosphorus and potassium content (μg^{-1} g^{-2}); *c*, pH levels.

TABLE 1

Notable Rainfall and Associated Hydrological Events in Leeward Southeastern O'ahu

Event	Gauge	24-hr Extreme (mm)	Date	Yr (Mon. Total)
Verified long-duration flooding events				
1967–1968 winter (flooding noted February 1968)	Makapu'u	245	18 December	1967 (439 mm)
		80	17 January	1968 (188 mm)
1987–1988 winter (flooding noted January 1988)	Paikō Drive	212	12–13 December	1987
		171	18–19 December	1987
		114	1 January	1988
1990–1991 winter (flooding noted March 1991)	Paikō Drive	175	19 March	1991
		208	20–22 March	1991
Other hydrological events				
1932–1933 winter (flooding noted March 1933)	Makapu'u	58	February	1933
		56	March	1933
1968–1969 winter (dense *M. villosa* noted May 1969)	Makapu'u	52	30 November	1968
		90	30 November	1968
		43	December	1968 (>243 mm)
		91	January	1969 (>251 mm)
1983–1984 winter (dense *M. villosa* noted December 1984)	Makapu'u	103	December	1984
2003–2004 winter (shallow flooding noted January 2004)	Hawai'i Kai Golf Course	25	1 January	2004
		149	2 January	2004
2003–2004 summer (no flooding August 2004)	Hawai'i Kai Golf Course	115	August	2004

Source: National Climate Data Center (2002).

(1967, 1988, and 1991), we took the value for the least of these as our datum (1988). On this basis we identified 14 calendar years between 1911 and 2004 in which the annual rainfall, largest monthly total, and 24-hr extremes exceeded those totals in 1988 (Table 1, Figure 8). It is to be noted that extreme 24-hr events that produced floods were not isolated occurrences but tended to take place during years when the annual rainfall was well above the long-term mean for the Makapu'u station (680 mm) and, perhaps more important, were preceded by smaller but hydrologically important rainfall events. This suggests that the soil was near field capacity before the very high-intensity 24-hr event occurred that produced the flood. Using Soil Conservation Service number method (Foote et al. 1972, Dunne and Leopold 1978), we estimated that nearly twice the runoff is produced with wet antecedent moisture conditions as occurs under dry antecedent conditions. In 11 of the 14 cases, the years both preceding and following were also wetter than average. Figure 8 shows that rainfall events that produce long-duration floods occur on the average every 6.5 yr although there are periods as long as 14 yr when no such event took place (e.g., between 1968 and 1982).

Thirteen years have now elapsed since the last long-duration flooding of 'Ihi'ihilauākea Crater, and this may account in part for the poor condition of the *M. villosa* at the site. However, it is also possible that conditions may have changed that influence the flooding regime or the ecological opportunities for *M. villosa*.

In the past, dense *M. villosa* was noted on a number of occasions when flooding would not have been expected based on our criteria. The winter season of 1932–1933 is of particular note because there is some evidence of flooding at the crater. Botanists R. J. Baker and M. Chong made two separate voucher collections on 25 March 1933, and Baker noted that *M. villosa* was growing in "moist soil beside a small temporary pond"

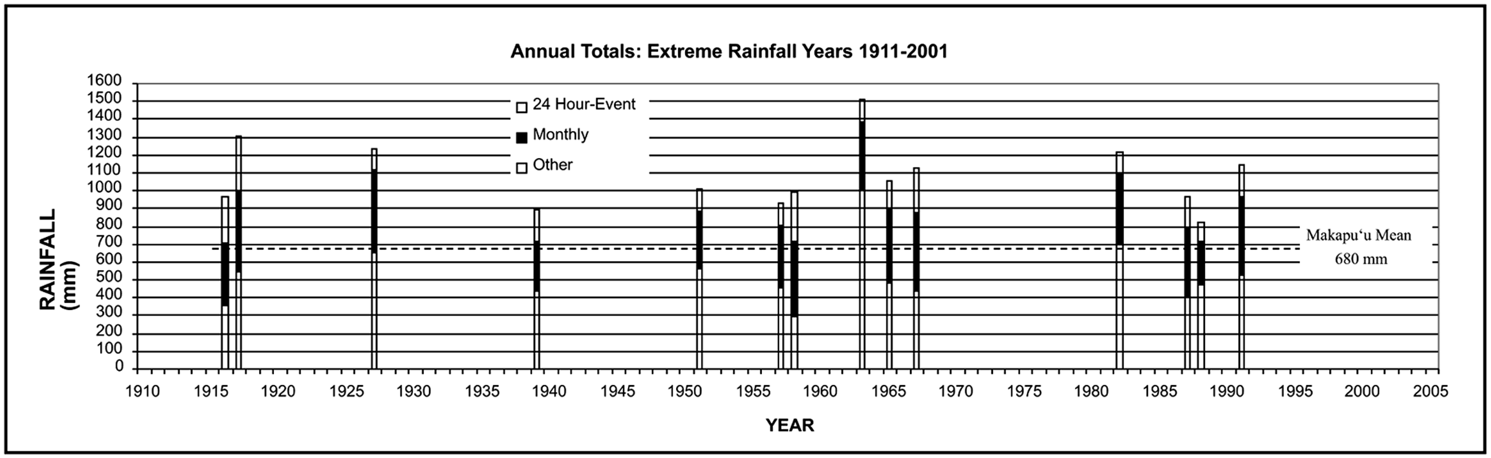

Figure 8. Extreme rainfall events between 1911 and 2001 that exceeded amounts received in 1988. In all years except 1963 and 1967 the largest 24-hr rainfall event occurred in the wettest month for the year.

(BISH 11104). Chong described the location as being at the "edge of swamp" (BISH 92002). These observations seem to indicate that *M. villosa* had experienced at least short-term flooding and was in a healthy state despite the facts that the previous January had been unusually dry and the highest rainfall events were 58 mm and 56 mm, respectively, in February and March and that 5 yr had elapsed since the 1927 rainfall event, which we calculate to have been the previous long-term flood.

In November 1978 a photograph taken by Charles Lamoureux showed *M. villosa* thickly carpeting the crater floor. The months of October and November 1978 were unusually wet and had received, respectively, 209 mm and 117 mm although the largest 24-hr event was only 51 mm. Breugmann collected *M. villosa* in February 1985, indicating on the voucher that *M. villosa* formed a "dense cover over much of crater floor but rapidly being covered by introduced species" (BISH 503861, 503862, and 503863). The last high-intensity event had been 103 mm in December 1984.

DISCUSSION AND CONCLUSIONS

Three long-duration floods were documented with confidence and used as a basis to estimate the frequency of such events. The minimum meteorological condition that produced them occurred in 1988, when 114 mm of rain fell on 1 day but on soil that had been moistened by much rain over 3 prior weeks. Based on conditions of 1988, we estimated that rainfall events of this magnitude occurred on the average every 6.5 yr but periods as long as 14 yr elapsed without them. Data suggest that the cover of *M. villosa* tends to be greatest following long-duration floods but then declines as flood-intolerant species gradually reestablish their populations. The extremely low cover of *M. villosa* currently may be the result of the fact that 13 yr have elapsed since the last long-duration flood. It is to be noted that 24-hr rainfall events of 149 mm and 115 mm occurred during the period of this study in 2004 and produced only short-duration floods or none at all. This suggests that the precondition of the soil was unsuitable for flooding because it could absorb moisture. Yet events of similar intensity had produced flooding in the past. Two possible explanations are that the soil had not been brought to near field capacity by previous rain (this was almost certainly the case for the August 2004 event) or that increased evaporation had effectively dried the soil from previous rain. Ecological changes have occurred in the crater over recent years that may have altered the rate at which the soil dries.

The Koko Head cone is a severely degraded habitat that has lost most of its mantle of soil and native species. Truncated soil horizons and exposed *P. pallida* roots suggest how much has been stripped away from the sloping surfaces of the crater. However, photographs from 1941 to 2001 do not show continuing erosion on a large scale and so suggest that most of the erosion occurred in the nineteenth or early twentieth centuries. On the other hand, the photographs do indicate that the canopy cover of *P. pallida*, the single tree species in the bottom of the crater, is undergoing decline. A canopy dieback is also evident from the many lifeless stems that protrude above the thinly foliated living canopy. The cause was not investigated in this study but might represent senescence of the last cohort of plants that germinated from seed before cattle were removed from the area. The diminished vigor of *P. pallida* may have facilitated the invasion by sun-loving grasses such as *Panicum maximum* that appeared between 1961 and 1984 and *Cenchrus ciliaris* that appeared in 1990 and whose spread coincided with the decline in *M. villosa*. It may be of importance that patches of *M. villosa* that survive are either under the *P. pallida* canopy or in association with the deep-rooted *Cynodon dactylon*, which may help exclude the taller perennial grasses.

The documented change in species composition and vigor may have important ecological implications for the condition of *M. villosa* populations in the crater. The dieback of *P. pallida* would be predicted to reduce water loss by transpiration, whereas the increase in leaf area of the understory, induced by the invasion of the tall perennial bunchgrasses

Panicum maximum and *Cenchrus ciliaris*, might be expected to increase water loss by transpiration. Data presented here cannot show whether these changes produced a net gain or loss of soil water by transpiration; however, the famously deep-rooted *P. pallida* is likely to be drawing on different sources of moisture than the grasses, which have shallow, fibrous roots. The effect of a changed rate of water loss by transpiration would be important because it would speed or slow the drying of the soil and determine its moisture status and thus absorptive capacity in the face of extreme rainfall events. A soil effectively dried out by more rapid transpiration would have greater ability to take in the moisture and thus reduce the likelihood of surface accumulation. Evidence of flooding from 1933, which may have been induced by small rainfall events in February (58 mm) and March (56 mm), is consistent with soils remaining moist due to lower transpiration rates.

Long-duration flooding, when it does occur, will presumably result in the drowning of all species in the crater except for *M. villosa* and *Cynodon dactylon* and thus provide an opportunity for the fern to regenerate. However, in years when no long-duration flooding occurs, the increased pressure from grass species that have newly invaded the site may prevent *M. villosa* from growing as abundantly or vigorously as it once did. The survival of *M. villosa* at ʻIhiʻihilauākea is therefore much more dependent on the viability of sporocarps stored in the soil, which could regenerate after a flood even if the vegetative form of *M. villosa* was completely excluded by competition at other times.

Because new perennial grasses *Panicum maximum* and *Cenchrus ciliaris* now dominate the open space in the bottom of the crater floor, the survival of *M. villosa* at the site has become more dependent on extreme events to eliminate them. Hence the length of viability of the sporocarps is an important consideration and should be tested to determine if it is as long as that of related species. Between long-duration floods, which may be decreasing in frequency, the fern is predicted to be a less-conspicuous part of the ecosystem unless the grasses can be suppressed by mowing, as has proven successful at other sites. This would have the effect of not only decreasing competitive pressure on *M. villosa* but also creating hydrological conditions that might induce more frequent flooding.

Literature Cited

Allsop, A. 1952. Longevity of *Marsilea* sporocarps. Nature (Lond.) 169:79–80.

Ben-Dor, E. 1989. Determination of organic matter content in arid-zone soils using a simple "loss-on-ignition" method. Commun. Soil Sci. Plant Anal. 20:1675–1695.

Bruegmann, M. M. 1986. The phenology, tissue water relations, and taxonomy of *Marsilea villosa*. M.S. thesis, University of Hawaiʻi at Mānoa, Honolulu.

Dunne, T., and L. B. Leopold. 1978. Water in environmental planning. W. H. Freeman and Co., New York.

Egler, F. E. 1947. Arid southeastern Oʻahu vegetation, Hawaiʻi. Ecol. Monogr. 17:383–435.

Foote, D. E., E. L. Hill, S. Nakamura, and F. Stephens. 1972. Soil survey of the islands of Kauaʻi, Oʻahu, Maui, Molokaʻi, and Lānaʻi, State of Hawaiʻi. U.S. Department of Agriculture, Soil Conservation Service with the University of Hawaiʻi, Agricultural Experiment Station, Washington, D.C.

Forbes, C. N. 1920. Notes on *Marsilea villosa* Kaulf. Occas. Pap. Bernice Pauahi Bishop Mus. 8:47–49.

Fosberg, F. R. 1961. Guide to excursion III, 10th Pacific Science Congress. Pacific Science Congress and University of Hawaiʻi, Honolulu.

Giambelluca, T. W., M. A. Nullet, and T. A. Schroeder. 1986. Rainfall atlas of Hawaiʻi. Report R-76. Hawaiʻi Department of Land and Natural Resources, Division of Water and Land Development, Honolulu.

Hodder, R. M., and W. A. Low. 1978. Grazing distribution of free-ranging cattle at three sites in the Alice Springs district, central Australia. Aust. Rangeland J. 1:95–105.

Holland, R. F. 1976. The vegetation of vernal pools: A survey. Pages 11–15 *in* S. Jain, ed.

Vernal pools: Their ecology and conservation. Institute of Ecology, University of California, Davis, Publication 9.

Johnson, D. M. 1985. New records for longevity of *Marsilea* sporocarps. Am. Fern J. 75:30–31.

———. 1986. Systematics of the new world species of *Marsilea* (Marsileaceae). Monogr. Syst. Bot. 11:87.

Mahlberg, P. G., and S. Yarus. 1977. Effects of light, pH, temperature, and crowding on megaspore germination and sporophyte formation in *Marsilea*. J. Exp. Bot. 28:1137–1146.

National Climate Data Center. 2002. NCDC summary of the day: West 2 2002. CD-ROM. Earthinfo Inc.

Palmer, Daniel D. 2003. Hawaiʻi's ferns and fern allies. University of Hawaiʻi Press, Honolulu.

Pukui, M. K., and S. H. Elbert. 1986. Hawaiian dictionary. Rev. and enl. ed. University of Hawaiʻi Press, Honolulu.

Rhodes, E. R., P. Y. Kamara, and P. M. Sutton. 1981. Walkley-Black digestion efficiency and relationship to loss on ignition for selected Sierra Leone soils. Soil Sci. Soc. Am. J. 45:1132–1135.

Smith, Clifford. 2004. http://www.botany.hawaii.edu/faculty/cw_smith/cen_cil.htm.

Tryon, R. M., and A. F. Tryon. 1982. Ferns and allied plants: With special reference to tropical America. Springer-Verlag, New York.

U.S. Department of Agriculture, Weather Bureau. 1922. Summary of the climatological data for the United States, by sections. Climatological data herein from the establishment of stations to 1918, inclusive. Hawaii section. Washington, D.C.

———. 1960. Climatic summary of Hawaii. Supplement for 1919 through 1952. Washington, D.C.

U.S. Fish and Wildlife Service. 1993. *Marsilea villosa* recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. Manual of the flowering plants of Hawaiʻi. Rev. ed. University of Hawaiʻi Press and Bishop Museum Press, Honolulu.

Wester, L. 1989. Restoration of *Marsilea villosa* population: Experiment in weed management. Newsl. Hawaii Bot. Soc. 28:63–70.

———. 1994. Weed management and the habitat protection of rare species: A case of the endemic Hawaiian fern *Marsilea villosa*. Biol. Conserv. 68:1–9.

Wester, L., and T. Ikagawa. 1988. Weed invasion of *Marsilea villosa* population at ʻIhiʻihilauākea Crater, Koko Head, Oʻahu. Newsl. Hawaii Bot. Soc. 27:87–101.

Wilkinson, M. 1997. Status of the *Marsilea villosa* population at ʻIhiʻihilauākea Crater, Oʻahu. Newsl. Hawaii Bot. Soc. 36:12–18.

Zedler, P. H. 1987. The ecology of southern California vernal pools: A community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85.

Appendix

Species Cover and Frequency Variation in ʻIhiʻihilauākea Crater, 1988 to 2004

		1988		1990		1991		2003		2004	
	Species	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.
#	*Marsilea villosa*	2,955	53	2,969	53	4,067	53	34	22	77	12
	Panicum maximum	178	18	963	31	794	30	1,087	43	1,499	46
	Cenchrus ciliaris	0	0	17	13	0	0	1,151	45	1,358	40
#	*Echinochloa colona*	1,193	52	1	35	3	32	0	4	55	25
#	*Merremia aegyptia*	0	32	0	29	0	5	27	42	1,040	44
#	*Cynodon dactylon*	68	12	197	17	118	16	234	19	415	18
#	*Digitaria insularis*	177	7	276	47	256	19	0	0	0	1
#	*Chloris barbata*	5	16	551	42	0	0	0	15	134	33

Appendix (continued)

Species	1988 Cov.	1988 Freq.	1990 Cov.	1990 Freq.	1991 Cov.	1991 Freq.	2003 Cov.	2003 Freq.	2004 Cov.	2004 Freq.
# *Setaria verticillata*	414	31	5	9	0	1	2	15	173	21
Asystasia gangetica	4	7	120	1	13	0	99	34	207	34
Sida fallax	0	1	80	34	0	0	19	21	36	18
Hyptis pectinata	0	0	32	17	0	0	1	6	99	23
# *Xanthium strumarium*	61	36	0	0	0	16	0	0	0	0
Emelia sonchifolia	0	0	5	17	6	3	0	0	36	27
Verbesina encelioides	0	0	0	0	0	0	0	1	40	20
# *Solanum americanum*	38	36	0	0	0	0	0	0	0	3
Atriplex semicbaccata	0	1	0	0	0	0	13	11	7	6
Portulaca oleracea	9	34	0	9	0	2	0	21	1	12
# *Malvastrum coromandelianum*	0	0	7	23	0	0	0	1	0	1
Boeharvia repens	0	0	5	2	0	0	0	0	0	0
Bothriochloa pertusa	0	0	5	4	0	0	0	0	0	1
Lycopersicon esculentum	0	7	0	0	0	2	0	1	5	34
# *Macroptilium lathroides*	0	17	0	14	0	17	0	9	5	21
# *Sonchus oleraceus*	0	16	0	12	0	1	0	0	3	12
Phyllanthus debilis	0	1	0	0	0	0	0	4	2	4
Stapelia	0	0	0	0	0	0	0	4	2	2
Waltheria americana	0	1	2	21	0	0	0	0	0	0
Desmanthus virgatus	0	0	0	2	1	2	0	3	0	1
Lantana camara	0	1	0	6	1	4	0	6	0	6
# *Ageratum conyzoides*	0	7	0	1	0	0	0	0	0	0
Bidens pilosa	0	9	0	13	0	3	0	2	0	3
Cenchrus echinatus	0	0	0	11	0	0	0	0	0	0
Chamaesyce hirta	0	1	0	1	0	0	0	0	0	0
Chenopodium murale	0	0	0	0	0	0	0	0	0	1
Coccinia grandis	0	0	0	0	0	2	0	0	0	0
Commelina diffusa	0	0	0	1	0	0	0	1	0	2
Coronocarpus didymus	0	1	0	0	0	0	0	0	0	2
Cuscuta sandwichiana	0	0	0	0	0	0	0	0	0	1
Leucaena leucocepahala	0	0	0	1	0	4	0	0	0	0
Momordica charantia	0	7	0	3	0	6	0	0	0	3
Ocimum gratissimum	0	0	0	4	0	0	0	0	0	0
Passiflora foetida	0	3	0	4	0	2	0	0	0	0
Portulaca pilosa	0	0	0	1	0	0	0	0	0	0
Stachytarpheta jamaicensis	0	1	0	1	0	0	0	0	0	0
Unknown grass	0	0	0	0	0	0	0	2		0
Bare ground	198	10	65	9	41	3	2,633	53	106	16
Richness		28		34		21		25		33

Note: Cover for each species was estimated as a percentage for each 10 by 10 m quadrat and totaled for the whole area surveyed. The maximum possible cover was 5,300 m^2. Frequency was determined as the number of quadrats in which a species was present out of a total of 53.

#Species noted at the site by Fosberg (1961).

Postscript

Although O'ahu experienced some heavy rains between 15 February and 30 March 2006, only 431 mm fell at Hawaii Kai Golf Course gauging station and the highest 24 hour rainfall event was 66 mm. This did not cause long term flooding at Ihi'ihilauakea Crater. However, the population of *M. villosa* at Makapu'u recovered from the fire of the previous summer.