THE DISTRIBUTION OF A MALE STERILE FORM OF *TI* (*CORDYLINE FRUTICOSA*) IN POLYNESIA: A CASE OF HUMAN SELECTION?

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Cordyline fruticosa (L.) Chev. is a woody monocot in the family Laxmanniaceae (Chase *et al*. 1996, Fosberg 1985). The approximately 20 species in this genus have a Southern Hemisphere distribution, with the greatest diversity concentrated in Australia and New Zealand (Conran 1998). The exact area of origin of *C. fruticosa* is unknown. It is thought to have originated in Southeast Asia and then to have been domesticated in New Guinea (Yen 1987). However, preliminary molecular phylogenetic investigations have shown *C. fruticosa* to be most closely related to *Cordyline* species from tropical North Queensland, Australia (Simpson 2000). It has been suggested that *C. fruticosa* does not have a natural distribution and that it arose by human domestication from another species (Yen, pers. comm.). From a botanical perspective, questions as to the geographic origin and phylogenetic placement of *C. fruticosa* have yet to be addressed adequately. Within Polynesia, *Cordyline fruticosa*, the *ti* plant, is ubiquitous in its distribution and ethnobotanical use (Whistler 1991). *Cordyline* pollen appears in the palynological record around the same time as taros, bananas, sugar cane, breadfruit and other common Polynesian-introduced plants, and the cordyline is considered to be an aboriginal introduction to the islands (M. Prebble, pers. comm.).

Ti was presumably carried by early Polynesians for its importance in costume making, for wrapping food and religious uses, and as a food source (Merlin 1989, Whistler 1992). Various colour varieties were present before Western contact, but this study focuses on a large non-variegated green form that is common throughout Polynesia. The green form can be circumscribed based on its names, appearance and uses across Polynesia. All varieties of *C. fruticosa* are known generally by the name of *ti*, *si*, *ki* or *tsi* in Polynesia. A descriptive modifier is generally added to specify the green form, which are often cognate words among archipelagoes (Ehrlich 1999, 2000; Pétard 1946). Names for the green form include *la-i* (Hawai'i), *auti* (Marquesas), *rau ti* (Tahiti), *lau ti* (Cooks), *ti karokaro* (Rapa), *ti pore* (New Zealand), *ti vao* (Samoa), *si* (Tonga), *tsi ngau* (Niue) and *qai* (*nggai*) (Fiji) (Brown 1931, Degener 1930, Parham 1972, Pétard 1946, Smith 1979, Sykes 1970, Tregear

1891, Walsh 1901). For consistency, I will refer to the green form by the name of *ti* across all archipelagoes. Most archipelagoes have varieties within the green form: Tahiti reportedly had over ten, the Marquesas had four, Mangareva had three (Brown 1931, Henry 1928, Hiroa 1938). Most varieties of the green form appear to vary slightly in leaf shape or quality, or in rhizome characteristics and suitability for eating (Brown 1931, Henry 1928).

In this paper, I will discuss the distribution and uses of *ti* across the Polynesian region, paying special attention to variation in its reproductive capacity. Given that asexually propagated crops are of extreme importance in the agricultural systems of Oceania, a loss of fertility in *ti* may suggest that sterile cultivars were intentionally sought out and distributed by the people who made various nutritional and cultural uses of the plant. I present pollen fertility and cytological data from the Polynesian green *ti* in the context of Polynesian settlement patterns in order to investigate and discuss the evidence for intentional selection for a sterile cultivar. I suggest that there is support for the case of human selection for the sterile *ti* cultivars.

PLANT MORPHOLOGY

Most species descriptions of the green form in regional floras emphasise the large stature, broadly lanceolate leaves with acuminate tips, glossy green colour and white flowers tinged with pink (Brown 1931, Cheeseman 1903, 1925, Christopherson 1935, Degener 1930, Hillebrand 1888, Smith 1979, Wilder 1931, Yuncker 1943). Cheeseman's description in the *Manual of the New Zealand Flora* (1925) calls the New Zealand green *ti* "the common Polynesian form of *C. terminalis*" (=*C. fruticosa*[1]). He comments that the green form in New Zealand (called *ti pore* by the Māori) has generally been found in abandoned Māori cultivations and survives in remnant populations from a period when it was grown by the Māori for food purposes, noting "the plant was originally introduced by the Maori on their first colonization of New Zealand" (Cheeseman 1925:310). Cheeseman (in Best 1925:135) comments that the "…north and south range [of *ti pore*] is from the Hawaiian Isles to the Kermadec Group", but given its then recent discovery by botanists on the North Island, he says "its introduction into New Zealand across 600 miles of ocean would present no difficulties". Incidentally, *ti pore* was later named *C. cheesemanii* by Thomas Kirk (Cheeseman 1925). In Rarotonga, Wilder (1931) describes the variety locally known as *lau ti* as the "*Cordyline terminalis* of Cheeseman's list" (referring to Cheeseman's Rarotongan flora from 1903) that "produces a large fibrous tuber, which, when baked in a native oven, yields a sweet juice". Brown (1931:141)

reports, "there seems to be no reason to believe that the ti cultivated by the Hawaiians is specifically different from that of the Marquesans"; in Hawai'i, there is no evidence of the existence of any varieties but *la'i*, the green form, before contact with Europeans (Abbott 1992). These comparisons among archipelagoes imply the existence of a green form that can consistently be recognised from island to island throughout Polynesia.

Many authors distinguish the green form from other colour varieties (particularly red ones). Colour varieties appear to have been present in some, but not all, Polynesian archipelagoes before European contact, with increasing numbers brought in after (Pétard 1946). Brown's (1931) dichotomous key separates the green *ti* from several colour varieties present in the Marquesas. For Hawai'i, Krauss (1974:215) also made a distinction between the "green-leafed, common ti" and modern "cultivated varieties and hybrids produced as ornamentals". Christophersen (1935:48-49) reported that *ti vao* is the name for the "wild" *ti* growing in Samoa as a common shrub in the forest up to 1500 metres or more, which is different from other colour varieties that are cultivated in villages. Yuncker (1943:33) also makes such a distinction between a form that is frequently found in the forests of Niue that can be used for food and the "variety with red leaves and flowers …cultivated as an ornamental about dwellings". Sykes (1970:255) observed that the red-leaved cultivar is not planted in Niue anymore, but that the green form is common in most types of ecosystems.

USES OF THE *TI* PLANT

Regional floras and ethnographies consistently reinforce a common series of material, spiritual and nutritional uses that provide a basis for the circumscription of green *ti* as a cultural entity. Skirts, necklaces, crowns and other clothing as well as ornamentation can be made by braiding or lacing together the leaf blades (Brown 1931, Degener 1930, Ehrlich 1999, Fornander 1916-20:668, Handy and Handy 1972, Krauss 1974). Other sources mention the use of the leaves for thatching roofs (Christophersen 1935, Ellis 1963, Fornander 1916-20:668, Métraux 1940). The leaves are described as being highly valued for their use as food wrappers (Degener 1930, Handy and Handy 1972, Hillebrand 1888, Sykes 1970). They have strong but flexible secondary veins with a parallel arrangement that allows them to be easily folded. The leaves contain no poisonous or disagreeable tasting sap so that meats and other foods can be wrapped in them and cooked in earth ovens (Brown 1931, Degener 1930, Sykes 1970). Leaves are also highly resistant to wilting and decomposition, and can be used to line pits dug for the fermentation of breadfruit (Brown 1931, Ellis 1963,

Ragone 1991). Green *ti* is reported to play an important role in rituals and ceremonies and is commonly planted in sacred sites (Handy and Handy 1972, Henry 1928, Oliver 1974, Pétard 1946). *Ti* plants are widely believed to offer protection from bad luck, spells or evil spirits; for these reasons, *ti* is often planted to form living fences around houses and the leaves are commonly carried while travelling (Handy and Handy 1972, Krauss 1974). Because it propagates easily and grows vigorously, green *ti* could be deliberately planted for political or religious purposes, such as to demarcate boundaries or mark shrines (Ehrlich 2000, Pukui *et al.* 1972). It is also reported to have been planted in the mountains to mark trails, to provide leaves for the thatching of temporary upland shelters and to make rain capes or sandals (Handy and Handy 1972).

Probably the most important single use of the green form of *Cordyline fruticosa* is the use of its tuberous underground stems, its rhizomes, for food. The cooked rhizomes of this form have been used extensively throughout Polynesia and can be eaten alone, used for sweetening other foods or fermented and/or distilled into an intoxicating beverage (Best 1925, Dening 1974, Ellis 1963, Pétard 1946). The large tuberous rhizomes are cooked in large earth ovens or *umu*, and become soft and molasses-like after one to several days of cooking (Cheeseman 1903, Wilder 1931, Yuncker 1943). Removal of the rhizomes from the ground and preparation of the *umu* requires significant effort, and the making of *umu ti* was commonly a community-wide event (Carson 2002, Cox 1982, Fankhauser 1989, Hiroa 1938). Preparing the *umu ti* required that a large pit be dug and filled with large amounts of firewood and stones. Rhizomes weighing from 4.5 to 22 kg were removed from the ground and put in the oven in bundles marked for each family. Sometimes they were cooked with giant taro (*Alocasia macrorrhiza*) or breadfruit (*Artocarpus altilis*) (Cheeseman 1901, Dening 1974, Henry 1893, Hiroa 1938). It appears that the consumption of *ti* rhizomes was largely divorced from the sacred status and ritualistic uses of its leaves. The significance, however, of eating cooked *ti* rhizomes may have differed among archipelagoes (Carson 2002, Ehrlich 2000, Merlin 1989). Consumption in Hawai'i is reported to have been either restricted to a certain social class, special occasions or times of famine; in New Zealand, it was a staple food (along with other endemic NZ *Cordyline* species) (Abbott 1992, Best 1925, Cheeseman 1901, 1903, Fornander 1916-20, Handy and Handy 1972, Walsh 1901). Particular rituals, such as the fire-walking ceremony in the Society Islands, are sometimes associated with the cooking of *ti* rhizomes (Henry 1893), and there is evidence that this ritual previously existed in other areas (e.g., Samoa, New Zealand) but has since fallen out of practice (Carson 2002, Gudgeon 1899). In some cases the *ti* oven

was associated with human sacrifice (Fornander 1916-20, Savage 1962). Fankhauser (1986 in Carson 2002:347) suggests "throughout Oceania there was a certain amount of ceremony surrounding the cooking of *Cordyline*…due to the magico-religious beliefs attached to *Cordyline*" (including NZ endemic species). Therefore, although there is evidence that *ti* was an important source of food, despite the fact that its uses and practices are likely to have differed among archipelagoes, it may not be possible to exactly categorise the cooking of *Cordyline* as either a sacred or secular activity.

"WILD", NATURALISED AND DOMESTICATED *TI*

Cheeseman's "common Polynesian form" of *C. fruticosa* can be circumscribed by morphological descriptions in regional floras, by local names for the plant that distinguish it from other colour and cultivated varieties, and by a suite of uses for *ti* that are shared among archipelagoes. It appears that green *ti* grew, was collected and used in both cultivated and "wild" contexts (Cheeseman 1925, Handy and Handy 1972, Hiroa 1938, Williams 1992). Propagation through stem cuttings is easy and cuttings grow readily, even without care (Henry 1928). The presence of green *ti* in most ecosystem types led some early workers to believe that it was indigenous to Polynesia, although most scholars now agree that *ti* was an aboriginal introduction to the islands (Cheeseman 1901, Handy and Handy 1972, Whistler 1992). From its distribution on most Polynesian islands, it would appear that once *ti* was introduced, it escaped cultivation and became naturalised through seed dispersal, most likely by birds. In the cultural region of West Polynesia (Samoa, Tonga, Niue) and Fiji, the green form (referred to as *ti vao*, *si*, or *qai/nggai*) is a common component of the forest understory (Ehrlich 1999, Smith 1979, Whistler 1992). It appears in ecological transects of almost every ecosystem type in Samoa (Whistler 1978). Its Samoan name, *ti vao*, can be translated literally as "forest ti" (Cox 1982:394). Fruits are described in published descriptions and are easily observed in the field and on herbarium specimens (Parham 1972, Smith 1979) (Fig. 1). Signs of herbivory on the mature red fruits indicate that birds may be vectors for their dispersal. In West Polynesia, green *ti* appears to be reproducing sexually and is naturally and widely distributed.

In contrast, many regional botanists have noted the absence of fruiting *ti* plants in the cultural region of East Polynesia (Hawai'i, New Zealand, and the Marquesas, Cook, Austral, Society and Gambier Islands) (Abbott 1992, Nadeaud 1897, Walsh 1901, Yen 1987, also W.L. Wagner, W.A. Whistler, J-Y. Meyer and G. McCormack, pers. comms). None of the

Figure 1: Fruiting *Cordyline fruticosa*/*ti vao* from Savai‘i, Samoa.

herbarium specimens of the green form of *C. fruticosa* from East Polynesian archipelagoes that I have studied were in fruit, and species descriptions of *C. fruticosa* in regional floras and other published sources generally do not discuss fruit morphology (Brown 1931, Pétard 1946, Wagner *et al.* 1990, Wilder 1931), although there are exceptions. Hillebrand (1888) describes yellow globose berries of the Hawaiian *ti*, and Degener (1930:95) reported that this yellow fruit matures to bright red, noting that only "very rarely does a flower mature into a… berry". Krauss (1974:215) noted that the "green-leafed, common ti seldom flowers" in Hawai‘i. Cheeseman described in his New Zealand flora (1925:310) that the berries of green *ti* plants are "globose, 1/3" diameter". However, other sources report that the New Zealand *ti* is sterile (Ehrlich 2000, Walsh 1901). After a discussion of methods of its propagation in New Zealand, Walsh (1901:304) comments that "so far as I have been able to learn, the ti pore does not seed in New Zealand". Waldern *et al.* (1999) report that green *ti* on Henderson Island is reportedly sterile, but fruiting is common on Pitcairn Island. For the Society Islands, Nadeaud reported in 1897: "It is remarkable that *Cordyline terminalis* does not produce fruits in Tahiti. During my second visit to this island I charged the inhabitants to search for fruits, but in vain. During my sojourn I examined a large number of Ti in flower and did not see a single fruit" (Nadeaud 1897, quoted in Welsh 1998:301).

If East Polynesian *ti* plants do not commonly produce fruit, the distribution of the green form of *C. fruticosa* on East Polynesian archipelagoes must be primarily (if not completely in some areas) explained by intentional planting of clones or by the rooting of broken stem sections from existing plants, which readily propagate vegetatively. The idea of a sterile form dependent upon humans for its reproduction would seemingly be difficult to reconcile with its broad distribution the islands of East Polynesia, where it is often described as "growing wild" in native forests, at high elevations, and in isolated and extreme environments such as sheer cliffs (Gill and Sykes 1996, Handy and Handy 1972, Hiroa 1938, Merlin 1985, Métraux 1940, Wilder 1931). As Fornander wrote, in Hawai'i "it grows in valleys, on hills, mountain ridges and side-hills" (1916-20:668).

Douglas Yen studied several green *ti* plants on the grounds of the Bishop Museum in Hawai'i and found that their flowers had inviable pollen (Yen 1987). This observation may explain why fruits rarely form: viable pollen is simply not available to successfully fertilise the ovules. If pollen inviability does indeed result in a lack of seed set in Hawaiian *ti*, it is likely that green *ti* on other archipelagoes may have inviable pollen as well. The purpose of this study is to investigate the geographic extent and biological basis of sterility in green Polynesian *C. fruticosa*. Based on Yen's observations, I will characterise pollen sterility of the green form of *C. fruticosa* throughout Polynesia, as pollen viability on other archipelagoes has not been previously studied. The biological process underlying pollen sterility is not known for Hawaiian *ti*, although a change in chromosome number was suggested to be the cause in the *Manual of the Flowering Plants of Hawai'i* (Wagner *et al*. 1990). In this paper, I will examine the suggestion that a change in chromosome number may underlie pollen sterility in Hawaiian green *ti* plants. Finally, evidence of intentional selection for sterile *ti* plants and associated features will be considered in light of the ethnobotanical importance of green *ti* throughout Polynesia.

INVESTIGATING POLLEN STERILITY: MATERIALS AND METHODS

To establish fertility or sterility of the green form of Polynesian *Cordyline fruticosa*, I studied pollen stainability across the entire Polynesian triangle region. Flowering specimens were collected on the islands of Kaua'i and O'ahu in the Hawaiian Islands, and on the island of Mo'orea, Society Islands. Additionally, flowering material from herbarium sheets was obtained from 11 Polynesian archipelagoes and Fiji. In an effort to exclude colour varieties from the study, specimens that had obvious leaf variegation or references to leaf colour on the specimen label were not considered.

This was only necessary in a few cases; the overwhelming majority of *C. fruticosa* herbarium specimens from Polynesia were of the green form. In total, 85 herbarium specimens were included in the study (see Appendix 1). Pollen grains were stained with lactophenol analine blue dye; stainability of pollen was used as a proxy for assessing fertility. Lactophenol analine blue binds to the cytoplasm of fertile pollen grains and stainability of pollen is a strong indication of normally developed pollen and pollen fertility (Kaul 1988).

Anthers were removed from closed flowers on all specimens. A single anther was placed on a microscope slide in a drop of lactophenol analine blue, following Hauser and Morrison (1964). The anther was macerated and the anther sacs removed. A cover slip was mounted and pollen was observed at 400x using a Leica DMRB compound microscope. Two hundred pollen grains were counted per slide and the percentage of fertile grains tabulated. Round grains and those that were darkly and uniformly stained were scored as fertile. Grains that were poorly stained, not stained at all, and/or folded or misshapen were scored as sterile (Fig. 2). I statistically tested whether pollen stainability is randomly distributed with respect to the divide between East and West Polynesia. Because the data tended towards either complete fertility or complete sterility, a non-parametric two-sample rank test was employed. I used the normal approximation to the Mann-Whitney test, which measures the probability that differences in the sums of the ranked percentages of fertile pollen from East and West Polynesian specimens could have arisen by chance given the sample size (Zar 1999).

To test whether sterility might be associated with a change in chromosome number, meiotic chromosome squashes were performed. In the field, floral buds were excised from inflorescences and fixed in Farmer's solution (3:1 100% ethanol:glacial acetic acid) for 24 hours. Buds were then transferred
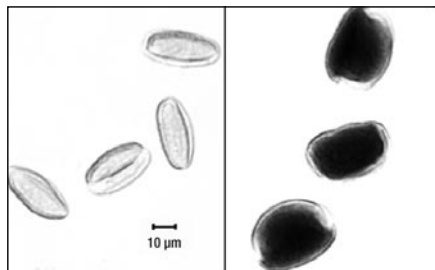

Figure 2: Examples of inviable and viable *C. fruticosa* pollen.

to a 70% ethanol solution and held at 40ºF. Immature flowers were dissected and anthers were placed in a drop of acetocarmine dye on a glass slide and macerated with a glass rod. The slide was heated over an alcohol lamp and stirred with a metal dissection needle. Excess tissue was removed, a drop of Hoyer's solution was added, and a cover slip placed over the top. The slide was then turned upside down onto a sheet of bibulous paper and pressure was applied. Chromosomes were counted and photographed at 1000x using a Leica DMRB compound microscope.

INVESTIGATIVE RESULTS

The pattern of pollen stainability shows a striking divide between West Polynesia (and Fiji) and East Polynesia (Table 1). Although some West Polynesian specimens were sterile or had less than 50 percent pollen stainability, most specimens showed greater than 85 percent stainability (Fig. 3). This contrasts sharply with the almost uniform pollen sterility in East Polynesian specimens. Despite low sample sizes in some areas, pollen
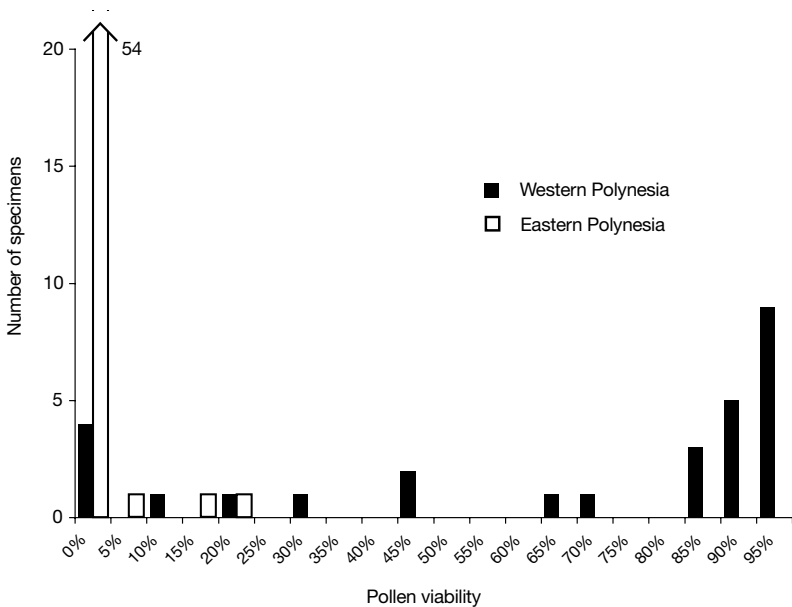

Figure 3: Percent viable pollen from herbarium specimens from West Polynesia and Fiji (in black) and East Polynesia (in white).

stainability in all East Polynesian specimens, except for the Society Islands, was less than five percent. These results were highly statistically significant, showing that West Polynesian accessions systematically outrank East Polynesian accessions in terms of percent pollen stainability at P>0.001.

Results of the chromosome squashes did not support the assertion that sterility in East Polynesian *ti* plants is caused by octoploidy. Accession AH164 from Kaua'i, Hawai'i showing 0 percent stained pollen had approximately 19 pairs of chromosomes at first metaphase of meiosis (Fig. 4). A count of 2n =19 II is in agreement with other published counts for the species and the reported base number for the genus (Matthew and Vijayavalli 1989, 1990; Sato 1935).

Table 1: Pollen viability of *C. fruticosa* by archipelago with comparative data from *Artocarpus altilis* (breadfruit). Numbers of accessions sampled are in parentheses. *Cordyline* data are reported as median percentages (see Appendix for a complete report). Breadfruit fertility is defined as the degree of seededness in various cultivars (as reported in Ragone 2001).

Location (# *Cordyline fruticosa* accessions)	*Cordyline fruticosa* Pollen stainability (median)	*Artocarpus altilis* Fertility (seededness)	*Artocarpus altilis* Ploidy
Western Polynesia + Fiji			
Fiji (9)	97.0%	normal (3)	diploid
Samoa (13)	88.0%	normal (3)	diploid
		partial (1)	diploid
		sterile (1)	triploid
Tonga (4)	91.8%		
Niue (2)	69.5%		
Eastern Polynesia			
Societies (12)	2.8%	partial (1)	diploid
		sterile (3)	triploid
Cooks (1)	0.0%	sterile (2)	triploid
Marquesas (3)	0.0%	sterile (3)	triploid
Hawai'i (34)	0.0%	sterile (1)	triploid
Australs (6)	0.0%		
Kermadecs (1)	4.5%		
Henderson/Pitcairn (2)	0.0%		

DISTRIBUTION AND PROPAGATION

Pollen viability in green *C. fruticosa* is variable among the archipelagoes of the Polynesian triangle. West Polynesian green *ti* plants generally showed high proportions of fertile pollen, which is in keeping with observations of seed set, dispersal and a broad distribution over a range of ecological systems. East Polynesian specimens were overwhelmingly pollen-sterile, confirming Yen's observations of sterile pollen in Hawai'i and extending them to apply throughout East Polynesia. This result would appear to support the paucity of observations of seed set, but creates something of a paradox with its broad distribution on East Polynesian islands, including remote, high elevation and rugged sites. If East Polynesian *ti* plants only rarely produce fruit, it becomes difficult to explain observations of green *ti* growing in isolated areas away from human settlement. The specimens used in this study were not specifically collected from villages; many were collected during expeditions by the authors of several regional floras and ethnographies from a variety of localities including native forests, cliffs and ridges (Brown 1931, Christophersen 1935, Degener 1930, Setchell 1926, Smith 1979, Yuncker 1943) (see Appendix 1 for collection information). Given this, *ti* plants with sterile pollen do not appear to be necessarily associated with human habitation, whereas human propagation could easily explain the presence of green *ti* at low elevations near villages. Therefore, the main problem is to explain how *ti* might have become established at high elevations. If East Polynesian green *ti* does not generally reproduce sexually through seed set and dispersal, there are several other mechanisms that may account for the presence of green *ti* in remote areas. If there were
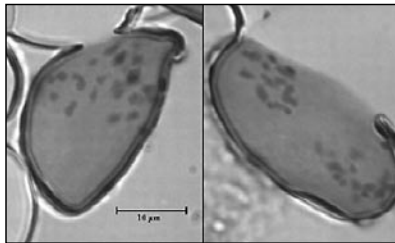

Figure 4: Chromosomes of *C. fruticosa* at first metaphase of meiosis in pollen parent cells of male-sterile accession AH164 from Kaua'i, Hawai'i. Although Hawaiian *ti* plants have been reported to be octoploids, this squash shows the chromosome number to be closer to the diploid base number for the genus, consistent also with published counts for the species.

reasons for people to propagate or casually cultivate *ti* at high elevations, vegetative propagation through broken stem pieces could at least partly account for the presence of *ti* in remote areas.

There is evidence for intentional propagation, casual cultivation, and utilisation of *ti* outside of the village setting. Best (1925:135) reports "it is clear that *C. terminalis*…[was] preserved by the Maori and planted as a food product, though this does not imply cultivation in the sense in which the *kumara*, yam, *taro* and gourd were cultivated". According to Handy and Handy (1972:224) "…ti roots were gathered from the forest in large quantities and steamed in great ovens". This is supported by archaeological evidence from excavations for the H-3 highway on 'Oahu, Hawai'i. *Ti* ovens were found up to 305 m in elevation on the foothill ridges of cliffs and talus slopes below, but these ovens were not clearly associated with habitation sites (Williams 1992). *Ti* was also used outside of the village setting to mark boundaries, trails and shrines (Handy and Handy 1972). Pukui *et al*. (1972:125) explain that "the family altar was the *Pohaku o Kane*… it was a single stone monument and… [altar] with *ti* and other greenery planted about". These shrines could often be found at boundaries or passes between cliffs (Ehrlich 2000, Valeri 1985). *Ti* plants were also valuable to have while traveling since rain capes and sandals could be made with the leaves (Krauss 1974). Bird catchers in Hawai'i thatched their temporary upland shelters with *ti* leaves during hunting expeditions. They were called *hale la-i* '*ti*-leaf houses' (Handy and Handy 1972).

Ti plants are known to propagate readily, with little or no care: "[p]lanting requires simply the cutting of a stalk, piece of stalk, or root, and sticking it in the ground, where it grows without cultivation" (Handy and Handy 1972:222). Greenhouse studies at the University of California, Berkeley show that *ti* stems root quickly whether submerged in water or planted in or simply lying on top of soil, oriented either vertically or horizontally (Hinkle, unpublished data). *Ti* plants are also known to be incredibly hardy; they can survive in disturbed areas and poor soils, and can even persist through typhoons and fires (Merlin 1989). Although there is no specific data available about the life span of *ti* plants, some anecdotal information from a local informant in Mo'orea, Society Islands, a man in his 70s who has a *ti* plant growing on his property, who remembers it being sizeable even during his youth, indicates that *ti* plants are capable of surviving 100 years and possibly many more. A related species, the New Zealand cabbage trees (*Cordyline australis*) commonly persist over 100 years, in some cases up to 1000 (Simpson 2000). In sum, it seems reasonable to conclude that casually cultivated or intentionally planted green *ti* at shrines, boundaries or trail sides in remote sites were able to thrive and survive for many years.

Setchell (1926:154) reports green *ti* to be "frequent in moist, shady gulches… above the falls". *Ti* plants commonly grow on small ledges of sheer cliff faces in vertical succession adjacent to waterfalls (see Fig. 5). One possibility is that broken stem pieces may have tumbled down these steep drainages and were able to take root. I was able to observe this in an isolated gulley in Tahiti. A broken *ti* branch was lying on bare soil at the base of a cliff, directly below a large *ti* plant growing on the cliff's edge. Roots had begun to emerge out of the nodes of the broken branch. Although a single observation cannot confirm the universality of this process, certainly rooting stem fragments account for some proportion of the "wild" *ti* that can be seen growing in remote areas. A second possibility, one that does not necessarily preclude the first, is that a small amount of sexual reproduction is occurring, resulting in occasional fruit formation. Bird-mediated seed dispersal could then result in the occasional distribution of green *ti* in remote sites. These plants could then asexually propagate themselves in the manner suggested above.

Figure 5:   *Ti* growing on cliff face near waterfall. (Photo by author.)

THE BIOLOGY OF POLLEN STERILITY

Although the pattern of pollen sterility in Polynesia is striking, the biological explanation for sterility is less clear. An interesting correlate to pollen sterility and seedlessness is a change in chromosome number, such as in triploid breadfruit cultivars (*Artocarpus altilis*) (Ragone 2001). *The Manual of the Flowering Plants of Hawai'i* (Wagner *et al.* 1990) suggests that Hawaiian *ti* plants are octoploids ("$n≈152$"), and some authors have suggested that this offers an explanation for sterility and seedlessness in Hawaiian *ti* plants (Ehrlich 1999, Wagner *et al.* 1990). However, Wagner *et al.* did not perform this count and they do not give a citation for it (D.R. Herbst and W.L. Wagner, pers. comms). Only one report of octoploid pollen ("$n≈76$") has ever been published (Rattenbury 1957). This count was from an unaccessioned plant from a private garden in Auckland, New Zealand, and has not been confirmed in any other published chromosome counts. Chromosome counts of *C. fruticosa* have never been performed in the context of its archaeological and ethnobotanical importance in Polynesia. The cytological results reported here are in agreement with all published accounts for the species besides Rattenbury (1957) and, having been performed on a Hawaiian accession confirmed to have 0 percent viable pollen, suggest that Hawaiian *ti* plants (and the green *ti* from other archipelagoes) are not octoploids.

Octoploidy is an unlikely explanation for pollen sterility and seedlessness in any case because even polyploidy (e.g., tetraploidy, octoploidy) is generally associated with normal pollen and seed set. Odd polyploids (e.g., triploids) often have dosage imbalances of the chromosomes at meiosis that result in unequal numbers of chromosomes in the pollen grains and ovules. In the case of odd polyploidy, seeds cannot develop because the chromosomes cannot usually pair correctly. Breadfruit provides an illustrative example; all triploid accessions are pollen sterile and seedless (Table 1) (Ragone 1991, 2001). However unlike triploidy, octoploidy would not necessarily lead to dosage imbalances at meiosis because chromosomes can be equally divided. In octoploid plants, each pollen grain and ovule would have a complete set of chromosomes that could potentially pair upon fertilisation, leading to normal seed development. Because seeds are either extremely rare or completely absent in East Polynesian *ti* plants, octoploidy is unlikely to explain pollen sterility or seedlessness in *ti*.

Because the developmental pathways of pollen and ovules are independent, it is possible that pollen sterility can be accounted for by a mutation in the developmental or expression pathways of the androecium (the pollen producing organs) (Kaul 1988). In some plants, the connection between

pollen sterility and seedlessness is that there is no viable pollen available in a population to fertilise the ovules. If this were the case with *ti*, the introduction of viable pollen to pollen-sterile *ti* plants should result in seed set if the gynoecium (ovule producing organs) were functional. Horticultural *C. fruticosa* varieties have fertile pollen and set seeds. Therefore, the introduction of fertile pollen to the stigmas of pollen-sterile *ti* plants should presumably lead to fruit production. The pollen-sterile green form and fertile modern horticultural forms are often grown together and cross-pollination by bees can be easily observed, yet seed set in the pollen-sterile form still appears to be absent. This suggests that there may also be an independent mutation in the gynoecium during the development of ovules that prevents seed set in pollen-sterile *ti* plants. The presence of allelic mutations in both the androecium and gynoecium at high frequencies in East Polynesian archipelagoes may have led to pollen sterility and seedlessness becoming prevalent or ubiquitous in those populations. Such an explanation is somewhat unsatisfying because it requires two independent mutational events; still, multiple mutations seem more likely than octoploidy to explain the widespread pollen sterility and seedlessness in East Polynesian *ti* plants. Because stained pollen occurs in East Polynesian accessions, albeit in extremely low proportions (particularly in the Society Islands), it is possible that what underlies sterility does not interfere with normal pollen development *in every case*. Extensive sampling of pollen across many archipelagoes would confirm the proportions of viable to inviable pollen that could serve as an important clue as to the nature of the biological process underlying pollen sterility.

Information about the genetic diversity within and between populations may suggest the degree to which gene flow can explain the maintenance of putative pollen sterility traits in populations. Crossing studies with viable pollen introduced from fertile plants could help to determine if *ti* plants that produce sterile pollen are capable of seed production. Further cytological studies, including more accurate counts of chromosome numbers and observations of chromosome behaviour at meiosis, would be useful to rule out aneuploidy or dysploidy (the loss or gain of a subset of chromosomes) as the cause of pollen sterility and seedlessness.

POLLEN VIABILITY AND THE COLONISATION OF POLYNESIA

The difference in pollen viability between West and East Polynesia creates a striking pattern that also appears to correspond with a significant cultural divide between West and East Polynesia (Burrows 1939). Archaeological evidence indicates that Polynesian culture appears to have developed in

relative isolation in Tonga and Samoa beginning around 800-500 B.C. (Kirch and Green 2001). The colonising peoples to this area were part of the Lapita cultural complex, an extinct culture defined principally by a particular style of pottery that can be traced back to Near Oceania (Kirch 1997). Stratified sequences of artefacts in Samoa indicate a gradual transformation of material culture from Lapita to Polynesian between 1000 B.C. and A.D.1 (Kirch and Green 2001). Voyaging out of this homeland area is evidenced by artefacts from the Cook Islands that date to approximately A.D.1 (Kirch 1984, 2000). The low frequency of dispersal out of West Polynesia coupled with rapid expansion and limited secondary contact throughout East Polynesia most likely contributed to a major bottleneck in the genetic diversity of people, commensal plants and animals, religious and cultural practices, and language (Kirch and Green 1987).

If such a bottleneck did in fact occur, supporting evidence should show shared features that distinguish East from West Polynesia. The relative uniformity in East Polynesia with regards to shared religious deities and customs, linguistic affinities and a common material culture creates a notable contrast with West Polynesia and supports the notion of a bottleneck (Bellwood 1989, Burrows 1939, Kirch 2000). In terms of *C. fruticosa*, although its distribution and use in regions outside Polynesia is well known, the proximate ancestor for Polynesian *ti* plants, like other cultural information, arguably has its homeland in West Polynesia, making it an appropriate proxy for events in Polynesian prehistory. The findings reported here, that East Polynesian green *ti* plants show almost complete pollen sterility, further supports the idea that a bottleneck may have occurred as a result of limited dispersal out of West Polynesia followed by rapid expansion into the vast East Polynesian area.

Interestingly, a concordant pattern of sterility and seedlessness at the West-East Polynesia split can be seen in breadfruit (*A. altilis*), an important staple starch crop throughout Polynesia. Virtually all breadfruit cultivars are pollen sterile and seedless in East Polynesian archipelagoes despite the presence of primarily seeded varieties in West Polynesia (Table 1) (Ragone 2001). The consumption of breadfruit is well documented in West Polynesia, with many similarities to East Polynesia. Its almost uniform sterility in East Polynesia suggests, however, that there may have been changes in the ways it was used or in its relative importance (Carson 2002, Cox 1982, Ehrlich 1999, 2000). The change to seedlessness in breadfruit may represent a preference for high-yield and storable foodstuffs. Reducing the number of seeds increases the proportion of edible fleshy tissue, and crops that are asexually propagated produce more reliable phenotypes than sexually reproducing ones so that preferred varieties can be preserved. Seedless

breadfruit may have been preferred for pit fermentation because the quality of the fermented product, *ma* (Marquesas), *mahi* (Cook and Society Islands) or *masi* (Samoa), is apparently reduced unless the seeds are removed due to high tannin content (Ragone, pers. comm.). Therefore, seedlessness in breadfruit may also be associated with an increased emphasis on pit fermentation in East Polynesia, resulting in storable food resources that can be used when other resources are not available (Ragone 1991:207).

HUMAN SELECTION FOR SEEDLESSNESS IN *TI*

In the case of *Cordyline fruticosa*, it is possible that there was a preference for sterile *ti* plants and their associated features, and that the distribution of this form in Eastern Polynesia was intentional. Unlike the breadfruit, however, it is more difficult to speculate upon the specific features associated with sterile *ti* plants that might make them more desirable than fertile plants. When released from the metabolically costly task of seed production, many plants allocate more resources to storage (Ehrlen and Van Groenendael 2001). One possibility is that sterility results in larger, sweeter and possibly less fibrous rhizomes that are better suited for their use as food. If sterility does in fact result in rhizomes more suitable for eating, it would be compelling indirect evidence that Polynesians were selecting for large rhizomes. Despite the widespread use of *C. fruticosa* in regions outside of Polynesia, the eating of rhizomes appears to be uniquely Polynesian (Abbott 1992, Ehrlich 2000). It may be no accident that the innovation of *ti* consumption is associated with increasing geographic isolation. Stochastic and catastrophic events, population pressures and short-term climatic shifts can result in local extirpation of resources, particularly given the small geographic area of most islands (Carlquist 1974, MacArthur and Wilson 1967). The impacts of such events are magnified in such cases of extreme isolation because resources can not be replenished easily. Therefore, it may have been advantageous to have an additional food source on the small, isolated islands of Polynesia.

An interesting example from New Zealand supports the idea that East Polynesian settlers may have selected sterile *ti* plants for their use as food. In New Zealand, there are five endemic *Cordyline* species (Moore and Edgar 1970). Maori settlers evidently adapted both the ceremony and practice of baking *C. fruticosa* rhizomes (*umu ti*) to the New Zealand endemic tree, *Cordyline australis* (Fankhauser 1989). There is evidence of selection for various *C. australis* cultivars, the most notable named *ti tawhiti* or *ti para*, known by its cultivar name of *C. australis* "Thomas Kirk" (Best 1925, Harris and Heenan 1991, Simpson 2000). This cultivar does not flower, and has a weak and flexible stem and a rhizome system that prevents it from

attaining the large stature of *C. australis*. Its rhizomes appear to be less fibrous, which may explain why it was preferred as a food source (Best 1925, Simpson 2000). Best (1925:137) reports that "…it was not necessary to hew or chip the outside off [of the *ti para*] prior to cooking in the steam oven" and "the bark is much thinner, and smooth, not rugged"; for this reason it was "the most highly prized" for cooking. W. Colenso (in Best 1925:137) wrote,

> Ti para…was propagated by its side-shoots and suckers… from what I have heard from the Maoris… it did not produce flowers. Is this another curious instance of a plant losing its powers of producing blossoms, etc., through long and continuous cultivation from its suckers?" It appears to be of some significance that the favourable morphological characteristics of the rhizome are associated with a lack of flowering and fruit production in this *C. australis* cultivar.

Given the evidence of cultivar selection for *Cordyline australis* in New Zealand, it is possible that *C. fruticosa* could have also undergone selection for rhizome characteristics. However, it is also possible that there was selection for leaf size, particularly given that most East Polynesian modifiers to the word "*ti*" refer to the leaf (*lau*, *rau*, *'au*, *la*) and not the rhizome. Lastly, it is possible that asexuality confers greater ecological tolerance and that sterile plants persist simply because they propagate more easily. Comparisons between sterile and fertile green *ti* plants with regards to morphological features particularly of their leaves and rhizomes would help to shed light on the significance of sterility of East Polynesian *ti* plants reported in this study.

*   *   *

These results are a first step toward characterising the geographic extent of pollen sterility in Polynesian green *ti* plants and understanding the biological processes that result in their pollen sterility and seedlessness. The almost uniform pollen sterility in East Polynesian green *ti* corresponds with archaeological and ethnographic evidence of a cultural divide at the split between West and East Polynesia, a pattern that is concordant with pollen sterility and seedlessness in East Polynesian breadfruit. Although the basis for pollen sterility is unknown, the present findings suggest that *ti* plants with sterile pollen have not undergone a change in chromosome number. Pollen sterility and seedlessness in East Polynesian green *ti* may suggest human selection for morphological features, such as rhizome characteristics, that may be associated with sterility.

ACKNOWLEDGEMENTS

NOTES

1. *C. terminalis* and *C. fruticosa* are botanical synonyms. The specific epithet was changed by R. Fosberg (1985).

APPENDIX (starts overleaf)

Appendix 1

Locality	Herbarium	Herbarium number	Author (collection number)	Collection date	Viable pollen
Austral Islands-Raivavae, Pic Rouge, northwest side, woods.	BISH	112685	St. John, H., Fosberg, F. R. (15950)	5-Aug-34	0.0%
Austral Islands-Raivavae, south side of pass, south of Raiurua.	BISH	112684	St. John, H.., Fosberg, F. R. (15815)	3-Aug-34	4.5%
Austral Islands-Rapa, Maungaeae, east of Mangaoa Peak.	BISH	112704	St. John, H., Maireau, J. (15357)	4-Jul-34	0.0%
Austral Islands-Rapa, Morangala.	BISH	112716	Stokes, A. M. (85)	7-Jul-21	0.0%
Austral Islands-Stream near Mutuaura.	BISH	112687	Fosberg, F. R. (12052)	5-Sep-34	0.5%
Austral Islands-Tubuai, Taitaa. N. E. slope.	BISH	112681	St. John, H. (16341)	16-Aug-34	0.0%
Cook Islands-Rarotonga, Avatiu.	BISH	112712	Wilder, G. P. (916)	3-Aug-29	0.0%
Hawaiʻi-Oahu, Honolulu.	UC	964089	Bryan, E. H., Jr. (1035)	27-Feb-36	4.5%
Hawaiʻi-Hawaiʻi, Puna District. Ahupuaʻa of Halepuaʻa.	BISH	656031/667211	Yoshida, L. (79.073)	8-Mar-79	0.0%
Hawaiʻi-Kauaʻi, Allerton Garden, Kalaheo.	BISH†		Hinkle, A. E. (151)	18-Jan-03	1.5%
Hawaiʻi-Kauaʻi, cliff above highway 560 West.	BISH†		Hinkle, A. E. (157)	19-Jan-03	1.5%
Hawaiʻi-Kauaʻi, highway 560 at milepost 5.	BISH†		Hinkle, A. E. (158)	19-Jan-03	3.0%
Hawaiʻi-Kauaʻi, highway 560W, beyond mile 5.	BISH†		Hinkle, A. E. (159)	19-Jan-03	0.0%
Hawaiʻi-Kauaʻi, Kalaheo, Allerton Garden.	BISH†		Hinkle, A. E. (162)	20-Jan-03	4.0%
Hawaiʻi-Kauaʻi, Kalaheo, Allerton Garden.	BISH†		Hinkle, A. E. (163)	20-Jan-03	1.5%
Hawaiʻi-Kauaʻi, Kalaheo, Allerton Garden.	BISH†		Hinkle, A. E. (164)	20-Jan-03	0.0%
Hawaiʻi-Kauaʻi, Limahuli Garden.	BISH†		Hinkle, A. E. (160)	19-Jan-03	1.0%
Hawaiʻi-Kauaʻi, Limahuli Garden.	BISH†		Hinkle, A. E. (161)	19-Jan-03	6.0%
Hawaiʻi-Kauaʻi, private garden at 3927 Olano Rd, Kaloa.	BISH†		Hinkle, A. E. (150)	18-Jan-03	0.5%

Location	Herbarium	Collection no.	Collector	Date	%
Hawai'i-Kaua'i, private garden at Kaloa and Aloha Rd, Kaloa.	BISH†		Hinkle, A. E. (149)	18-Jan-03	1.0%
Hawai'i-Kauai, north side of Haupu.	BISH	121196	MacDaniels, L. H. (714)	16-Feb-27	0.0%
Hawai'i-Lanai, Koele.	BISH	121221	Munro, G. C. (248)	1915	0.0%
Hawai'i-Lanai, Koele.	BISH	121200, 121201	Munro, G. C. (577)	28-Feb-30	0.0%
Hawai'i-Maui.	BISH	121227	Munro, G. C.	n/a	0.0%
Hawai'i-Molokai, w. ridge of Hanomuni (?)*.	BISH	413372	St. John, H. (25,184)	23-Dec-53	0.0%
Hawai'i-Oahu, Hillebrand's Glen.	MO	786772	Forbes, C. N.	28-Dec-09	0.0%
Hawai'i-Oahu, Honolulu, cultivated from wild state.	BISH	121230	Bryan, E. H. (1035)	27-Feb-36	0.0%
Hawai'i-Oahu, Honolulu, Nuuanu Valley.	BISH	121212	MacDaniels, L. H. (169)	Jan-27	0.0%
Hawai'i-Oahu, Honolulu, private garden of Otto Degener.	CANB	297626	Degener, O, Degener, I. (35,039)	Jan, 1980	0.0%
Hawai'i-Oahu, Honouliuli, Waianae Mts, east of Palikea.	UC	1729870	Bean, R. S. et al (441)	23-Feb-30	1.0%
Hawai'i-Oahu, Lyon Arboretum, Middle Lawn (unaccessioned).	BISH	56807/771071	Nagata, K. (530)	6-Jan-69	0.0%
Hawai'i-Oahu, Makua, Keaau Makua Forest Reserve.	BISH	121229	Davis, H.	25-Nov-32	0.0%
Hawai'i-Oahu, Manoa Cliffs trail.	BISH	504184	Takeuchi, W., Pyle, L. (1932)	19-Jan-85	0.0%
Hawai'i-Oahu, Moanahua (?) Valley	BISH	121219	Bryan, W. A.	13 Dec 1903	0.0%
Hawai'i-Oahu, Palolo Valley.	MO	1086350	Degener, O. (9066)	12-Feb-28	0.0%
Hawai'i-Oahu, Punaluu.	BISH	121210/121209	St. John, H. (10082)	30-Nov-29	0.0%
Hawai'i-Oahu, right fork of Wailupe Valley.	BISH	121224	Garber, D. W., Forbes, C. M. (189)	12-Jan-20	0.0%

continued next page

Locality	Herbarium	Herbarium number	Author (collection number)	Collection date	Viable pollen
Hawai'i-Oahu, southeast slope of Kaola.	CANB	33918	Degener, O., Park, Takamoto (10,469)	2 Feb 193?	2.0%
Hawai'i-Oahu, Waikane Ditch Trail.	BISH	468053/468050	Takeuchi, W., Imada, Tate (1882)	17-Dec-84	0.5%
Hawai'i-Oahu, Waimanalo.	BISH	497198	Char, W. (172)	15-Feb-82	0.5%
Hawai'i-Oahu.	BISH	121217	Rock, J. F.	n/a	2.5%
Henderson Island-Northwest end, cliffs above landing.	BISH	112706	Fosberg, F. R. (11351)	21-Jun-34	0.0%
Kermadec Islands-Raoul Island. Road from Matirohia to Fishing Rock.	AK	227727	Cooper, R.	1-Jun-56	4.5%
Marquesas-Fatu Hiva, Upper Omoa Valley in ancient native plantations.	BISH	112732-5	Brown, F. B. H. (883)	20-Jun-22	0.0%
Marquesas-Nuku Hiva, Taipivai, low elev.	BISH	112695-9	Brown, F. B. H., E. D. W. (1126)	27-Jun-22	2.0%
Marquesas-Nuku Hiva, Taipivai.	BISH	112725-9	Brown, F. B. H. (1125)	27-Jun-22	0.0%
Pitcairn Island-Flatlands.	BISH	112707	Fosberg, F. R., Clark, R. (11240)	13-Jun-34	0.0%
Society Islands-Mo'orea, Pao Pao Valley, near trail to Trois Pinus.	BISH†		Hinkle, A. E. (269)	9-Jul-03	2.5%
Society Islands-Mo'orea, Pao Pao Valley, near trail to Trois Pinus.	BISH†		Hinkle, A. E. (271)	9-Jul-03	4.0%
Society Islands-Mo'orea, Faatoai Valley.	UC	1362515	Smith, H. M. (25)	25-Jul-67	0.0%
Society Islands-Mo'orea, Faatoai Valley.	MO	1973841	Smith, H. M. (129)	17-Jun-67	21.0%
Society Islands-Raiatea, Tetro Islet.	BISH	112693	St. John, H., Wight, S. G. (17219)	4-Oct-34	0.0%

Location	Herbarium	Number	Collector	Date	%
Society Islands-Raiatea, third valley south of Faaroa Bay.	BISH	13810	Moore, J. W. (288)	11-Nov-26	3.0%
Society Islands-Taha'a, Mt. Purauti, e. side.	BISH	112692	St. John, H. (17339)	10-Oct-34	3.0%
Society Islands-Tahiti, Mt. Aorai, Orange Ravine.	UC	1388561	Quayle, E. H. (104)	5-Oct-21	2.0%
Society Islands-Tahiti, Paea, Papehue.	MO	3271180	Tilden, J. E. (364)	Jun-10	0.5%
Society Islands-Tahiti, Teahupoo, Ronai (?).	BISH	18028	Grant, M. L. (3898)	2-Jul-30	19.0%
Fiji-Kambara.	BISH	112808	Smith, A. C. (1273)	27-May-34	97.0%
Fiji-Kandavu. Mount Mauke Levu.	BISH	112814	Smith, A. C. (222)	23-Oct-33	98.0%
Fiji-Matuku.	BISH	112804	Bryan, E. H. (255)	4-Jul-24	98.0%
Fiji-Namosi, Nabukavesi.	BISH	34070	Koroiveibau, D. (11591)	16-Jan-59	4.5%
Fiji-Ovalau.	UC	948877	Bryan, E. H. Jr. (607)	15-Oct-24	0.0%
Fiji-Viti Levu, Ra, Vicinity of Rewasa, near Vaileka.	BISH	112809	Degener, O. (15,400)	May-41	21.0%
Fiji-Viti Levu, Serua, between Ngaloa and Wainiyambia.	BISH	112791	Smith, A. C. (9663)	Dec-53	0.0%
Fiji-Viti Levu, Tailevu. East of Wainimbuka River, near Ndakuivuna.	BISH	112795	Smith, A. C. (7047)	15-Apr-53	97.0%
Fiji-Viti Levu, southeast slopes of Korolala (?) mountain.	BISH	112793	Gillespie, J. W. (2296)	15-Aug-27	99.0%
Niue-1 mile south of Alofi village.	BISH	112775	Yuncker, T. G. (9615)	12-Jan-40	49.5%
Niue-Alofi village.	UC	843801	Yuncker, T. G. (10043)	5-Feb-40	89.5%
Samoa-Savai'i, Laleaula.	BISH	112762	Ex Museo botanico Berolinensi	13-Apr-05	96.0%
Samoa-Savai'i, Vaipoali.	MO	1621530	Ex Museo botanico Berolinensi	17-Apr-05	33.5%

Locality	Herbarium	Herbarium number	Author (collection number)	Collection date	Viable pollen
Samoa-Tau, in thicket along trail to Fitiuta.	BISH	112748	Yuncker, T. G. (9047)	26-Sep-39	86.0%
Samoa-Trail down to Vatia, Tutuila Island.	UC	215812	Setchell, W. A. (332)	11-Jul-20	93.5%
Samoa-Tutuila, Tafuna, rocky soil.	BISH	112754	Wisner, A. W. (55)	20-Feb-59	94.5%
Samoa-Tutuila, undergrowth in moist forest.	BISH	112761	Brown, E. H. (74)	12-Apr-24	88.0%
Samoa-Tutuila.	BISH	112763	Garber, D. W. (808)	14-Dec-24	46.0%
Samoa-Upolu, Aleisa, Potoga Plantation.	UC	1550121	Cox, P. A. (967)	17-Jun-86	0.0%
Samoa-Upolu, forest above Malololei.	BISH	112751	Christopherson, E. (252)	15-Aug-29	68.5%
Samoa-Upolu, Lefaga, Falaseʻela, very steep rocky coast.	BISH	28847	Bristol, M. L. (2320)	11-Sep-68	95.0%
Samoa-Upolu, Lefaga, Faleseʻela.	BISH	28508	Bristol, M. L. (1976)	25-Mar-68	74.0%
Samoa-Upolu, Mafafa Ridge, growing on side of road.	BISH	439411, 439412	Cox, P. A. (64)	29-Nov-78	93.0%
Samoa-Upolu, ridge between Mt. Fia Moe and Lake Lanotoo.	BISH	609259	Cox, P. A. (978)	19-Jun-87	97.5%
Tonga-Eua, between Pangai and Fuai.	BISH	112769	Yuncker, T. G. (15, 483)	25-Mar-53	97.5%
Tonga-Tofua Island	CANB	473171	Johnson, V. S. (17)	Jan-67	13.0%
Tonga-Tongatapu Island, near Haʻamonga,	UC	297467	Setchell, W. A., Parks, H. E. (15341)	Summer 1926	92.0%
Tonga-Tongatapu, Vahe Hahake.	UC	296902	Setchell, W. A., Parks, H. E. (15526)	Summer 1926	91.5%

* Some specimens have old and/or handwritten labels that were difficult to read.
BISH   Herbarium of the Bernice P. Bishop Museum
BISH†   voucher specimens were deposited in September 2003
UC   University Herbarium, University of California, Berkeley
CANB   Herbarium Australiense, C.S.I.R.O., Canberra, A.C.T.
MO   Missouri Botanical Garden Herbarium
AK   Auckland War Memorial Museum Herbarium

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