[1]Notes on the Natural History of *Cycas seemannii* (Cycadaceae)

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Abstract
Cycas seemannii occurs in several habitats in Vanuatu, New Caledonia, Fiji and Tonga, but is mostly coastal. Growth rates are about 5-15cm.yr^{-1} and sex ratios observed were almost neutral. Mechanisms to survive in adverse environments are discussed. Female plants were found to produce, on average, longer leaves with more leaflets than male plants. Larvae of an unidentified moth, which are parasitised by at least two species of wasps, mine the leaflets of C. seemannii. Reproduction occurs mainly by seeds and bulbils. Wind appears to be the major pollination agent. Seed dispersal, other than oceanic, appears to be inefficient.

***Keywords**: Cycas seemannii, cycads, South Pacific, ecology, natural history*

1 Introduction
Cycas seemannii A.Br. (Subsection *Rumphiae* K.D. Hill, 1994) is found in all the three major Eastern Melanesian archipelagos (Vanuatu, Fiji and New Caledonia) and also extends to the Polynesian island of Tonga. It is cultivated in Samoa (A. Whistler pers. comm.). The species, which has been severely reduced by intensive shifting agricultural practices, grows on calcareous beach dune sands and coral limestone formations and may extend to various inland substrates (Hill 1994).

In Vanuatu, *C. seemannii* is widespread throughout its 80 islands (Schmid 1975). However, it is not abundant on New Caledonia (Laubenfels 1972) and is likely to have arrived relative recently on this old Gondwanaland island (Hill, 1996; Keppel, 1999). The species occurs throughout the entire Tonga group (Yuncker, 1959; Franklin *et al.*, 1999). It is especially abundant on the island of 'Eua (Drake *et al.* 1996), while it is almost extinct in the wild on Tongatapu (K.D. Hill pers. comm.). In Fiji, despite continuing to decline, *C. seemannii* seems to be still moderately common, especially on Vanua Levu (Keppel 1999). A species of *Cycas*, possibly *C. seemannii*, occurs on Tikopia (Kirch and Yen 1982) and may also occur on islands of the extended Santa Cruz group.

Little is known about the ecology of *C. seemannii*. In Fiji, it is found infrequently, in gullies or on well-drained slopes of the "talasiga" vegetation (Guppy, 1906; Mead, 1928; Derrick, 1951; Parham, 1972; Lees, 1989) – the fire-prone grasslands on the drier side of the larger islands in the Fiji Group. In some places it may be a prominent component of coastal vegetation (Laubenfels, 1972; Schmid, 1975; Drake *et al.*, 1996).

In this paper I report my observations on the natural history of *C. seemannii*, which were made during my study of the genetic structure and morphology of the species (Keppel 1999). These observations serve as a starting point for future, more detailed ecological research on the species.

1.1 Study sites
The results presented here were obtained from observations and studies on cycads in both natural populations and in cultivation at The University of the South Pacific (USP) and the Sacred Heart Cathedral in Suva, Fiji. In addition, four natural populations, one each in New Caledonia (Baie des Tortues, a few kilometres south-east of Bourail), Vanuatu (Devils Point on Efate), Fiji (a wild population growing in a plantation of *Pinus caribaea* at the Nabou Pine Station, western Viti Levu; at 209 m a.s.l., 5 - 10 km from the coast) and Tonga (southernmost tip of 'Eua) were studied in greater detail (Figure 1).

2 Materials and Methods
The year in which individuals of *C. seemannii* were planted at the University of the South Pacific was determined where possible to estimate growth rate (R.H. Phillips and L. Mataitini, pers. comm.).

In each of the 4 populations studied in detail, 30 individuals were chosen at random. From each of these an entire leaf was removed to measure the various leaf characters and to obtain a sample for starch gel electrophoresis (results for the latter are reported in Keppel 1999). The sex of individuals was determined where possible. Females were identified by the presence of megasporophylls. Height and diameter of individuals were recorded. In the population in New Caledonia, this was done for 100 individuals and the resulting data grouped into height classes and a graph of frequency against height was plotted to estimate the age structure of the population.

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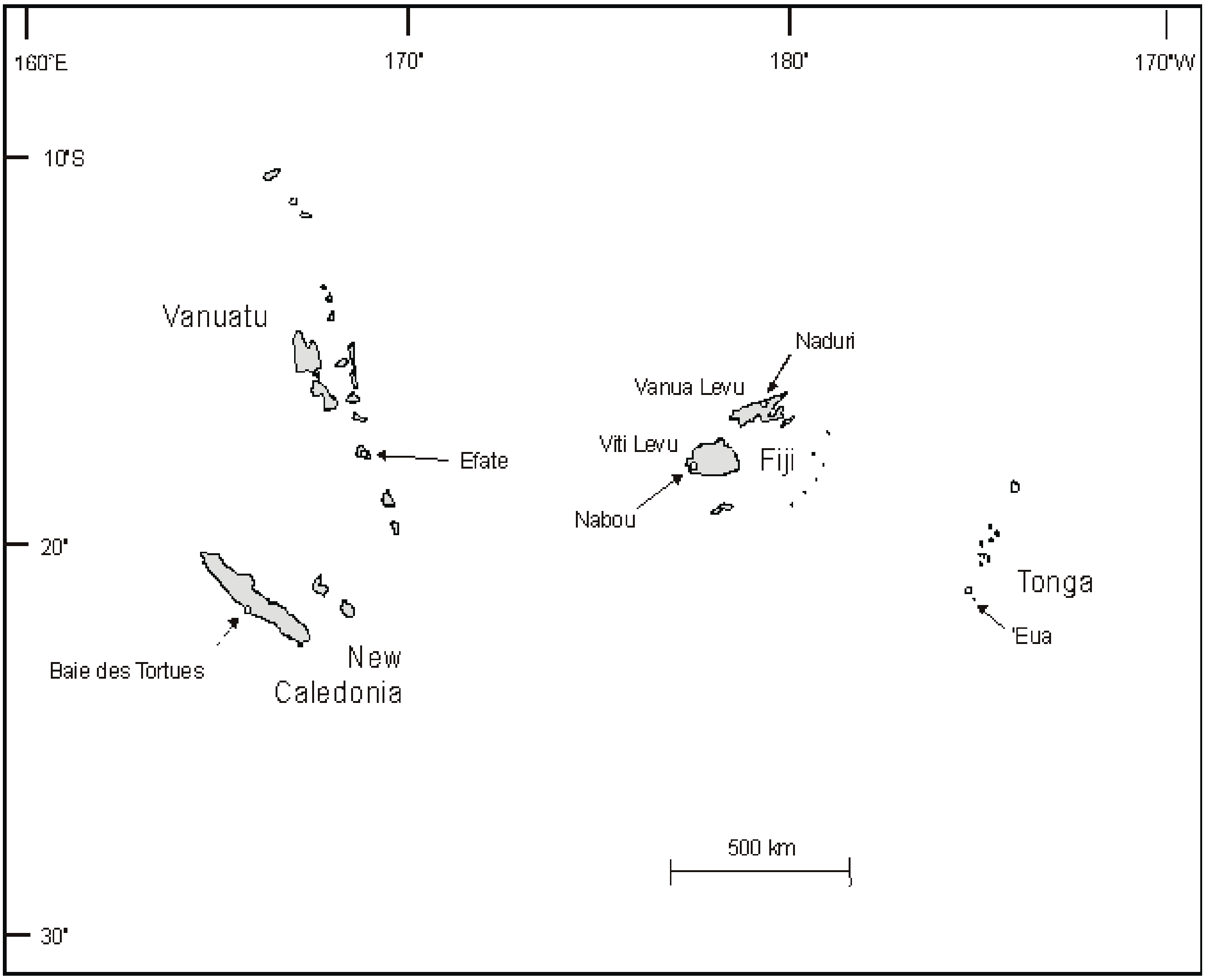

Figure 1: Location of study sites

Twelve pupae of a moth caterpillar mining the leaflets of *C. seemannii* were placed into a covered, aerated petri dish. A single moth (not identifiable, T. Edwards, pers. comm.) and 4 wasps were collected from the petri dishes. The wasps were identified by C. Burwell of the Queensland Museum.

3 Observations

3.1 Distribution

C. seemannii is widely distributed and occupies a variety of habitats. At the Baie des Tortues more than 200 individuals (reaching up to 9m in height) grew on a soil-covered limestone terrace on cliffs overhanging the ocean, dominated by a dense thicket of *Leucaena leucocephala*, a serious weed on the island (T. Jaffré pers. comm.). Some cycads extend into the adjacent steep-sloped *Araucaria columnaris*-dominated littoral forest. Similarly, cycads grow on a limestone terrace above almost vertical cliffs on 'Eua (Tonga) in a population numbering at least a thousand plants. They form a prominent component of the understory of the cliff vegetation and *Hernandia-Terminalia* coastal forest (Drake *et al.* 1996), rarely exceeding 5 m in height and growing on a relatively thin soil layer with limestone outcrops.

On Efate in Vanuatu the cycad is part of a lowland rainforest ("medium-stature forest heavily covered with liana", Mueller-Dombois and Fosberg 1998) about 500 m from the coastline on steep soil-covered slopes with some limestone outcrops. A small area of the population was visited. A few cycads penetrate the canopy and reach up to 12 m in height. There are some remnant trees of *C. seemannii* in a coconut plantation on the adjacent coastal plain.

In Fiji *C. seemannii* seems to occur in most island groups, having been observed on Viti Levu, Vanua Levu, Ovalau, the Kadavu Group, the Yasawa Group (M. Fisher, pers. comm.), Taveuni (M. Tuiwawa, pers. comm.), the Lau Group (Fuller and Jones, 1999; L. Mataitini, pers. comm.), on the small basaltic island of Yanuyanu-i-loma in the Kadavu Group and at 600m elevation in the Nausori Highlands. However, the species occurs most commonly in coastal habitats, on well-drained slopes in the lowland rainforest and in the talasiga. The Nabou population consists of several groups of trees of 20-70 individuals that reach up to 7 m in height. They are present on slopes with generally poor talasiga soils (Latham 1979, 1983). These clusters are fragmented relics of a once larger population.

Although being moderately abundant, cycads are decreasing through anthropogenic activities. Many of the populations visited in Fiji show fire damage and no or poor regeneration (Keppel 1999).

3.2 Growth

C. seemannii usually has an unbranched, erect stem but two, three or rarely more branching events may occur, usually as a response to physical damage. Bulbils, if produced, may also develop into branches. Tilted and 'creeping' stems are not uncommon. These often curve slightly upward to expose the crown of leaves to the maximum sunlight.

Cycads have an inconsistent growth rate, which is different for each individual, even under similar environmental conditions (Giddy 1974). Several factors seem to affect the growth rate, two of which may be soil quality and sex of the plant. Plants cultivated in poor soil on reclaimed land of the SPAS (School of Pure and Applied Sciences) Palm Garden grew slower than those grown in the soil of the Cycad Garden and the Botanical Garden, all at USP (Table 1). Similarly, trees in the limestone population on 'Eua, Tonga, were much smaller (up to 5 m in height) compared to those (up to 12 m) in the rainforest at Efate (Vanuatu). Also, a female planted beside a male at the same time in the SPAS Palm Garden had a faster average growth rate of 7.78cm.yr^{-1} as compared to and 5.83cm.yr^{-1} (Table 1). Other cultivated plants of *C. seemannii* seem to parallel this trend of faster growing femalesThe height structure of the New Caledonian population at the Baie des Tortues shows a gradual decline in the number of individuals with increasing height class (Figure 2). The lower number of individuals in the smallest size class may indicate a recent increase in juvenile mortality and reduced regeneration. Pedestrian tracks through the thicket and the dominance of *Leucaena leucocephala* also indicate that the population is disturbed.

3.3 Tolerance

The tolerance of *C. seemannii* to a wide range of environmental conditions is reflected by the variety of habitats it occupies. Fiji's dry and fire-prone talasiga, rainforest (Devil's Point in Vanuatu), cliffs exposed to strong winds and salt spray (Baie des Tortues, New Caledonia), limestone terraces with a low cover of soil ('Eua, Tonga) and goat-denuded basaltic substrate (Yanuyanu-i-loma, Kadavu, Fiji) are examples.

However, *C. seemannii* is only found in well-drained habitats, as it appears to be intolerant to water-logging (R.H. Phillips pers. comm.). Although adult leaves are able to withstand salt spray, young, developing leaflets do not seem to posses this ability. Several trees of the cycad population on the cliffs of the Baie des Tortues in New Caledonia had new leaves that were withered, diminutive and black, possibly as a result of salt spray.

Resprouting of broken stems damaged by strong winds, fires or by falling trees was found in some plants of all populations surveyed, a phenomenon also observed in other species of the subsection *Rumphiae* (Norstog and Nicholls, 1997; Marler and Hirsch, 1998). Plants are also observed to produce new leaf flushes almost immediately after defoliation through hurricanes or fires.

The production of aerial roots on damaged trunk sections is common. This may provide attachment to detached trunk pieces and anchorage for uprooted trees. At Devils Point (Vanuatu), a cycad with a procumbent trunk was, in addition to its normal root system, attached to the ground by three stem-like connections from its trunk. These may have formed from aerial roots.

I visited the Nabou population twice (March 1998 and again in May 1999). Between these visits part of the population had been burnt by fire (in December 1998/ January 1999), which had spread from a sugar cane plantation a few kilometres away. A particular fragment of this cycad population that had consisted of about 400 individuals in 1998 was reduced to about 50 plants in 1999. Many of the surviving trees were damaged. The outer protective layer of persistent leaf bases was charred and had cracked under the extensive heat, making the stem vulnerable to invasion by insects and pathogens.

Leaves of cycads in Nabou had fewer leaflets and were less spinescent after the fire compared to before (Table 2). Significantly smaller average trunk diameter after the fire could mean that older plants are more susceptible to fire.

Table 1. Growth rate estimates of ***Cycas seemannii.*** All plants are cultivated at The University of the South Pacific. Zero height was assumed upon planting. Height in 1999 was measured on the 20th September 1999.

Code	Sex	Location	Year Planted	Height in 1999 (cm)	Growth Rate (cm.yr^{-1})
CS 10	Female	SPAS Garden	1982	140	7.78
CS 11	Male	SPAS Garden	1982	105	5.83
CS 12	Male	Botanical Garden	1988	178	14.83
CS 13	Male	Botanical Garden	1988	141	11.75
CS 14	Male	Cycad Garden	1988	120	10.00

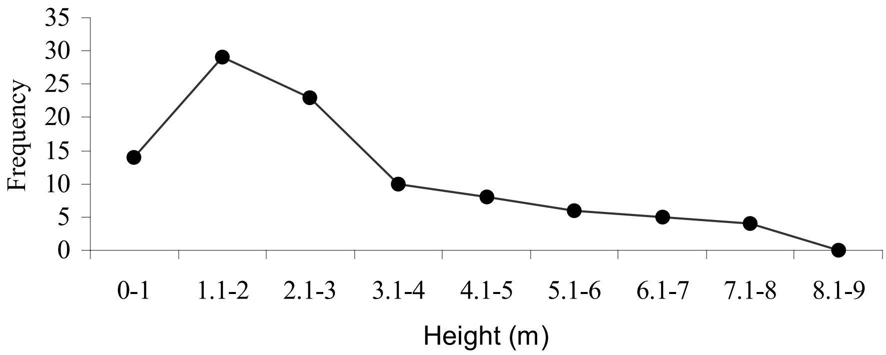

Figure 2: Height class distribution in the *Cycas seemannii* population near Bourail in New Caledonia.

Table 2. Leaf morphology of a cycad population at Nabou, Viti Levu, Fiji before (May 1998) and after (May 1999) a fire. % petiole length = percentage of the total leaf length constituted by the petiole. % spinescence = percentage of the total length of the petiole covered by spines.

Character	1998 (n = 37)	1999 (n=30)	t-test (P)
	Mean ± S.D.	Mean ± S.D.	
Trunk height (cm)	296.4 ± 111.3	291.3 ± 120.7	0.859
Trunk diameter (cm)	20.4 ± 16.5	16.0 ± 4.5	0.001
leaf length (cm)	143.3 ± 27.5	144.3 ± 21.3	0.859
Leaflet number	200.1 ± 39.5	181.8 ± 26.0	0.027
Width (mm)	9.9 ± 1.5	10.2 ± 1.1	0.484
Length (cm)	18.1 ± 2.7	18.0 ± 2.7	0.862
Petiole % of whole leaf	17.5 ± 3.4	17.8 ± 3.4	0.702
Petiole % spinescence	10.0 ± 9.3	6.0 ± 6.3	0.041
Petiole length	24.7 ± 5.5	25.5 ± 4.9	0.547

It has been found that the corraloid roots of *Macrozamia riedlei* produce more nitrogen after a fire than normally (Grove *et al.* 1980). During the second visit to the cycad population in Nabou, after the fire, *Ficus vitiensis* (Moraceae) and *Alphitonia zizphoides* (Rhamnaceae) were observed to occur mostly within 1 to 2m from a trunk of a cycad, probably because of nitrogen enrichment by cycads and their symbiotic cyanobacteria.

3.4 Leaf predation

Caterpillars of a small moth (unidentified) were found to reduce the photosynthetic potential of leaves by tunnelling through leaflets of *C. seemannii*. Sections of the affected leaflet die. However, the caterpillars do not damage the petiole, rachis and midrib of leaves. Being nocturnal, the activities of the caterpillars are seldom observed. When mature, the caterpillars weave two or more leaflets together and pupate between them. Despite being protected by the leaflets, the pupae are parasitised by at least three species of wasp (one species of *Tineobius* (Eupelmidae) and two species of *Brachymeria* (Chalcididae)).

3.5 Reproduction

Male and female plants produce cones at approximately the same time in natural populations. Several female plants of *C. seemannii* cultivated at USP, possibly originating from different populations, failed to produce fertile seeds between 1997 and 2000, perhaps because their cone production was not synchronised.

Cone production may be more energy consuming for male plants than it is for females. In cultivation, the leaves of some male plants begin to dry up soon after cone production, while female cycads are seemingly unaffected. Also female plants have, on average, longer leaves with more numerous and wider leaflets compared to male plants (Table 3).

The frequency of cone production seems to differ between populations. In all populations investigated in Fiji and on ‘Eua, Tonga, coning appears to be an annual event. Cone production of female plants seems to occur only every second or third year at the Baie des Tortues (megasporophylls remain attached to the plant for up to three years).

Circumstantial evidence suggests that pollination in *C. seemannii* is wind-mediated. A female plant cultivated at the Sacred Heart Cathedral in Suva, Fiji, is shielded from the impact of wind on three sides by surrounding buildings, so that wind currents can only enter in one direction. Male plants are planted at the side of the wind impact and at exactly opposing sides. Although several seeds on the leeward side also develop, the great majority of seeds on this plant are found on the windward side of the cycad. These results agree with the findings by Niklas and Norstog (1984) on the potential effect of wind on *Cycas* cones. Seeds are lacking in the rainforest cycad population on Efate but present on female cycads that grow in the coconut plantations on the adjacent coastal plain. This suggests that wind is the major, if not only, pollination agent of *C. seemannii*. However, male cones produce heat, are malodorous and have microsporophylls that are often much tunnelled by insects, suggesting that detailed examinations of cones and exclusion experiments need to be conducted during coning in natural populations, before definite conclusions can be drawn.

In the absence of seeds, rainforest cycads must have alternative reproductive strategies. Bulbils, which generally form as a response to injury, are relatively common in the Efate rainforest population. These may occasionally become detached and develop into new individuals. Cycad trunks may also be broken when other, bigger trees fall on them. Such severed sections may take root and provide another way of vegetative reproduction.

Seed dispersal in *C. seemannii* seems to be limited. Developing seedlings were generally found clustered around the mother tree. In trees growing along slopes seedlings were observed 2 m downhill. On ‘Eua there is no regeneration (after removal) of cycads on agricultural land that has been left unattended for 10 years or more.

The germination of mature seeds usually takes 6 – 8 months, but may take up to 12 months or more (R.H. Phillips pers. comm.). Seedlings only produce one or two leaves in the first leaf flush and then progressively more up to 50 or more in adult plants. On one plant on ‘Eua, Tonga, a seed that had germinated (but not yet produced a leaf) was found attached to the megasporophyll, but this case of vivipary seems to be exceptional.

Sex ratios of populations could not be determined in populations where females cone irregularly (New Caledonia) or only when emergent (Efate). The other two populations investigated had a nearly neutral sex ratio for the small samples investigated (Table 4).

Table 4. Sex Ratios for the populations in Nabou, Viti Levu, Fiji and on ‘Eua, Tonga.

Population	Number of Males	Number of Females	Sex Ratio
Nabou (n=37)	19	18	1.056
’Eua (n=32)	17	15	1.133

4 Discussion

The seeds of *Cycas seemannii* have positive buoyancy in seawater and are believed to have colonised the Pacific by oceanic dispersal (Guppy, 1906; Dehgan and Yuen, 1983; Hill, 1996). Presence of seeds in drift also supports this colonisation theory (Ridley, 1930; Smith, 1990). That the dispersal abilities of the species are nevertheless limited is seen by the fact that it has not been able to naturally colonise the islands of Samoa. Beaches and coastal forests are, therefore, likely to have been the first habitat of the species and many populations are still found in littoral habitats (Hill 1994). The seeds are too big to have transoceanic avian dispersal.

Once established, *C. seemannii* could have dispersed further inland to occupy the elevations at which it is found today. Both biotic and abiotic factors probably contributed to this dispersal. Tidal currents of river systems, although seeds tend to sink in brackish water, and exceptionally high tsunamis, can potentially transport the seeds and bulbils of the species up to at least 100 m elevation (Moore and Moore, 1984; Young and Bryant, 1992). However, establishment in the Nausori Highlands at 600 m altitude and in other inland locations is likely to have been animal-mediated. Bats (Pijl 1957) and now extinct, giant ground-dwelling birds (Balouet and Olson, 1989; Steadman 1993, 1995 and 1997) are possible vectors. Man can also not be discounted as a potential dispersal agent, considering the present and former cultural and nutritional importance of *C. seemannii* (Seemann, 1865-73; Pant, 1973; Kirch and Yen, 1982; Thaman, 1992; Keppel, 1999). Anthropogenic changes since the Holocene are believed to have reduced the number of populations and individuals of the species by direct destruction, increased frequency of fires and, possibly, through the extinction of bird dispersers (Keppel 1999).

Seed dispersal in the species appears to be poor unless ocean-mediated. The limited ability for dispersal may explain the patchy distribution of the species. Only seemingly rare, long-distance dispersal events can carry seeds into a suitable habitat and allow establishment. Once a few trees are established, the gravity-dispersed seeds gradually colonise the area around these founder trees, causing the formation of a patch.

The talasiga may be a secondary habitat because its greatest expansion is thought to have been anthropogenic and within the last 150 years (Latham 1979 and 1983; Southern, 1986) and because of the seemingly limited dispersal ability of the cycad. *C. seemannii* may, therefore, not characteristically be associated with the talasiga but instead be a relic of the previous forest vegetation, probably having survived because of its greater tolerance to fire and general resilience as compared to other forest plants.

Adaptations of *C. seemannii* to survive hardships and catastrophic events such as fire, hurricanes and salt spray, include xerophytic leaves, coralloid roots, a deep reaching root system, rapid new growth on severed stems and the quick production of a new leaf-flush. The great plasticity of the leaf morphology (Keppel 1999) may also contribute to the adaptability of the species. The large number of individuals, at least 300, that were killed in the Nabou population during the fires, probably aggravated by fallen pine needles, show that cyads are however susceptible to fire, despite having some tolerance. Similar observations have been made in other cycad species (Norstog and Fawcett, 1992; Wilson, 1993).

The observed growth rate in cultivated specimens of *C. seemannii* were values similar to that observed in other cycad species (Giddy, 1974; Tang, 1995; Vogel *et* *al.*, 1995), and appears to depend on environmental factors and sex of a plant. The faster growth of female plants could imply that in the genus *Cycas*, unlike in other genera where the female plants expend more energy on reproduction than do male plants (Clark and Clark, 1987; Ornduff 1987 and 1990), the male plants need to invest relatively more resources into reproduction.

Insects appear to be the pollination agent in most cycad species (Norstog, 1987; Ornduff, 1991; Vovides, 1991; Vovides *et al.*, 1997), yet no pollinators were observed for *C. seemannii* and it appears that the species is wind-pollinated. Even if its ancestor had been insect pollinated, the pollinator may not have had the ability to cross the ocean with the cycad seeds.

The approximately neutral to slightly male biased sex ratios agree with observations in other species of cycads (Clark and Clark, 1987; Ornduff, 1987, 1990 and 1993; Connell and Ladd, 1993).

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