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Pollen evidence for plant introductions in a Polynesian tropical island ecosystem, Kingdom of Tonga

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Introduction

The dynamic nature of tropical Pacific ecosystems results from chance migrations and the evolution of founder species, as well as from physical factors such as changes in sea level, ocean currents, tectonic processes and climate (Hope 2001). In addition, this region's vegetation is constantly adjusting through succession to local perturbations like landslides and tropical cyclones. These ecological and physical processes are compounded by continued immigration of new species, competition, extinctions and extirpation of species. For many island ecosystems the most dramatic impact on species composition results from the arrival of humans and their 'co-voyaging' plants and animals (Hope 2001). The degree to which climatic or other natural variations, versus human impacts, have caused recent environmental fluctuations in island ecosystems is an ongoing debate (cf. Nunn 1994; Burney 1997).

In this paper, I examine palynological evidence for plants introduced to several islands in the three main island groups of Tongatapu, Ha'apai and Vava'u in the Kingdom of Tonga. My purpose is to briefly document the history of the tropical rainforests of Tonga as they can be reconstructed from pollen cores, to understand the role that humans played in the development of the Tongan flora, and to discuss plant introductions to the islands by both Polynesian and later European settlers.

Losses or increases in plant species on remote islands are controlled by many factors, including habitat change, natural factors, and loss of dispersers or pollinators. Habitat change in Pacific tropical ecosystems may be due to human factors, including fire, habitat destruction (deforestation) and the introduction of exotic animals or plants (Southern 1986; Hope and Pask 1998; Stevenson 1998; Hope et al. 1999; Haberle et al. 2001; Stevenson et al. 2001; Haberle 2007). Natural factors such as tropical cyclones (Franklin et al. 2004), sea-level variation (Dickinson et al. 1994; Dickinson 2001, 2003), or the effects of ENSO (Haberle and David 2004) cause disturbances to island ecosystems. The loss of animal pollinators or dispersers, triggered by human or natural causes, can further disrupt reproduction and establishment

of plant species (McConkey and Drake 2006, 2007; Steadman 2006; Prebble and Dowe 2008). As Hope (2001) points out, tropical Pacific islands support rain-green forests with relatively high numbers of endemic species. Variations in local species diversity and ecological adaptations between island groups confound the task of understanding present vegetation dynamics, and make deciphering palaeoecological interactions a particularly daunting task. Thus, palaeoecological data often are needed to help unravel the history of an island's ecology. Here, I address one of the historical questions regarding Pacific ecosystems asked by Hope (2001:172): Have human populations caused major changes in species composition and ecological processes?

Kingdom of Tonga

The Kingdom of Tonga, lying southwest of Samoa and east of Fiji, is comprised of more than 170 islands and covers a vast area of the south Pacific Ocean from 15° 30' to 22° 20' S latitude, and between 173° 00' and 177° 15' W longitude (Figure 1). Tonga is formed by a north-south alignment of islands that includes the three main uplifted limestone island groups of Vava'u, Ha'apai and Tongatapu. The Tofua Volcanic Arc to the west of these limestone islands is made up of the younger volcanic islands and sea mounts that run from the northernmost island of Niuafo'ou to 'Ata in the south. The highest point in the archipelago is Koa, an extinct volcano with an elevation of 1046 m. Recent eruptions and earthquakes, including an eruption of a submarine volcano on March 19, 2009, southwest of Tongatapu, demonstrate the ongoing volcanic and tectonic activity of the islands.

The Kingdom of Tonga has a mild tropical maritime climate dominated by the south Pacific trades for most of the year. Annual temperature and precipitation average 21°C and 1780 mm on Tongatapu, and 23.5°C and 2340 mm on Vava'u (Thompson 1986). The climate is slightly wetter in the Austral summer than in the somewhat drier and cooler winter. The islands lie in the track of tropical cyclones, being struck by an average of two tropical cyclones per year (Franklin et al. 2004).

Tonga is part of the southwestern Pacific region of the Indo-Malesian floral realm described by van Steenis (1979) in which floral impoverishment increases with distance from tropical Southeast Asia. Tropical shoreline vegetation is typical of many Pacific islands (Whistler 1992a). More species-rich lowland rainforests are found on the larger islands (Tongatapu, 'Eua and Vava'u), with somewhat more depauperate forests in Ha'apai and on the smaller islands. The islands of 'Eua and 'Uta Vava'u contain more diverse forests due to their larger sizes and greater elevational range (more than 300 m) (Figure 2). A range of botanical inventories document the flora of Tonga (Yuncker 1959; Sykes 1977, 1981; Palmer 1988; Stoddart 1992; Whistler 1992a, 1992b; Drake et al. 1996; Mueller-Dombois and Fosberg 1998; Franklin et al. 1999; Park and Whistler 2001; Wiser et al. 2002; Franklin 2003; Franklin et al. 2006). Park and Whistler (2001) estimate Tonga has about 450 indigenous and 240 introduced plant species. Polynesian introductions (about 40 species) to Tonga tend to be trees or herbaceous cultigens that are dispersed by people or native fauna, whereas European introductions (as many as 200 species) are primarily herbaceous species that are dispersed by wind or epizoochorously by humans or their domestic animals (Fall et al. 2007). Nomenclature (including Tongan and English names where known) follows Smith (1979, 1981, 1985, 1988, 1991) and Whistler (1991) (Table 1).

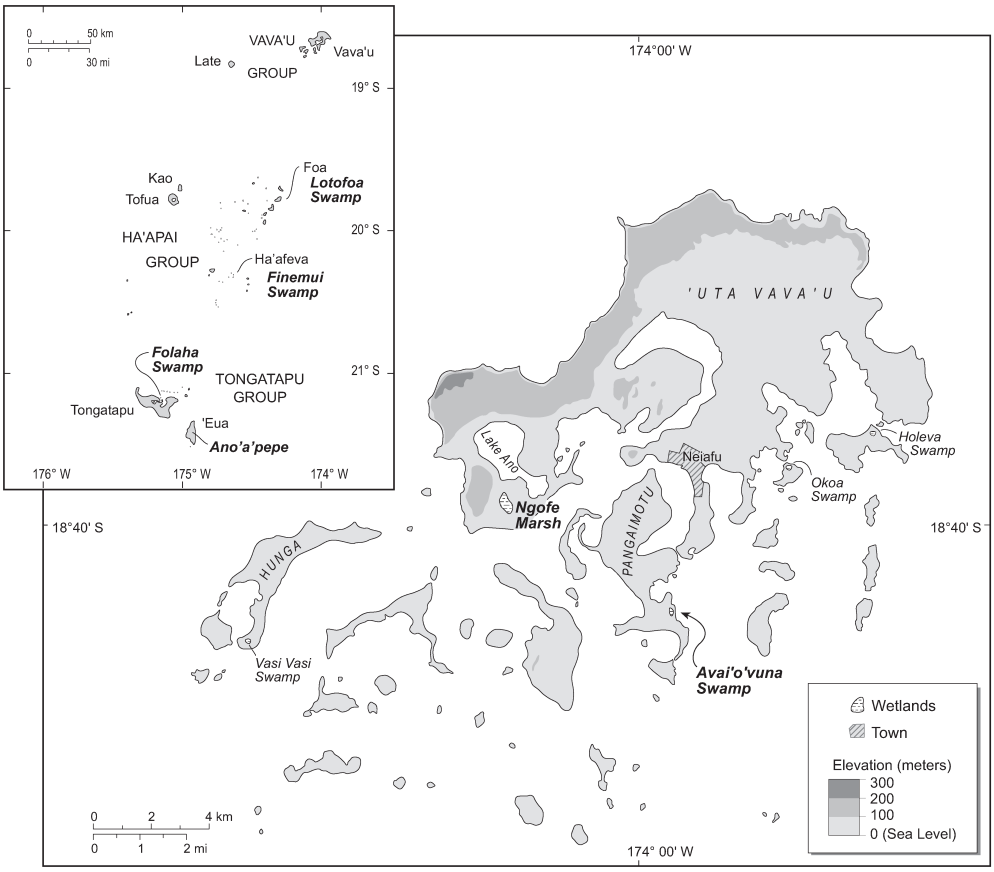

Figure 1. Location of the Kingdom of Tonga. Large map shows the Vava'u island group with the location of the Ngofe Marsh and the Avai'o'vuna Swamp. Inset shows three main island groups (Vava'u, Ha'apai and Tongatapu) where sediment cores were collected. Ha'apai island group: Lotofoa Swamp on Foa, and Finemui Swamp on Ha'afeva. Tongatapu island group: Folaha Swamp in Fanga 'Uta Lagoon on Tongatapu, and Ano'a'pepe on 'Eua (see Table 2 for descriptions of coring localities). Figure by Barbara Trapido-Lurie

Figure 2. Rainforest on 'Uta Vava'u. Photograph by P. Fall

Table 1. Plant taxa mentioned in text including scientific authorities, Tongan and English names (where known). Nomenclature follows Smith (1979; 1981; 1985; 1988; 1991) and Whistler (1991) (Table 1 continues on page 257)

Taxon	**(*Tongan*; English names)**
Acrostichum aureum L.	(*hakato*; golden leatherfern)
Alphitonia zizyphoides (Spreng.) A. Gray	(*toi*)
Alternanthera sessilis R. Br. ex DC	(*loseli*; joyweed)
Barringtonia asiatica (L.) Kurz	(*futu*; fish poison tree)
Bruguiera gymnorrhiza (L.) Lam.	(*tongo lei*)
Calophyllum inophyllum L.	(*feta'u*; beach mahogany; oil nut tree)
Calophyllum neo-ebudicum Guillaumin	(*tamanu*)
Canarium harveyi var. *harveyi* Leenh.	(*'ai*)
Casuarina equisetifolia J.R. & G. Forst.	(*toa*; ironwood; she-oak)
Cocos nucifera L.	(*nui*; coconut)
Colocasia esculenta (L.) Schott.	(*talo*; taro)
Cordyline fruticosa (L.) A. Chev.	(*si*; ti; good luck plant)
Cyperaceae	(sedge family)
Dysoxylum forsteri (Juss.) DC	(*mo'ota*)
Dysoxylum tongense A.C. Smith	(*mo'ota mea*)
Elaeocarpus tonganus Burk.	(*ma'ama'alava*; blue berry tree)
Eleocharis dulcis (Burm. f.) Trin. ex Hensch.	(*kutu*; water chestnut)
Ellatostachys falcata (Seem.) Radlk.	(*ngatata*)
Erianthus	(plume grass)
Erythrina fusca Lour.	(*ngatae fisi*; Fijian coral tree)
Erythrina variegata L.	(*ngatae*; coral tree)
Excoecaria agallocha L.	(*feta'anu*; blind-your-eye mangrove)
Flacourtiaceae	(Flacourtiaceae family)
Freycentia urvilleana Hombron & Jacqinot	(*kahikahi*)
Gardenia augusta (L.) Merr.	(*siale matalateau*; double gardenia)
Gardenia tannaensis Guillaumin	(*siale lotuma*; gardenia)
Gardenia taitensis DC. Prodr.	(Tahitian gardenia)
Garuga floribunda Decne.	(*manaui*)
Glochidion ramiflorum J.R. & G. Forst.	(*manolo*)
Guettarda speciosa L.	(*puopua*; beach gardenia)
Hedycarya dorstenioides A. Gray	
Hernandia nymphaeifolia (Presl) Kub.	(*fotulona*; lantern tree)
Hibiscus tiliaceus L.	(*fau*; beach hibiscus)
Homalanthus nutans Benth. & Hook. f. ex Drake	(*fonua mamala*; bleeding heart tree)
Homalium	(*moto*)
Inocarpus fagifer (Parkinson) Fosb.	(*ifi*; Tahitian chestnut)
Ipomoea batatas L.	(*kumala*; sweet potato)
Leguminosae	(legume family)
Lepironia articulata (Retz.) Domin	(*kutu kofe*; blue rush)
Ludwigia octovalvis (Jacq.) Raven	(*loaana*; water primrose)
Macaranga haveyana (Muell. Arg.) Muell. Arg.	(*loupata*; giant leaf plant)
Mallotus	(kamala tree)
Malvaceae	(mallow family)
Maniltoa grandiflora (A.Gray) Scheff.	(*pekepeka*; dove tree; handkerchief tree)
Melastomataceae	(Melastomataceae family)
Meliaceae	(Meliaceae family)
Mimosa pudica L.	(*mateloi*; sensitive plant)
Miscanthus floridus (Labill.) Warb.	(*kaho tonga*; reed)
Monimiaceae	(Monimiaceae family)
Moraceae	(fig family)
Morinda citrifolia L.	(*nonu*; Indian mulberry)
Narenga	(genus in the grass family)
Neonauclea fosteri (Seem.) Merr.	(*afa*)
Onagraceae	(primrose family)

Taxon	(*Tongan*; English names)
Pandanus tectorius Parkinson	(*fafa*; screw-pine)
Pandanus veitchii Hort.	(*hauai'i*)
Pandanus whitmeeanus Mart.	(*paongo*)
Papillionaceae	(pea family)
Phyllanthus amicorum G.L. Webster	
Pinus caribaea Morelet	(*paini*; Caribbean pine)
Planchonella	(*kalaka*)
Pleiogynium timoriense (DC.) Leehn.	(*tangato* or Burdekin plum)
Poaceae	(grass family)
Podocarpus pallidus N.E. Gray	(*uhiuhi*)
Polygonum dichotomum Bl. Bijar (synonym *Polygonum glabrum*)	(dense-flower knotweed)
Pometia pinnata J.R. & G. Forst.	(*tava*; island lychee)
Psidium guajava L.	(*kuava*; guava)
Rhizophora mangle	(*tongo*; mangrove)
Rhus taitensis Guillemin	(*tavahi*; island sumac)
Saccharum officinarum L.	(*to*; sugarcane)
Saccharum spontaneum L.	(wild sugarcane)
Sapotaceae	(sapote family)
Schizostachyum glaucifolium (Rupr.) Munro	(*kofe*; bamboo; Polynesian 'ohe)
Sclerostachys	(genus in the grass family)
Solanum amicorum Benth.	(*polo tonga*)
Solanum nigrum L.	
Stachytarpeta urticifolia (Salisb.) Sims	(*hiku 'i kuma*; blue rat's-tail)
Stenochlaena palustris (Burm.) Beddome	(*pasivaka*; climbing fern)
Syzygium	(*fekika*)
Thespesia populnea (L.) Solander ex Correa	(*milo*; portia tree)
Trema cannabina Lour.	(*mangele*; poison bush)
Tricale	(grass hybrid of *Triticum* and *Secale*)
Triumfetta rhomboidea Jacq.	(*mo'osipo*; burr bush)
Urticaceae	(nettle family)

Polynesian settlers reached Tonga by 2850 yr BP (Burley 1998). Lapita culture has been documented on Tongatapu (Poulsen 1987; Burley and Dickinson 2001), Ha'apai (Burley 1994; Burley et al. 1999) and Vava'u by about 2700-2800 yr BP (Burley and Connaughton 2007). European contact with Tonga was initiated by Dutch sailors in 1616 and by Abel Tasman in 1643 (Whistler 1991). The next European contact was made by James Cook in 1773, 1774 and 1777; missionary settlement soon followed in the late 1700s. Only 37 of the islands are inhabited today, with the majority of the Tongan people living on the main islands of Tongatapu, Ha'apai, or 'Uta Vava'u, the largest island of Vava'u.

Palynological records from Tonga

Sediment cores have been retrieved from a variety of small wetlands found throughout the Kingdom of Tonga (Table 2). Sediments were collected by the author on several islands in the Vava'u Island Group in 1997 and 1998, including cores from the islands of Pangaimotu (Avai'o'vuna Swamp) and 'Uta Vava'u (Ngofe Marsh) (Fall 2005). In the Ha'apai Islands, Flenley and others (1999) collected cores from two small basins on the islands of Ha'afeva (Finemui Swamp) and Foa (Lotofoa Swamp). In the Tongatapu island group, a sediment core was collected from the island of 'Eua in 1998 from a small lake in the highlands, Ano'a'pepe (Lake of the Butterflies) (Fall unpublished). In addition, Ellison (1989) reported on a series of sediment cores from a mangrove swamp on the main island of Tongatapu.

The evidence for indigenous or pre-Polynesian vegetation, Polynesian plant introductions and later European-introduced plants from these sediment records will be used to outline floral changes in Tonga over about the past 7000 years. Particular attention is directed to Polynesian and European plant introductions, as documented by pollen records in Tonga, and to plant taxa showing substantial declines or increases in abundance associated with Lapita colonisation through later European settlement.

Table 2. Sediment cores collected for pollen analyses in the Kingdom of Tonga

Island Group							
Core locality	**Island**	**Latitude**	**Longitude**	**Elevation (m)**	**Approximate age range**	**Length of core (m)**	**Reference**
Vegetation surrounding coring locality							
Vava'u Island Group							
Ngofe Marsh	'Uta Vava'u	18°39'53" S	174°02'40" W	20	6000-0 yr BP	3.4	Fall unpublished
Cyperaceae (*Eleocharis dulcis and Lepironia articulata*) marsh surrounded by Poaceae, *Stachytarpeta urticifolia*, *Ludwigia octovalvis*, *Erythrina variegata*							
Avai'o'vuna Swamp	Pangaimotu	18°41'44" S	173°59'02" W	1.5	4500-0 yr BP	1.5	Fall 2005
Coastal forest of *Pandanus tectorius*, *Cocos nucifera* and *Hernandia nymphaeifolia*, *Cocos* plantation, and *Colocasia* swamp							
Ha'apai Island Group							
Lotofoa Swamp	Foa	19°44'48" S	174°18'27" W	3	6700-0 yr BP	3.13	Flenley et al. 1999
Ludwigia octovalvis, Cyperaceae and Poaceae swamp surrounded by *Erythrina variegata*							
Finemui Swamp	Ha'afeva	19°56'45" S	174°42'35" W	6	5800-0 yr BP	3.33	Flenley et al. 1999
Polygonum cf. *glabrum* swamp with *Ludwigia octovalvis*, Poaceae, Cyperaceae, Cocos *nucifera*							
Tongatapu Island Group							
Folaha Swamp	Tongatapu	21°11' S	175°11' W	0.4-0.9	6900-0 yr BP	3.2	Ellison 1989
Rhizophora mangrove at lagoon edge with *Bruguiera*, *Acrostichum aureum*, *Excoecaria*, *Hibiscus tiliaceus* and *Stenochlaena palustris*							
Ano'a'pepe	'Eua	21°24'03" S	174°55'05" W	250	Undated	0.6	Fall unpublished
Small lake (1.5 m deep) in the upland rain forest with Poaceae and Cyperaceae, surrounded by *Calophyllum neo-ebudicum*, *Dysoxylum tongense* and *Ellatostachys falcata*							

Vava'u Island Group

Vava'u is the northernmost of the three limestone island groups that make up the Kingdom of Tonga. The main island of 'Uta Vava'u forms the northern edge of an uplifted limestone platform, including several embayments and the brackish water Lake Ano. The limestone platform of Vava'u slopes southward, where its subsidence has produced numerous smaller islands (Dickinson and Burley 2007). Several swamps were examined in Vava'u, including the two discussed here – Ngofe Marsh and Avai'o'vuna Swamp – for their potential to provide palaeoecological data on pre-settlement forests and subsequent vegetation change associated with settlement by Lapita and later cultures (Fall 2005). Avai'o'vuna Swamp is a very small basin about 5 m x 10m in size that lies about 1.5 m above mean sea level on the eastern shore of Pangaimotu Island. The swamp is a sedge wetland surrounded by coastal forest trees, *Pandanus tectorius, Hernandia nymphaeifolia* and *Cocos nucifera*, set among more extensive

Cocos plantations on the island. *Colocasia esculenta* and *Ipomoea batatas* are cultivated in wetter soils. Ngofe Marsh is a sedge, grass and reed marsh on the eastern flank of Mount Mo'ungalafa on 'Uta Vava'u, separated from Lake Ano by a low rise. Vegetation on Ngofe Marsh is dominated by *Eleocharis dulcis* and *Lepironia articulata*, with grasses, sedges, *Stachtarpeta urticifolia*, *Polygonum dichotomum*, and the swamp tree *Erythrina variegata* at the edge of the marsh (Figure 3).

Figure 3. Ngofe Marsh on 'Uta Vava'u, Vava'u island group. Photograph by P. Fall

The coastal wetland Avai'o'vuna Swamp produced a 2 m sediment record, documenting sea-level variation, fire history and vegetation change. During a marine high-stand from 4500 to 2600 yr BP, the swamp was dominated by mangroves, including *Rhizophora mangle* and *Excoecaria*, the coastal trees *Barringtonia, Pandanus tectorius* and *Cocos nucifera*, and Malvaceae (perhaps *Thespesia populnea*), and was surrounded by lowland rainforest with *Hedycarya*, *Calophyllum* (presumably *C. inophyllum*), *Rhus*, Papillionaceae and *Alphitonia* (Fall 2005). After about 2600 yr BP, sea level dropped and fire, as attested by the appearance of microscopic charcoal in the sediments, became common. The recent vegetation around the swamp is dominated by mangroves (*Excoecaria*), coastal forest (*Pandanus tectorius* and *Cocos nucifera*), successional forest (*Macaranga*), and open vegetation of sedges, grasses and ferns. Past rainforest dynamics have included shifts to *Homalanthus* and *Macaranga* as secondary taxa, with declines in pollen from rainforest trees, including *Hedycarya, Calophyllum*, *Elaeocarpus,* Monimiaceae*, Neonauclea, Pleiogynium* and Papillionaceae (Fall 2005).

Plant taxa more common at Avai'o'vuna Swamp before Polynesian colonisation included *Hedycarya, Neonauclea, Guettarda* and *Solanum* (possibly *S. amicorum*) (Fall 2005). Following Polynesian colonisation, rainforest trees, particularly *Hedycarya*, *Calophyllum, Elaeocarpus* and *Rhus,* declined in abundance. Plants that increased and/or were possibly introduced by Polynesian settlers include cultivated grass (Poaceae >40-50 µm), *Casuarina, Erythrina* and *Canarium*.

Ngofe Marsh produced a record indicating that the basin contained a lake between about 7000 and 3000 yr BP. Associated rainforest taxa included *Elaeocarpus, Dysoxylum, Ellatostachys,* Flacourtiaceae*, Garuga, Hedycarya, Maniltoa*, Melastomataceae and Papillionaceae. Microscopic

charcoal first appears in sediments from about 2800 yr BP, coincident with the arrival of Lapita people on Vava'u (Burley and Connaughton 2007). Along with the abundant charcoal, the infilling of the lake and the spread of plants on to the marsh is attested by dramatic increases in Poaceae and Cyperaceae pollen and fern spores after 2800 yr BP. The lowland rainforest surrounding Ngofe Marsh became less diverse after this time, with significant losses in most rainforest trees, accompanied by the notable expansion of *Pandanus tectorius* and *Macaranga*. Plant taxa with truncated records at Ngofe Marsh following Polynesian colonisation include *Dysoxylum, Garuga, Homalium, Maniltoa, Pleiogynium, Syzygium*, *Freycentia* and one type of *Pandanus*. Cultivated grass (Poaceae >40-50 µm; grains often have a double pore, or rarely a triple pore), *Colocasia, Pometia* and *Erythrina* are likely Polynesian introductions.

Ha'apai Island Group

The middle island group of Ha'apai is made up of a multitude of small low limestone islands and atolls to the east and the two more recent, larger and higher volcanic islands of Kao and Tofua at the western edge. Flenley and others (1999) examined two small swamps in Ha'apai on the islands of Ha'afeva and Foa for their potential to provide palaeoecological information applicable to Lapita and later archaeological sites investigated by Burley and colleagues (Burley 1994; Burley et al. 1999, 2001). The two swamps examined, Finemui (on Ha'afeva) and Lotofoa (on Foa), were most likely former lagoons within the atolls (Flenley et al. 1999). Both basins are surrounded by herbaceous and shrub vegetation. Finemui Swamp is dominated by *Polygonum* cf. *glabrum*, with other herbaceous plants, including *Ludwigia octovalvis* and plants in the Poaceae and Cyperaceae families. *Cocos nucifera, Inocarpus fagifer, Morinda citrifolia* and *Erythrina variegata* are marginal trees. Lotofoa Swamp is characterised by *Ludwigia octovalvis*, plants in the Cyperaceae, Poaceae and Leguminosae families, as well as ferns, *Erythrina* and other trees.

Basal organics began to accumulate in Finemui Swamp about 5770 yr BP (Flenley et al. 1999). The indigenous or pre-settlement vegetation at Finemui Swamp is interpreted as a brackish or freshwater wetland, which was replaced by a fern and *Polygonum* swamp, with the coastal trees *Hibiscus* and *Trema* (Flenley et al. 1999). Pollen from *Elaeocarpus, Trema,* Urticaceae/Moraceae and Meliaceae/Sapotaceae is indicative of the surrounding rainforest trees. The record also demonstrates a slight sea-level rise before disturbed sediments that are hypothesised to relate to the Lapita phase. Flenley and others (1999) also associate Lapita occupation with an expansion of *Glochidion* pollen (interpreted as a possible opening in the forest canopy) and increases in *Pandanus*, *Casuarina* and *Cocos nucifera* pollen, all of which could have been encouraged by planting. Peaks in Cyperaceae and Poaceae pollen and monolete fern spores seen at Finemui Swamp also are associated commonly with forest disturbance on other Polynesian islands (Parkes et al. 1992; Kirch et al. 1995; Kirch 1996; Parkes 1997; Flenley et al. 1999). The modern environment of Finemui Swamp is dominated by *Polygonum*, Cyperaceae and ferns, with *Cocos nucifera* and *Trema* as the most common dryland trees, accompanied by *Pandanus* and *Gardenia*, Elaeocarpaceae and *Macaranga*. Herbaceous plants include Poaceae and weedy taxa. Probable recently introduced species include *Gardenia, Stachytarpheta, Ipomoea* (*Ipomoea* cf. *batatas*) and *Solanum* (*S*. cf. *nigrum*) (Flenley et al. 1999).

Similarly, Flenley and others (1999) interpret the vegetation at Lotofoa Swamp before Polynesian settlement as a fern wetland surrounded by a coastal forest of *Pandanus* and *Hibiscus*, as well as *Podocarpus, Mallotus* and *Planchonella* trees. Lotofoa Swamp became an *Excoecaria* swamp during Polynesian settlement, and provides evidence of *Cocos* pollen. The modern vegetation at the swamp is represented by Cyperaceae and Poaceae pollen and fern spores. Dryland vegetation surrounding Lotofoa Swamp has been deforested, perhaps followed by the planting of *Cocos, Gardenia, Trema* and *Triumfetta*. Probable Polynesian introductions to

Ha'apai include *Ipomoea* cf. *batatas, Cocos* and *Casuarina*, accompanied by an expansion of *Pandanus* (Flenley et al. 1999).

Tongatapu Island Group

Ano'a'pepe, on the island of 'Eua, is a small lake about 1.5 m deep surrounded by plants in the Cyperaceae and Poaceae families. The forest surrounding the lake is dominated by *Calophyllum neo-ebudicum, Dysoxylum tongense* and *Ellatostachys falcata,* as is typical of upland rainforests on 'Eua (Drake et al. 1996). Although the rainforest immediately surrounding the lake is undisturbed, plantations of *Pinus caribaea* grow nearby. Approximately 1 m of organic gyttja was recovered from Ano'a'pepe in 1998; pollen preservation was good in the uppermost 50 cm of the core (Fall unpublished). The presence of microscopic charcoal, the abundance of Poaceae (including grains >40-50 µm; see discussion below), Cyperaceae pollen and fern spores, and the presence of pollen from introduced trees (e.g. *Pinus* and *Mimosa* in the upper few centimetres) suggest a relatively recent age (at least post-Polynesian) for this core.

Ellison (1989) collected a series of sediment cores from Fanga 'Uta Lagoon on Tongatapu to investigate sea-level change. A basal age of about 6900 yr BP demonstrates that the lagoon was a brackish marsh dominated by Cyperaceae and *Acrostichum aureum,* which lay about 1 m above modern mean sea level. This interpretation agrees with Dickinson and Burley's (2007:247) inference of a marine high-stand that peaked about 5000 yr BP, and a subsequent draw-down of sea level beginning about 3000 yr BP. A late Holocene sea-level drop is represented by a mangrove forest designated by pollen from *Hibiscus*, *Bruguiera*, *Excoecaria* and *Stenochlaena palustris* spores. The uppermost peat samples contain pollen from the introduced tree *Psidium guajava*.

Introduced plants

A number of tree, crop and ornamental plants was introduced to Tonga and cultivated by its Polynesian and European inhabitants. Analysis of pollen from the small marshes and swamps on Tonga, described above, provides a unique window into the human ecology of these islands. Based on ethnographic information and early botanical collections, Whistler (1991) provides a valuable compendium of the plants of Tonga, their names and their uses. Drawing on Whistler's (1991) observations of cultivated or aboriginal introductions, I discuss useful tree and herbaceous cultigens for which we have a palynological record, as well as inadvertent introductions. Interestingly, many taxa known to be European introductions do not appear in pollen records, perhaps reflecting a combination of palynological invisibility and restricted distributions. Although a wide range of taxa introduced by Polynesians is signalled palynologically, other Polynesian introductions, such as *Colocasia escuelenta* and *Ipomoea batatas*, may be invisible for the same reasons (Haberle 1995; Haberle and Atkins 2005). The subsequent discussions note the species most likely responsible for each pollen type represented in the subfossil record (pollen identification often is limited to genus, type or family), listed by scientific name with authority, followed by the Tongan and English names (in parentheses), as available (after Whistler 1991).

Pollen evidence for Polynesian introductions

Canarium harveyi var. *harveyi* is indigenous to Tonga, where it is found today mostly as a cultivated tree in villages. Its edible almond-like seeds, timber and sap are used by Tongans (Whistler 1991). *Canarium* pollen appeared in small amounts in both Ngofe Marsh and Avai'o'vuna Swamp before Lapita settlement, but is more abundant and consistent in the

Table 3. Plant taxa that first appear (FAD) in sediment cores from Tonga or show an increase in pollen in the uppermost sediments after Lapita (Polynesian) colonisation

Botanical species	Island	Core	Evidence	Reference
Canarium harveyi Leenh.	Pangaimotu, Vava'u	Avai'o'vuna Swamp	Pollen increase c. 2600 BP	Fall 2005
	'Uta Vava'u, Vava'u	Ngofe Marsh	Pollen increase c. 2600 BP	Fall unpublished
	'Eua	Ano'a'pepe	FAD pollen (recent)	Fall unpublished
Casuarina equisetifolia L.	Pangaimotu, Vava'u	Avai'o'vuna Swamp	FAD pollen c. 2600 BP	Fall 2005
	Ha'afeva, Ha'apai	Finemui Swamp	Pollen increase c. 2000 BP	Flenley *et al.* 1999
	'Eua	Ano'a'pepe	FAD pollen (recent)	Fall unpublished
Cocos nucifera L.	Pangaimotu, Vava'u	Avai'o'vuna Swamp	Pollen increase c. 1000 BP	Fall 2005
	'Uta Vava'u, Vava'u	Ngofe Marsh	Pollen increase after 4000 BP	Fall unpublished
	Ha'afeva, Ha'apai	Finemui Swamp	Pollen increase after 1800 BP	Flenley *et al.* 1999
	Foa, Ha'apai	Lotofoa Swamp	FAD pollen c. 2900 BP	Flenley *et al.* 1999
Colocasia esculenta (L.) Schott.	Pangaimotu, Vava'u	Avai'o'vuna Swamp	FAD pollen c. 2600 BP	Fall 2005
	'Uta Vava'u, Vava'u	Ngofe Marsh	FAD pollen c. 2000 BP	Fall unpublished
	'Eua	Ano'a'pepe	FAD pollen (unknown age)	Fall unpublished
Cordyline fruticosa (L.) A. Chev.	Pangaimotu, Vava'u	Avai'o'vuna Swamp	FAD pollen c. 2600 BP	Fall 2005
	'Uta Vava'u, Vava'u	Ngofe Marsh	FAD pollen c. 2200 BP	Fall unpublished
Erythrina variegata L.	Pangaimotu, Vava'u	Avai'o'vuna Swamp	FAD pollen c. 1500 BP	Fall 2005
	'Uta Vava'u, Vava'u	Ngofe Marsh	FAD pollen c. 2400 BP	Fall unpublished
Gardenia tannaensis Guillaumin	Pangaimotu, Vava'u	Avai'o'vuna Swamp	FAD pollen c. 2200 BP	Fall 2005
	Ha'afeva, Ha'apai	Finemui Swamp	Pollen increase c. 2200 BP	Flenley *et al.* 1999
Ludwigia octovalvis (Jacq.) Raven	Foa, Ha'apai	Lotofoa Swamp	FAD pollen c. 2500 BP	Flenley *et al.* 1999
	'Uta Vava'u, Vava'u	Ngofe Marsh	Single Onagraceae grain c. 2000 BP	Fall unpublished
Pandanas tectorius Parkinson	Pangaimotu, Vava'u	Avai'o'vuna Swamp	Pollen increase c. 1500 BP	Fall 2005
	'Uta Vava'u, Vava'u	Ngofe Marsh	Pollen increase c. 2400 BP	Fall unpublished
	Ha'afeva, Ha'apai	Finemui Swamp	Pollen increase c. 2900 BP	Flenley *et al.* 1999
Poaceae (grains >40µm)	Pangaimotu, Vava'u	Avai'o'vuna Swamp	FAD pollen c. 2600 BP	Fall 2005
	'Uta Vava'u, Vava'u	Ngofe Marsh	FAD pollen c. 2800 BP	Fall unpublished
	'Eua	Ano'a'pepe	FAD pollen (unknown age)	Fall unpublished
Poaceae	Foa, Ha'apai	Lotofoa Swamp	Pollen increase c. 3100 BP	Flenley *et al.* 1999
	Ha'afeva, Ha'apai	Finemui Swamp	Pollen increase c. 900 BP	Flenley *et al.* 1999
Polygonum dichotomum Bl. Bijar	Ha'afeva, Ha'apai	Finemui Swamp	Pollen increase c. 1600 BP	Flenley *et al.* 1999
	'Uta Vava'u, Vava'u	Ngofe Marsh	Pollen increase c. 1000 BP	Fall unpublished
Pometia pinnata J.R. & G. Forst.	'Uta Vava'u, Vava'u	Ngofe Marsh	FAD pollen c. 2500 BP	Fall unpublished
Stenochlaena palustris (Burm.) Beddome	Foa, Ha'apai	Lotofoa Swamp	FAD pollen c. 1100 BP	Flenley *et al.* 1999

Note: All ages estimated from sedimentation rates based on radiocarbon ages from each core. Ngofe Marsh and Avai'o'vuna Swamp each have two ^{14}C ages; Finemui and Lotofoa Swamps have one ^{14}C age each.

records following Polynesian settlement. These suggest aboriginal cultivation of this tree, leading to its modern distribution as a cultivated species in villages (Table 3).

Casuarina equisetifolia is suggested to have been either an indigenous tree or an aboriginal introduction to Tonga (Whistler 1991). Haberle (2007) documents the planting of *Casuarina equisetifolia* in New Guinea to aid nitrogen-fixing in the soil, noting that increased *Casuarina* pollen indicates arboriculture. Whistler (1991:125) notes that *Casuarina* often is cultivated in Tonga and that its hard wood is used for posts, tapa mallets, war clubs and other tools. Pollen evidence documents *Casuarina* trees in Tonga before human occupation of the islands, but its abundance and distribution on the islands may have been expanded by Polynesians. Pollen records from Ha'apai (Finemui Swamp) (Flenley et al. 1999) and Vava'u (Ngofe Marsh) (Fall unpublished) suggest that this tree was maintained and probably planted during Lapita occupation. *Casuarina* pollen first appears in Avai'o'vuna Swamp on Pangaimotu Island after Polynesian arrival (Fall 2005). Similarly, *Casuarina* pollen is found in pre-aboriginal sediments on Rapa and Rapanui, then shows a marked increase about 1000 cal. BP (Prebble 2008; Prebble and Wilmshurst 2009).

Cocos nucifera is thought to be an aboriginal introduction to Tonga, where it is cultivated widely in plantations throughout the islands. Coconut provides a liquid that can be substituted for water during periods of drought, meat that can be eaten, and oil that can be made from the nut. Virtually every part of the plant has a use, including its shell, leaves and roots (Whistler 1991:94). While *Cocos nucifera*-type pollen is found in sediments from Tonga prior to colonisation, one record in Ha'apai (Lotofoa Swamp) shows the first *Cocos* pollen coincident with the arrival of Lapita people. Other records from Ha'apai (Finemui Swamp) and Vava'u (Ngofe Marsh and Avai'o'vuna Swamp) document its expansion following Lapita settlement. Similarly, palaeoenvironmental records from Vanuatu (Spriggs 1984), Mo'orea (Parkes 1997) and the Cook Islands (Ellison 1994; Kirch and Ellison 1994) provide evidence for *Cocos nucifera* on Pacific islands prior to human settlement. *Cocos* palms may have been introduced by early Polynesian settlers on the Hawaiian Islands (Athens and Ward 1997) and by European immigrants to French Polynesia (Prebble 2008; Prebble and Wilmshurst 2009).

Colocasia esculenta was brought to Tonga by Polynesian settlers. This starchy cultigen is a staple crop and its many varieties introduced by aboriginal and more recent populations are cultivated widely (Whistler 1991:117). In Tonga, the earliest *Colocasia* pollen is found in Avai'o'vuna Swamp (at about 2600 yr BP), Ngofe Marsh (at about 1800 yr BP), and Ano'a'pepe on the island of 'Eua (in the upper sediments). Although *Colocasia* pollen is not preserved in some sedimentary basins (Haberle 1995), it has been associated with Polynesian settlement and cultivation in other parts of Polynesia, specifically Hawai'i (Athens and Ward 1993, 1997) and French Polynesia (Kennett et al. 2006; Prebble 2008; Prebble and Wilmshurst 2009).

Cordyline fruticosa is an aboriginal introduction to Tonga. The root of *Cordyline fruticosa* was consumed as food in the past; the plant is used today as an ornamental and its leaves are harvested for cooking or medicinal uses (Whistler 1991:111). The first appearance of *Cordyline* pollen at Ngofe Marsh at about 2200 yr BP and at Avai'o'vuna Swamp about 2600 yr BP corroborates the interpretation of *Cordyline fruticosa* as a Polynesian introduction to Vava'u. Prebble (2008) also found *Cordyline* pollen associated with aboriginal colonisation in sedimentary records from subtropical Polynesian islands.

Erythrina variegata, although thought to be an indigenous tree, today is found mostly in cultivation. *Erythrina fusca*, which grows in swamps and marshes on Tonga, may have been introduced to Tonga by Polynesians, perhaps from Fiji, as its Tongan name (*ngatae fisi*, Fijian coral tree) suggests (Whistler 1991:38-39). *Erythrina* trees are commonly found at the edges of wetlands like Ngofe Marsh on Vava'u and at Finemui and Lotofoa swamps on Ha'apai. *Erythrina* pollen appears for the first time in Ngofe Marsh about 2400 yr BP and in Avai'o'vuna Swamp about 1500 yr BP, after Lapita colonisation of Vava'u, supporting

Whistler's suggestion that one of the species of *Erythrina* is a Polynesian introduction, or that *Erythrina* became more prominent in the palynological record.

Gardenia taitensis is an indigenous littoral species in Fiji, which grows on Tonga (Smith 1988). *Gardenia tannaensis* is a tree that is cultivated and naturalised on Niuatoputapu and was probably introduced from Tanna, Vanuatu, where it is indigenous (Whistler 1991:111). *Gardenia augusta* is a European introduction (Whistler 1991:112). *Gardenia* pollen is found in pre-Lapita sediments in both Lotofoa and Finemui swamps (Flenley et al. 1999), strongly supporting Smith's (1988) idea that *Gardenia taitensis* is indigenous to Tonga. *Gardenia* pollen also is present in Lapita and post-Lapita-age sediments at both Finemui and Lotofoa swamps. Increased frequencies of *Gardenia* pollen in Lapita and particularly in post-Lapita sediments at Finemui Swamp (Flenley et al. 1999), and its first appearance in Avai'o'vuna Swamp at about 2200 yr BP (Fall 2005), lend support to the possibility of Polynesian planting or encouragement of *Gardenia* plants, or the increased palynological visibility of *Gardenia* on Tongan Islands.

Ipomoea batatas is an aboriginal introduction to Tonga, commonly found in cultivation today (Whistler 1991). Pollen identified as *Ipomoea* cf. *batatas* is noted in Finemui Swamp at a depth of 0.15-0.24 m (Flenley et al. 1999) and as two grains from Avai'o'vuna Swamp at 0 m and 0.24 m below the surface of the swamp (Fall 2005). This pollen type is very distinctive (Flenley et al. 1999), but normally is not preserved in sediments (Haberle and Atkins 2005). At Avai'o'vuna Swamp the presence of sweet-potato pollen fits the criteria outlined by Haberle and Atkins (2005) for its association with *Casuarina equisetifolia* silviculture, signalled by the first appearance of *Casuarina* pollen in this little swamp.

Ludwigia octovalvis, a pan-tropical species, is a native of tropical America and an introduction to the Pacific islands, where it is common in wetlands and is associated with *Colocasia* cultivation (Whistler 1995:113). *Ludwigia octovalvis* currently dominates the vegetation in some swamps and wetlands in Tonga. Of particular interest here, it grows at the edge of Ngofe Marsh in Vava'u (Fall unpublished) and in both of the swamps investigated by Flenley and colleagues (1999) on Ha'apai, where it dominates the vegetation in Lotofoa Swamp. Although Whistler (1995) suggests that *Ludwigia octovalvis* is a European introduction, the evidence presented below suggests it may have been introduced inadvertently by Polynesians. *Ludwigia* pollen is found associated with *Colocasia* pollen in Polynesian-age deposits in a sediment core from Hawaii (Athens and Ward 1997). *Ludwigia* pollen and seeds document this taxon as an inadvertent Polynesian introduction to Rapa (Prebble 2008). In Tonga, *Ludwigia* pollen first appears in Lapita-age sediments at Lotofoa Swamp (Zone LF 4) (Flenley et al. 1999). At Ngofe Marsh a single Onagraceae (cf. *Ludwigia*) pollen grain is found in association with *Colocasia* pollen in sediments dated to about 2000 yr BP. *Ludwigia octovalvis* is a common weed associated with *Colocasia escuelenta* fields throughout the Pacific (Kirch 1994). The discovery of *Ludwigia* pollen in Lapita-age ponds on Ha'apai and Vava'u suggests that *Ludwigia* was a Polynesian introduction to Tonga.

Pandanus tectorius is an indigenous and cultivated tree in Tonga. Whistler (1991:70-76) describes the many varieties and uses for the indigenous *Pandanus tectorius*, as well as for the Polynesian introduction *Pandanus whitmeeanus* and for *Pandanus veitchii*, which probably was introduced from Hawai'i. *Pandanus tectorius*-type pollen is present in Tonga in sediments deposited before colonisation by Polynesians, as it is on other Polynesian islands (Prebble 2008). However, *Pandaus tectorius*-type pollen is more abundant in Avai'o'vuna Swamp, Ngofe Marsh and Finemui Swamp after Lapita colonisation, supporting the suggestion that people may have planted *Pandanus tectorius* and encouraged its growth throughout the Tongan Islands.

Phyllanthus amicorum, although not mentioned in Whistler (1991), is an endemic tree or small shrub that grows today on 'Eua (Drake et al. 1996) and Vava'u (Steadman et al. 1999). While *Phyllanthus amicorum* or another species of *Phyllanthus* may have grown in

Tonga before human colonisation, *Phyllanthus*-type pollen makes its initial appearance in Avai'o'vuna Swamp in the upper sediments deposited in the past 300 years (Fall 2005). Poaceae pollen increases in all Tongan sediment cores coincident with Lapita settlement and burning. *Saccharum officinarum*, *Schizostachyum glaucifolium* and *Miscanthus floridus* are recognised as Polynesian introductions to Tonga (Whistler 1991). *Miscanthus floridus* was used for arrow shafts, pipes or construction (Whistler 1991:50). The two cane species *Saccharum officinarum* and *Schizostachyum glaucifolium* were cultivated grasses. The sweet stalks of *Saccharum officinarum* provided food and its leaves were used for thatch (Whistler 1991:124-5). *Schizostachyum glaucifolium* occasionally was cultivated or became naturalised, providing materials for poles, vessels, musical instruments and construction (Whistler 1991:57).

While small amounts of Poaceae pollen (1-2%) are found in Ngofe Marsh before Polynesian arrival, increases in Poaceae pollen (up to 270% calculated outside the terrestrial pollen sum), Poaceae pollen >40-50 µm (up to 85% calculated outside the terrestrial pollen sum), and Poaceae pollen with two to three pores (up to 45% calculated outside the terrestrial pollen sum) jump dramatically with the onset of burning of the marsh (denoted by the presence of microscopic charcoal) and the arrival of Polynesian colonists (Figure 4). Similarly, Poaceae pollen, particularly grains >40-50 µm, becomes more abundant in Avai'o'vuna Swamp about 2600 yr BP, and again coincident with the onset of microscopic charcoal deposition (Fall 2005). Ano'a'pepe on 'Eua contains Poaceae pollen >40-50 µm, some Poaceae with multipores, and microscopic charcoal throughout the 1 m core.

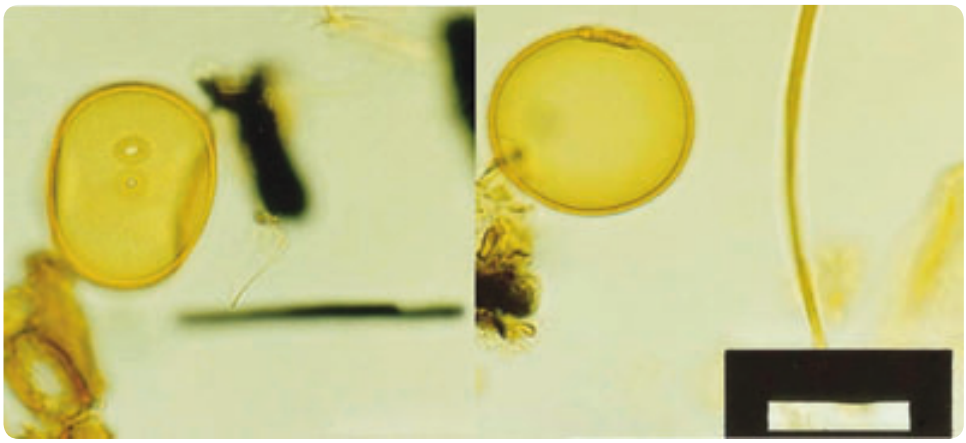

Figure 4. Poaceae pollen from Ngofe Marsh (scale bar = 50 µm [black rectangle]). Photo by P. Fall

The possibility that these Poaceae pollen grains from the Vava'u and 'Eua cores represent a cultivated or hybridised grass is strengthened by their larger size and multiple pores. Erdtman (1969) notes that hybridised cultigens in the Poaceae family may be diporate, multiporate or inapertuate (e.g. *Tricale,* a hybrid of *Triticum* and *Secale,* often has two or more pores). *Saccharum officinarum* hybridises with *Saccharum spontaneum*, as well as other genera, including *Erianthus, Miscanthus, Narenga* and *Sclerostachys* (Aitkens et al. 2007), perhaps leading to the production of these subfossil hybrid pollen grains. Thus, one of the cane or reed grasses brought by Polynesians to Tonga may have been cultivated on Vava'u and 'Eua.

Polygonum dichotomum (synonym *Polygonum glabrum*) has been suggested as a Polynesian introduction to Tonga (Smith 1981). This common wetland plant (Whistler 1992b) currently grows in Tongan swamps, including Finemui Swamp on Ha'afeva (Flenley et al. 1999), and dominates the marsh vegetation at Vasi Vasi Swamp on Hunga Island, Vava'u (Fall unpublished). *Polygonum* pollen first appears at Ngofe Marsh about 4000 yr BP, prior to Polynesian settlement, but is much more common on the marsh after 1000 yr BP. *Polygonum*-type pollen appears throughout the record at Avai'o'vuna Swamp. Although *Polygonum* pollen

is found in cores from Lotofoa and Finemui swamps on Ha'apai before Lapita colonisation, *Polygonum* pollen increases in Lapita and subsequent sediments at Finemui Swamp (Flenley et al. 1999).

Pometia pinnata is a large Polynesian introduced tree common in villages and plantations throughout the islands. Fruits of *Pometia pinnata* are similar to litchi in taste and appearance, and are highly valued by Tongans; its wood is used for timber, tapa pounders and other wooden tools (Whistler 1991:121). *Pometia* pollen first appears in Ngofe Marsh at 2500 yr BP, just after the arrival of Polynesians, suggesting that early colonists most likely brought this tree.

Pollen evidence for European introductions

Alternanthera sessilis is a European introduction that is used occasionally as an ornamental around houses (Whistler 1991:70). *Alternanthera* pollen appears in the uppermost sediments from Avai'o'vuna Swamp, Vava'u, attesting to its European introduction (Fall 2005) (Table 4).

Mimosa pudica is an introduced weedy shrub or small tree found in disturbed habitats (Whistler 1991:85). *Mimosa* pollen is quite abundant in a short core collected from the mud-water interface at Ano'a'pepe, the small lake in the upland rainforest, attesting to the recent introduction of *Mimosa pudica* to 'Eua.

Pinus caribaea was introduced to 'Eua, where today it is cultivated in plantations (Whistler 1991:100). Interestingly, although pine species are notoriously prolific pollen producers, and *Pinus caribaea* plantations grow within a few hundred metres of Ano'a'pepe, only three *Pinus* pollen grains have been recovered from a single sample collected at the surface (0 cm) of the lake. *Pinus* pollen is absent from both Avai'o'vuna Swamp and Ngofe Marsh on Vava'u. However, Flenley and others (1999) found small amounts of Pinaceae pollen in the two cores collected on Ha'apai, suggesting long-distance transport to these islands.

Psidium guajava is an introduced fruit tree which has become naturalised in pastures and disturbed areas (Whistler 1991:60). *Psidium guajava* is widespread in Tonga as a cultivated tree and as an adventive species. *Psidium* pollen appears in the upper peats at Folaha Swamp in Fanga 'Uta Lagoon, Tongatapu, dating to the historic period (50-150 yr BP) (Ellison 1989).

Stachytarpeta urticifolia is a weed introduced recently to Tonga (Whistler 1991:46). *Stachytarpeta urticifolia* grows in disturbed soils around swamps and is particularly common on the edge of Ngofe Marsh. *Stachytarpeta* pollen appears in the most recent sediments from Finemui Swamp on Ha'afeva, Ha'apai, in Zone FM 5 (Flenley et al. 1999).

Stenochlaena palustris, an epiphytic fern, grows on *Hibiscus tiliaceous* plants in the *Rhizophora* mangrove at the edge of Folaha Swamp in Fanga 'Uta Lagoon on Tongatapu (Ellison 1989). Whistler (1991:102) notes that it is relatively uncommon in most forests in Tonga. *Stenochlaena* spores were found in Zone LF5, the most recent sediments in the core from Lotofoa Swamp on Foa, Ha'apai (Flenley et al. 1999). Flenley et al. (1999) suggest that *Stenochlaena palustris* was introduced from Southeast Asia, where it is common today, became abundant on Ha'afeva Island, and then was extirpated.

Summary

Dramatic changes follow the settlement and modification of tropical Pacific Island ecosystems by human populations (Hope et al. 1999). The creation of anthropogenic landscapes in Oceania extended from New Guinea eastward with the Lapita culture, and became widespread throughout the Pacific islands (Kirch et al. 1995; Athens et al. 1996; Denham et al. 2003; Kennedy and Clarke 2004; Fairbairn 2005). Vegetation in the Kingdom of Tonga derives from long-distance dispersal (Carlquist 1967, 1974), transport by birds and bats (Rainey et al.

Table 4. Plant taxa that first appear (FAD) in sediment cores from Tonga or show an increase in pollen in the uppermost sediments after European colonisation

Botanical Species	Island	Core	Evidence	Reference
Alternanthera sessilis R.Br. ex DC	Pangaimotu, Vava'u	Avai'o'vuna Swamp	FAD pollen c. 300-0 BP	Fall 2005
Ipomoea batatas L.	Ha'afeva, Ha'apai	Finemui Swamp	FAD pollen historic	Flenley et al. 1999
	Pangaimotu, Vava'u	Avai'o'vuna Swamp	FAD pollen c. 300-0 BP	Fall 2005
Mimosa pudica L.	'Eua	Ano'a'pepe	FAD pollen 0 BP	Fall unpublished
Phyllanthus amicorum G.L. Webster	Pangaimotu, Vava'u	Avai'o'vuna Swamp	FAD pollen c. 300-0 BP	Fall 2005
Pinus caribaea Morelet	'Eua	Ano'a'pepe	FAD pollen 0 BP	Fall unpublished
Psidium guajava L.	Tongatapu	Folaha Swamp	FAD pollen historic (50-150 yr BP)	Ellison 1989
Stachytarpeta urticifolia (Salisb.) Sims	Ha'afeva, Ha'apai	Finemui Swamp	FAD pollen historic	Flenley et al. 1999

Note: All ages estimated from sedimentation rates based on radiocarbon ages from each core. Ngofe Marsh, Avai'o'vuna and Folaha swamps each have two ^{14}C ages; Finemui and Lotofoa swamps have one ^{14}C age each.

1995; Banack 1998) and human introduction and cultivation (Fall et al. 2007). Palynological evidence for Polynesian and later European plant introductions to Tonga comes from Holocene age sediment cores collected from Vava'u (Fall 2005), Ha'apai (Flenley et al. 1999), Tongatapu (Ellison 1989) and 'Eua (Fall unpublished).

Plants introduced commonly by Lapita colonists include both trees and herbaceous cultigens. In addition, indigenous plants may have been planted and cultivated by Polynesian settlers, allowing the expansion of their native habitats. Plants that were cultivated or whose ranges were expanded by Polynesians in Tonga are represented by pollen from the following tree species – *Canarium harveyi, Casuarina equisetifolia, Cocos nucifera, Erythrina variegata, Pandanus tectorius*, and *Pometia pinnata*. Woody shrubs introduced or cultivated by Polynesian settlers include *Cordyline fruticosa* and *Gardenia*. Herbaceous taxa introduced or expanded by early colonists consist of *Colocasia esculenta, Ludwigia octovalvis, Polygonum*, and a cultivated grass species. Pollen deposited in the past few hundred years provides evidence for European cultigens or inadvertent introductions. Pollen from tree species includes the planted *Pinus caribaea* found in plantations on 'Eua and the naturalised weedy species *Mimosa pudica* and *Psidium guajava*, found in very recent-age deposits. Historic-age deposits also contain pollen produced by herbaceous or shrubby vegetation, including *Alternanthera, Ipomoea* cf. *batatas, Phyllanthus* and *Stachytarpeta*, as well as *Stenochlaena* spores.

Pollen data provide a window to understanding many of the changes that have moulded the Tongan landscape. Polynesian colonists significantly modified their environment through the burning and clearing of indigenous rainforests, making way for cultivated root crops, grasses and ferns. These early settlers also brought a number of woody shrubs and useful tree species, and expanded their ranges, thereby encouraging the creation of anthropogenic forests, as well as open landscapes. European settlement of Tonga further added to the number of cultivated plants, promoted forest clearing and introduced new species, particularly weedy or unintentionally introduced plants.

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