

Morphological variation, an expanded description and ethnobotanical evaluation of *Cycas seemannii* A.Braun (Cycadaceae)

Gunnar Keppel^{1,2}

¹ Biology Division, School of Biological, Chemical and Environmental Sciences, Faculty of Science, Technology and Environment, University of the South Pacific, Suva, Fiji.

² Current Address: School of Integrative Biology, University of Queensland, St. Lucia, Brisbane, QLD 4072, Australia.

Abstract

Cycas seemannii (Cycadaceae) is a widespread and highly variable species. This study investigates morphological variability and ethnobotanical uses throughout the entire range (Torres Strait Islands, Vanuatu, New Caledonia, Fiji and Tonga) of the species. The morphological characters studied are highly variable among populations and unrelated to genetic differences. Characters are also more variable than previously assumed and because of this we provide an updated, detailed taxonomic description of *Cycas seemannii* based on extensive morphometric data, fieldwork and herbarium specimens. The plant is of great cultural importance in Vanuatu, its seeds are utilised as a source of starch and it is a widely cultivated ornamental. Possible consequences of the plant's decreasing cultural importance are discussed.

Keywords: *Cycas*, ethnobotany, morphology, morphometrics, taxonomy.

1. Introduction

Many plants respond to differences in environmental parameters, such as light, temperature, nutrients and moisture, by producing leaves of different morphology (Chabot and Chabot, 1977; Sultan and Bazzaz, 1993a, 1993b). For example, it has been found that many plants produce sun and shade leaves that differ in several morphological and anatomical features (Jackson, 1967; Smith and Nobel, 1977, 1978). This phenomenon of environmentally introduced phenotypic variation is known as phenotypic plasticity (Stearns, 1989), thought to be a mean of absorbing stress (Bradshaw and Hardwick, 1989).

The morphology of a plant contributes to its competitive ability in a particular environment (Baker, 1972; Sultan and Bazzaz, 1993a) and is, therefore, subject to natural selection. Hence, phenotypic plasticity may be of evolutionary importance as it may modulate the effects of natural selection by shielding genotypes (Sultan, 1987; Sultan and Bazzaz, 1993a). Not many studies on cycads have investigated the variability in the morphology of their leaves. A great amount of phenotypic plasticity seems to exist in species of *Zamia* (Newell, 1989). The occurrence of different sun and shade leaves was observed in *Zamia pumila* (Newell, 1985).

The Cycadaceae is a monogeneric family that is presently distributed from southern China to northern Australia and from the East African mainland to the island group of Tonga in the Southwest Pacific (Hill and Stevenson, 1998). While most taxonomists consent in accepting a single genus, *Cycas* L. (Chen *et al.*, 2004; see de Laubenfels and Adema, 1998), there has been and still is considerable confusion about the classification at the subgeneric level (Hill, 2004). *Cycas seemannii* A.Braun, which grows mainly in coastal habitats and is still moderately common in remote places of Vanuatu, New Caledonia, Fiji and Tonga (Hill, 1994a; Keppel, 2001), is a good example of the taxonomic confusion at the subgeneric level. After its initial brief description in 1876 (Braun 1876), it was considered a subspecies of *C. circinalis* L. (Schuster, 1932) and a form of *C. rumphii* Miq. (Kanehira, 1938), before Hill (1994a) elevated it once again to species status. Recently, de Laubenfels and

Adema (1998) considered *C. seemannii* identical to *C. celebica* Miq., a treatment that has not found much support (Hill, 2004; Chen *et al.*, 2004). The species has been declining because of shifting agricultural practices and other coastal development projects (Hill, 1994a; Keppel, 2002).

As all other species of the genus *Cycas* L. in the insular Southwest Pacific, *C. seemannii* is in Subsection Rumphiae of Section *Cycas* (Hill, 1994a). The Subsection is defined by the presence of a layer of spongy tissue within the buoyant seed, which probably allowed it to colonise the Pacific and eastern Africa relatively recently (Keppel *et al.*, 2008). Microsporophylls are also distinctive in many members of the group, being more or less dorsiventrally thickened, with short or vestigial, sharply upturned apical spines. Hill (1994a) also lists the two-year seed maturation period as a potentially distinctive character. However, this trait has been reported only in *C. seemannii*, *C. thourasii* R.Br. and *C. bougainvilleana* K.D.Hill (Hill, 1994a). About ten species comprise the subsection, nine of which have been formally described (Hill and Stevenson, 1998). The buoyant seeds have resulted in a wide distribution, extending from the African East Coast to Fiji and Tonga, and from New Guinea north to southern coastal Indochina.

The morphology of leaves is frequently used in the identification and delimitation of cycad species, because seeds, cones and cataphylls are often unavailable (Lindström, 2004). Another possible reason for this is the scarcity of characters because of the conservative morphology of cycads (generally a stem with a crown of pinnately divided leaves at the apex). The adequacy of this approach is questionable, as many species are quite variable in their leaf morphology (Newell, 1985, 1989; Hill 1995, 2004). Hill (2004) highlighted several seed and some sporophyll characters as the most consistent and most useful in delimiting different subgeneric lineages. Within the subsection Rumphiae stem minimum diameter, percentage of the petiole covered in spines, number of leaflets, length of leaflets, width of leaflets, basal width of leaflets, megasporophyll lamina length, and megasporophyll lateral spine number have been identified

as potentially being able to differentiate between different species (Lindström, 2004).

De Laubenfels (1972) and Smith (1979) provided brief descriptions of *C. seemannii* in New Caledonia and Fiji, respectively. A detailed description of the species was presented by Hill (1994a). However, his treatment was based on a limited number of specimens. The results here presented in the form of an expanded taxonomic description of *Cycas seemannii* reveal that the species is more variable than previously thought. Ethnobotanical uses of the species are also recorded. In addition, I assess the morphological variation among populations in various characters. This will allow determining which characters are the most variable among populations and therefore most plastic and likely to be least useful in delimiting *Cycas seemannii* and other *Cycas* species.

2. Materials and Methodology

2.1 Morphometric Analysis

Using quasi-random sampling (Keppel *et al.*, 2002) at least 30 individuals in each of the four populations (Baie des Tortues in New Caledonia, Devils Point in Vanuatu, Nabou in Fiji, 'Eua in Tonga – see Table 1 and Keppel (2002) for detailed descriptions of the populations) was sampled. On each plant the following characters were measure or counted:

- i) leaf length (as measured from the leaf base to the apex of apical leaflets)
- ii) leaf width (as measured at the widest point)
- iii) length of the petiole (as measured from the leaf base to the first leaflet)
- iv) length of petiole covered with spines (as measured from the first spine to the first leaflet)
- v) thickness of rachis at location of the first leaflet
- vi) number of leaflets
- vii) length of median leaflets (as measured from the origin to tip of the leaflet)
- viii) width of median leaflets (as measured at the widest point of the median leaflets)
- ix) thickness of median leaflets (as measured 1cm from the rachis and 1cm from the midrib)

The length of petiole and leaf length were used to calculate the percentage the petiole constitutes of the total leaf length, and the length of the petiole covered with spines and the total length of the petiole were used to calculate the percentage spinescence of the petiole. This was done because the percentage values are more constant than the length of petiole and the length of petiole covered with spines, respectively (Hill, 1994b; Lindström, 2004). Characters of male and female cones were also measured

where possible but were only sparingly and inconsistently available and, therefore, omitted from the analysis.

Data was analysed using SAS (SAS Institute Inc., 1988). Mean and standard deviation were calculated for all variables analysed. Correlation analysis between variables using the Pearson correlation coefficient, an ANOVA test with Duncan Multiple Range Test, a stepwise discriminant analysis, the discriminatory power variables using Wilks' Lambda, Mahalanobis Distances among populations and a canonical analysis were performed. Trunk height and trunk diameter were excluded from most analyses because the samples from New Caledonia and Vanuatu would have a lower average than the actual value, because some of the highest trees were not be sampled. The Mahalanobis distances were then compared with Nei's (1972) genetic distances (Keppel *et al.*, 2002). This comparison should be valid because the leaves measured were the same as those used for the genetic analysis using starch gel electrophoresis.

2.2 Taxonomic Description

The morphology of *Cycas seemannii* was studied by investigation and careful measuring of more than 250 living specimens in the natural environment or in cultivation and on herbarium specimens. Fieldwork was done throughout the entire range of the species by visiting populations on Vanua Levu and Viti Levu in Fiji, 'Eua in Tonga, Efate in Vanuatu and New Caledonia. The resulting data were incorporated into an expanded description based on that of Hill (1994a). Colour notations were added or improved by comparison to a standard color reference (Kornerup and Wanscher, 1967). *Cycas seemannii* is in the Subsection Rumphiae within the Section *Cycas*.

2.3 Ethnobotanical Information

People living close to populations of *Cycas seemannii* were informally asked, whether they had any names and/or uses for the plant to yield the ethnobotanical information here presented. If they did, I asked them to detail the uses. Additional information was obtained from literature and herbarium specimens.

3. Results

3.1 Morphometric Analysis

Average values for the various variables measured in the 120 individuals in the 4 populations are given in Table 2. All variables were found to vary considerably between populations (Table 3). The rainforest population in Vanuatu had the longest leaves, widest and longest leaflets and the greatest percentage of petiole length.

Table 1. Substrate, soil depth, annual precipitation, distance to ocean and percentage canopy cover of the study sites.

Location	Substrate	Soil Depth (cm)	Annual Precipitation (mm)	Distance to ocean (m)	Percentage Canopy Cover
Bourail, New Caledonia	Limestone	5	973 (La Tontouta)	5	40
Efate, Vanuatu	Limestone	5-20	2,332 (Vila)	100	100
'Eua, Tonga	Limestone	0-5	2,134 (Vavau)	5	60
Nabou, Fiji	Basalt	20 or more	1,842 (Nadi)	1,500	0

Table 2. Mean, standard deviation and maximum and minimum values for the morphometric characters measured. % petiole length percentage of total leaf length constituted by petiole. % spinescence = percentage of total length of petiole covered by spines.

Variable	Number of Individuals	Mean	Standard Deviation	Range (cm)
Leaf length	120	170.4cm	28.0	102.0 - 265.0cm
Leaflet number	120	158.6cm	33.9	93.0 - 242.0cm
Leaflet width	120	1.4cm	0.3	0.8 - 2.1cm
Leaflet length	120	24.3cm	4.9	14.3 - 35.0cm
Leaflet thickness	120	4.8mm	1.1	2.7 - 7.2mm
Rachis thickness	120	1.4cm	3.3	0.8 - 2.1cm
% petiole length	120	19.3%	5.1	0.6 - 46.5%
% spinescence	120	9.1%	10.5	0.0 - 52.0%
Midrib width	120	16.2mm	8.2	9.0 -101.0mm

Table 3. Significant ANOVA results and Duncan Multiple Range Test for the morphometric characters in the different populations. EU = 'Eua population. NB = Nabou population. NC = New Caledonia population. VA = Vanuatu population. % petiole length = percentage of total leaf length constituted by petiole. % spinescence = percentage of total length of petiole covered by spines. * = *F*-value significant at 1% level.

Variable	F-value	Duncan Grouping
Leaf length	24.95*	1=VA, NC; 2=EU; 3=NB
Leaflet number	25.85*	1=NB,NC; 2=VA; 3=EU
Leaflet width	93.62*	1=VA; 2=EU; 3=NC; 4=NB
Leaflet length	55.42*	1=EU,VA; 2=VA,NC; 3=NB
Leaflet thickness	94.73*	1=EU,NC; 2=VA; 3=NB
Rachis thickness	100.36*	1=EU,NC; 2=VA; 3=NB
% petiole length	5.58*	1=VA,EU; 2=EU,NB; 3=NB,NC
% spinescence	24.82*	1=NC; 2=VA,NB; 3=NB,EU

The coastal populations of Eua and New Caledonia had the thickest leaflets and rachises, while the grassland population in Nabou (Fiji) had the shortest leaves, the narrowest, shortest and thinnest leaflets and the thinnest rachises.

The thickness of the rachis is the single most important variable in differentiating the four populations. It is followed by leaflet number and leaflet width. All variables, except midrib width, had significant ($P = 0.01\%$) discriminatory power as measured by Wilks' Lambda value (Table 4). Morphologically, the population in Nabou is the most differentiated. It has Mahalanobis distances of 37-60 to other populations, while the other populations are comparatively similar with distances between 8 and 13.4 (Table 5). Mahalanobis distances do not correlate ($r = 0.0451$) with Nei's (1972) genetic distances.

3.2 Taxonomic Description

Cycas seemannii A.Braun, Sitzungsbericht der Gesellschaft Naturforschender Freunde zu Berlin: 114 (1876).

Synonyms:

Cycas circinalis subsp. *seemannii* (A.Braun) Schuster, Das Pflanzenreich 99 (4,1): 71 (1932).

Cycas rumphii forma *seemannii* (A.Braun) Kanehira, J. Jap. Bot. 14: 587 (1938).

Cycas rumphii var. *seemannii* (A.Braun) Parham, Agric. J. Fiji 19: 94 (1948). (*Cycas neocaledonica* Linden, Illustr. Horticole 28: 32 (1881); *nom. nud.*; also cited as Greguss or Linden ex Greguss (in reference to Greguss 1968: 42, 176). Greguss (1968) merely asserted that, on anatomical grounds, this was a species distinct from all others that he had studied.)

Type: Viti Levu and Ovalau, *Seemann* 572, 1860 (lecto type: K, isolecto type: BM, G).

Stem to 8 (-12)m tall, 10-25 (-35)cm in diameter, occasionally with one or more branches; light yellow to greyish brown (sometimes black on some sections due to fungal or lichen growth). Plant excretes viscous, transparent mucilage when wounded that hardens upon exposure to air. Leaves of mature plants are 120-250 (-300)cm long, 25-70cm wide, flat (opposing pinnae inserted at 180 degrees on rachis), with 90-300 pinnae, terminated by single pinna or paired pinnae or a spine 3-10mm long. When young, the leaves are greenish yellow and densely covered with an orange-yellow tomentum.

Distinctly recurved margins, decurrent for 4-10mm, narrowed to 4-9 mm at base (one-third to half of maximum width), 12-25 mm apart on rachis (spacing increases from the apex, where pinnae may slightly overlap, towards the petiole), slightly (rarely strongly) undulated, with an attenuate apex. Lower pinnae are usually reduced in size and pointing upwards at an angle of about 45° to the horizontal leaf plane. Midrib is not sharply raised, more or less equally prominent above and below, greenish yellow on the upper surface and yellowish green on the lower surface, 1.0-2.2 mm wide, 1.2-2.2 mm in height Cataphylls are narrowly triangular, densely shortly tomentose, yellowish brown in colour, 50-150mm long, weakly pungent.

Male cones begin to form under cataphylls (which form on the stem apex in late July), emerging as narrowly ovoid structures with yellowish white to pale yellow tomentum in late September, and progressively increase in size as tomentum becomes orange. At maturity (November to December) the cones are brown, narrowly ovoid, 35-75 cm long, 10-15 cm in diameter. Microsporophyll lamina are

30-50 mm long and 15-30 mm wide, with a fertile zone 25-45mm long, with a sterile apex that is 4-6 mm long, not recurved and an apical spine that is somewhat reduced, broad, sharply upturned, 2-8 mm long. The pale yellow pollen that is released between mid-November to mid-December has a musty smell. Peduncle is to 5 cm long, 6 cm wide, brown.

Megasporophylls begin to form under cataphylls (which form on the stem apex in late July) and emerge in a loose aggregation to form an ovoid, cone-like structure (a cluster of megasporophylls that is sometimes called a “pseudocone”) with pale yellow tomentum in late September. They progressively increase in size (the tomentum becoming orange) and are eventually displaced from the stem centre as new leaves are formed, causing the pseudocone to disintegrate. Megasporophylls are 20-45 cm long, greyish orange tomentose, with 4-10 (-12) ovules. Their lamina are 45-100 mm long, 20-50 mm wide, narrowly triangular, regularly dentate with 18-45 lateral spines (2-9 mm long) and an apical spine that is 10-30mm long. The megasporophyll apex is sometimes moderately to strongly downcurved, often lacking tomentum on its upper surface at maturity. Ovules are initially yellowish white and develop into seeds when fertilised. Unfertilised ovules are aborted and shrink into dark brown, flat, ovoid structures that are 5-20 mm long. Seeds are flattened, ovoid, 40-60 mm long, 30-52 mm in diameter and their sacrotesta is 3-5 mm thick. Young seeds are yellowish white in colour upon emergence of the megasporophylls from the stem apex but quickly become light yellow, yellowish green and, then, deep green. The sacrotesta is initially hard but begins to soften after about 12-18 months, as seeds change from deep green to orange, brownish orange, light brown, reddish brown and finally, dark brown, and begins to emit a fruity smell, resembling that of dried figs. The sacrotesta then slowly decays revealing the greyish yellow sclerotesta.

Distribution

Widespread on Pacific islands, including the Torres Strait Islands (Australia), Vanuatu, New Caledonia, Fiji and Tonga. The cycad species on the Santa Cruz Islands (Kirch and Yen, 1982), which is a group of relatively

remote islands administered by the Solomon Islands, may also be *Cycas seemannii*.

Conservation Status

Vulnerable A2c (Baille *et al.*, 2004), “Vulnerable” (Keppel, 2002), CITES - Appendix 2 (UNEP 2008)

Vernacular

Fiji:

Logologo (dialects of Bau, Bua, Macuata, Cakaudrove; pronounced: “longolongo”; villagers, pers. com.)

Roro (Seemann, 1865-73; Guppy, 1906)

Sisila (Nadroga dialect, Taqaqe villagers, pers. com.)

Tuawawa niu (Degener, 1949 - as used by a person from Ba district)

Wiro (Smith, 1979)

Note: “Logologo” is the most frequently used term for *Cycas seemannii* in Fiji, as Bauan is the “official” native language. “Lagalaga” and “lagolago” were also mentioned to refer to the species (Smith, 1979) but are likely to be the result of a misunderstanding and actually were pronounced logologo.

Niue:

Longolongo (cultivated; R. R. Thaman, pers. com.)

Tikopia: Rongorongo (Kirch and Yen, 1982)

Tonga:

Longolongo (Yunker, 1959)

Vanuatu:

Namele (Bislama dialect; S. Chanel, pers. com.)

No-moll (Eromanga; Hill, 1994a)

Mwele (Pentecost; P. Ala, pers.com.)

Nemol (Espiritu Santo; Guillaumin, 1938)

Namail (Maskelynes; Curry 853, herbarium specimen, 1992)

Note: there are several different dialects that are spoken in Vanuatu and the above vernacular is likely to be just a fraction of the total number of names that exist for the cycad. Bislama (“namele”) is the official language.

Table 4. Significant ($P=0.01\%$) Wilks' Lambda values of discriminatory power for morphometric characters.

Variable	Discriminatory Power (Wilks' λ)
Rachis thickness	0.2781
Leaflet number	0.1049
Leaflet width	0.0582
% spinescence	0.0424
Leaflet thickness	0.0318
Leaf length	0.0269
% petiole length	0.0241
Leaflet length	0.0227

Table 5. Mahalanobis distances (D^2 ; above the diagonal) and genetic distance (D, Nei 1972; below the diagonal) for the four populations of *Cycas seemannii*.

	‘Eua	Nabou	New Caledonia	Vanuatu
‘Eua	XXX	60.18	8.33	13.40
Nabou	0.1182	XXX	47.58	36.99
New Caledonia	0.2516	0.1530	XXX	9.20
Vanuatu	0.1508	0.0723	0.0507	XXX

The species is named after Berthold Karl Seemann, an English botanist appointed by Hooker at Kew Botanical Gardens to report on the native and cultivated vegetable products of Fiji (Knoll, 2001) and who was the first to collect the species. *Cycas seemannii* shows great variation in its leaf morphology. Plants from different populations often appear distinct even when transplanted and cultivated under similar conditions. For example, plants from 'Eua, Tonga, and New Caledonia have bigger seeds than material from Fiji and Vanuatu. *Cycas seemannii* occupies well-drained spots in coastal vegetation, dry and mesic forest and lowland rainforest. The species is common on limestone formations but may also be abundant on other substrates in non-coastal habitats (Hill, 1994a; Drake *et al.*, 1996; Keppel, 2001; Keppel and Tuiwawa, 2007). On New Caledonia it is mainly restricted to coastal habitats, possibly as a result of a more recent colonisation event (Hill, 1994a; Keppel *et al.*, 2002). In Fiji, the species may also be found in the "talasiga" grasslands, where it is likely to be a remnant of the forests of pre-European times, and occurs at altitudes of 600m in the Nausori highlands.

Selected Specimens Examined

AUSTRALIA: Murray Island, Torres Strait Islands, Queensland, Wannan 2886, 12/05/2003 (NSW).

FIJI: Yanuyanu-i-loma, Ono, Kadavu, Keppel 46, 13/04/2000 (SUVA). Sigatoka Valley, Keppel 34, 23/07/1999 (SUVA). Nawailevu, Bua, Vanua Levu, Keppel 7, 07/12/1998 (SUVA). Nabou Pine Station, Viti Levu, Keppel 4, 18/04/1998 (SUVA); Keppel 17/99, 18/05/1999 May 1999 (SUVA). Sigatoka Valley, Nadroga, Vodonaivalu SV 46/93 (SUVA). Nabau Forestry Reserve, Viti Levu, Hill 4387, 24/3/1993 (NSW). Naivasisi area, Mago Island, Lau Province, Tuisawau AT 0132, 17/08/88 (SUVA). Nawairoro, Dreke, Ba, Koroiveibau 14751, 27/06/1966 (SUVA). Seaqaqa, Macuata, Mc Paul 13198, 04/06/1962 (SUVA). Navuiyari, Nadi, Penisoni L., 19/01/1940 (SUVA).

NEW CALEDONIA: Baie des Tortues, Bourail, New Caledonia, Keppel 38, 07/07/1999 (SUVA). N of Houailu, Hill 4412, 1/05/1993 (NSW). Hienghene, Ilôt Hienga, McKee 31744, 20/08/1976 (NOU). Baaba-Plage, Sud-Ouest, McKee 23228, 06/01/1971 (NOU). Ile Néba, McKee 22724, 08/10/1970 (NOU). Dogny, Nothis 30, 27/02/1966 (NOU). Ilôt Porc Epic, Veillon 529, 18/11/1965 (NOU).

TONGA: Nuku'alofa, Tongatapu, Hill 4396, 30/3/1993 (NSW). Neiafu, Vava'u, Hill 4397, 1/04/1993 (NSW). Tofua Island, Johnson 118, 01/1967 (BRI).

VANUATU: Devils Point, Efate, Keppel 40, 10/07/1999 (SUVA). Malatao River District, Efate, Hill 4429, 05/05/1993, Sakao, Maskelynes, Malekula, Curry 853, 13/11/1992 (PVNH). Wousi, Santo, Bourdy 1162, 05/04/1987 (PVNH). Saritamata, Maewo, Bourdy 565, 23/08/1986. Tsibel, Malekula, Halle 6362, 6363, 02/10/1971 (PVNH).

3.3 Ethnobotany

Cycas seemannii is of great cultural importance in Vanuatu, where it is pictured on the national flag. Vanuatu consists of numerous different islands, most of which differ in their customs and traditions. Therefore, some of the uses described below may only be practised in certain parts of the country. Leaves of the plant have high cultural

status and are used to indicate taboo or restriction but are also a symbol of peace. The plant is ascribed mystic powers and Ala and Osborne (in press) report that "some tribes have beliefs involving the interchanging of the spirits of the cycad and of deceased persons". Cycad leaves are involved in conferring of status upon recipients in an act of initiation and such a rank may be displayed by wearing cycad leaves on belts or tattoos. The leaves are also held up during the guard-of-honour in funeral processions for high-ranking chiefs. (Thaman, 1992; Ala and Osborne, in press).

In addition, *Cycas seemannii* is planted along graves and in dance grounds in Vanuatu. Before ceremonial feasts, pigs are usually tied to it. Leaves of the plant were used to infer punishment upon people guilty of severe crimes by burning with hot leaves. The pinnae on a leaf maybe used for counting and recording numbers, such as the days remaining before important events or the number of people present at such functions. Leaves are also used to communicate messages. The dried sclerotesta of the seed has various uses ranging from cloth pins to various toys. Finally cycads are planted as ornamentals and their leaves are used for decoration in tribal costumes and for other purposes (Thaman, 1992; Ala and Osborne, 2009 in press).

The cultural importance of cycads in Vanuatu appears to be unparalleled in other Pacific countries and, probably, around the world. There are, however, indications that *Cycas seemannii* was of, at least some, cultural importance in Fiji. People living along the banks of the Navua River used the pith of the trunk to prepare cakes that were reserved for exclusive use by chiefs (Seemann, 1865-73, Seemann in Degener, 1949). However, this cultural usage of the plant seems to have been forgotten and no present cultural uses are known in Fiji. In Tonga, cycads are often planted on cemeteries for ornamental purposes and were cultivated for food (Pant, 1973). This practice could well have arisen from cultural traditions that are now forgotten.

Cycads were, probably, an important food plant for the first colonisers of Pacific Islands. In the absence of most present food plants, early inhabitants must have relied on edible products obtained from the native flora and fauna (Guppy, 1906). The seeds, after proper detoxification by washing (Thaman, 1992) or boiling (Degener, 1949), are edible. Often the megagametophyte in the seed is processed into a kind of flour and baked into a type of bread (Parham, 1948). The usage of seeds as an emergency food has been reported from Tonga (Yuncker, 1959), Fiji (Degener, 1949; Parham, 1948), and from New Caledonia (Massal and Barrau, 1956). Consumption of the pith obtained from the trunk, after having been made into a bread in a way similar to the seeds, has been reported from Fiji (Seemann, 1865-73) and probably also occurred in New Caledonia (Massal and Barrau, 1956). Male cones were also utilised as a food source in Fiji (Smith, 1979). The absence of reports on nutritional uses of the plant from Vanuatu may be related to its sacred status in that country.

In all countries of its occurrence, *Cycas seemannii*, is a widely planted ornamental and its leaves, which can retain a fresh appearance for several weeks, are used in decorations. In New Caledonia the empty sclerotesta of seeds were used to prepare rattles used in traditional dances. Inhabitants of Nawailevu Village in Bua on Vanua Levu, Fiji use the mucilage as glue. Considering that

cycads are known to be toxic (Whiting, 1963; Pant, 1973; Spencer *et al.*, 1987), there are surprisingly little reports on the toxic effects of this cycad. However, Fijian farmers in areas where the species occurs know that the consumption of cycad leaves has detrimental effects on cattle.

4. Discussion

This taxonomic description shows *Cycas seemannii* to be morphologically more variable than previously thought (Hill, 1994a). For example, the number of pinnae is reported to be 90 to 300 (compared to 140-230 reported previously; Hill, 1994a), percentage spinescence of the petiole up to 50% (20% previously), length of petiole 15-85cm (25-50cm), thickness of median pinnae to be 0.25-0.75 mm (0.35-0.45 mm), cataphylls to 150 mm (90 mm) long, male cones to 75cm (55cm) long, maximum number of ovules to be 12 (8), and maximum number of lateral spines on megasporophyll lamina to be 45 (30). In addition, standardised colour descriptions and a description of the development of megasporophylls are provided for the first time.

The observed morphological differences among populations seem to be related to the environmental variables of soil fertility, rainfall and amount of light. The population in Nabou is morphologically most distinct (Table 3). Less robust leaves may be caused by the poor fertility of grassland soils (Mueller-Dombois and Fosberg, 1998), lesser amount of rainfall on the western side of Viti Levu (Mueller-Dombois and Fosberg, 1998; Keppel and Tuiwawa, 2007), stress caused by periodical burning or be the result of inbreeding depression as this population, which is much disturbed by man, had zero heterozygosity (Keppel *et al.*, 2002). Leaves are longest in the populations in Vanuatu and New Caledonia, which occur in the shade of canopy trees. Probably as a response to the lower amount of incident light, the leaflets are widest in the two populations growing in forests (Vanuatu and 'Eua). The thicker leaflets and rachis observed in the New Caledonian and 'Euan population may be related to the influence of salt spray in these coastal populations.

Variation in leaf morphology among populations is considerable (Tables 2, 3). Individuals within populations are more similar to each other than to individuals of other populations (Figure 2). Morphological differences are seemingly not caused by genetic differences because there is no correlation between the morphological and genetic distances between populations (Table 5, $r = 0.21$). Therefore, leaf morphology seems to be, at least partially, an adaptation to environmental conditions. Ideally, experiments under controlled conditions should be conducted to further investigate the causes of phenotypic plasticity. However, the slow growth rate and a long maturation period of cycads (Giddy, 1974; Norstog and Nicholls, 1997) make such studies time-consuming and tedious.

The great variation in leaf morphology suggests that great care should be exercised in utilising foliage characters for species identification and in taxonomic keys. De Laubenfels and Adema (1998) provided a key (pg. 368) for *Cycas seemannii* (there regarded as *C. celebica*) that was partially based on leaflet width and spinescence of the petiole. This study shows leaflet width to be one of the most variable leaf characters in *Cycas seemannii* and

seems to depend much on environmental factors (Tables 3, 4). Similarly, the number of leaflets per leaf, proposed to be a diagnostic character in the subsection *Rumphiae* (Hill, 1994a), was very variable (between 93 and 242 leaflets in the individuals investigated here and up to 289 in an individual cultivated at the University of the South Pacific and should not be used for taxonomic purposes.

"Being generally more robust in all features" (Hill, 1994a, pg. 558) was the major differentiating character between *C. bougainvilleana* and *C. seemannii* in the initial treatment of the subsection *Rumphiae*. While this is a useful character in the field, some individuals of *C. seemannii* are similarly robust and the character is only of limited taxonomic utility. The truncate microsporophyll (Hill, 2004, pg. 35) therefore is the taxonomically most useful character in differentiating the two species and underlines the importance of using reproductive characters for taxonomic purposes. Whitmore (1980) advocated the exclusive use of reproductive characters when revising *Agathis*, another gymnosperm genus. Interestingly, he also noted bigger leaves in Solomon Island specimens of *Agathis macrophylla* compared to specimens of the same species from Fiji.

Cycas seemannii is of great cultural importance throughout Vanuatu. This status is unparalleled in other countries it occurs in. Considering the active trade that existed between the various Pacific islands in pre-European times (Kirch and Yen, 1982; Kirch and Hunt, 1988; Cann and Lunn, 1996), one would expect that exchange of customs and traditions also occurred. Indeed, the species appears to have had greater cultural role than it does presently in other Pacific countries. Indications for this to have been the case in Fiji are found in the literature (Seemann, 1865-73; Pant, 1973). The cultural importance of the plant has apparently been long forgotten and its use as a food plant is only remembered by few of the older persons, mostly those from the more remote islands. Most of the villages in Fiji visited by myself could not remember any uses for the plant and many younger people, especially on Viti Levu, could scarcely remember the native name of the plant.

Therefore, the cycad has lost much of its importance in the culture and nutrition of Pacific people. Plants of seemingly no importance to mankind are not looked after and often readily sacrificed for plants that are more useful. The vanishing importance of the plant to native inhabitants in combination with its predominantly coastal habitat, the predominant sites for economic development, impose a threat to the existence to this already declining cycad (Hill, 1994a; Keppel, 2002).

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References

- Ala, P., and Osborne, R. 2009 in press. Some observations on *Cycas seemannii* in Vanuatu. *The Cycad Newsletter*.
- Baillie, J.E.M., Hilton-Taylor, C. and Stuart, S.N. 2004. 2004 IUCN Red List of Threatened Species. A Global Species Assessment. IUCN, Gland, Switzerland and Cambridge, UK.
- Baker, H.G. 1972. Seed weight relation to environmental conditions in California. *Ecology*, **53**, 997-1010.
- Bradshaw, A.D. and Hardwick, K. 1989. Evolution and stress-genotypic and phenotypic components. *Biological Journal of the Linnean Society*, **37**, 137-155.
- Braun, A. 1876. Über zwei von Hildebrandt angeführte Cycadeen nebst Bemerkungen über einige andere Cycadeen. *Sitzungs-Bericht der Gesellschaft Naturforschender Freunde zu Berlin*, 113-125.
- Cann, R.L. and Lunn, J.K. 1996. Mankind and Pacific biogeography. In: *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia*. A. Keast and S.E. Miller (Eds). SPB Academic Publishing, Amsterdam, Netherlands, 437-443.
- Chabot, B.F. and Chabot, J.F. 1977. Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria vesca*. *Oecologia*, **26**, 363-377.
- Chen, C.J., Hill, K.D., and Stevenson, D.W. 2004. Comments on *Cycas*, *Dyerocycas*, and *Epicycas* (Cycadaceae). In: *Cycad Classification. Concepts and Recommendations*. T. Walters and R. Osborne (Eds), CAB International Publishing, Wallingford, Oxfordshire, UK, 57-68.
- Degener, O. 1949. *Naturalist's South Pacific Expedition: Fiji*. Paradise of the Pacific Ltd. Honolulu, Hawaii, USA.
- Drake, D.R., Whistler, W.A., Motley, T.J., and Imada, C.T. 1996. Rain forest vegetation of 'Eua Island, Kingdom of Tonga. *New Zealand Journal of Botany*, **34**, 65-77.
- Giddy, C. 1974. *Cycads of South Africa*. Struik Publishers, Cape Town, South Africa.
- Greguss, P. 1968. *Xylotomy of the Living Cycads – with a Description of their Leaves and Epidermis*. Akadémiai Kiadó, Budapest, Hungary.
- Guillaumin, A. 1938. A florula of the island of Espiritu Santo, one of the New Hebrides; with a prefatory note by the leader of the Oxford University Expedition to the New Hebrides, 1933-34 - John R. Baker. *Journal of the Linnean Society, Botany*, **51**, 547-566.
- Guppy, H.B. 1906. *Observations of a Naturalist in the Pacific between 1896 and 1899*. Volume II: Plant Dispersal. Macmillan and Co., Ltd, London, UK.
- Hill, K.D. 1994a. The *Cycas rumphii* complex (Cycadaceae) in New Guinea and the Western Pacific. *Australian Systematic Botany*, **7**, 543-567.
- Hill, K.D. 1994b. The golden cycad of Fiji. *Encephalartos*, **38**, 11-13.
- Hill, K.D. 1995. Infrageneric relationships, phylogeny, and biogeography of the genus *Cycas* (Cycadaceae). In: *Proceedings of the Third International Conference of Cycad Biology*. P. Vorster (Ed), Cycad Society of South Africa, Stellenbosch, South Africa, 139-162.
- Hill, K.D. 2004. Character evolution, species recognition and classification concepts in the Cycadaceae. In: *Cycad Classification. Concepts and Recommendations*. T. Walters and R. Osborne (Eds), CAB International Publishing, Wallingford, Oxfordshire, UK, 23-44.
- Hill, K.D. and Stevenson, D.W. 1998. *The Cycad Pages*. <http://plantnet.rbgsyd.gov.au/PlantNet/cycad>. (accessed March 2008)
- Jackson, L.W.R. 1967. Effect of shade on leaf structure of deciduous tree species. *Ecology*, **48**, 498-499.
- Kanehira, R. 1938. On the Micronesian species of *Cycas*. *Japanese Journal of Botany*, **14** 579-588.
- Keppel, G. 2001. Notes on the Natural History of *Cycas seemannii* (Cycadaceae). *South Pacific Journal of Natural Sciences*, **19**, 35-42.
- Keppel, G. 2001. Low genetic variation in a Pacific cycad: Conservation concerns for *Cycas seemannii* (Cycadaceae). *Oryx*, **36**, 41-49.
- Keppel, G., Hodgskiss, P.D. and Plunkett, G.M. 2008. Cycads in the insular Southwest Pacific: dispersal or vicariance? *Journal of Biogeography*, **35**, 1004-1015.
- Keppel, G., Lee, S.-W. and Hodgskiss, P.D. 2002. Evidence for long isolation among populations of a Pacific cycad: genetic diversity and differentiation in *Cycas seemannii* A. Br. (Cycadaceae). *Journal of Heredity*, **93**, 133-139.
- Keppel, G. and Tuiwawa, M. 2007. Dry zone forests of Fiji: species composition, life history traits, and conservation. *New Zealand Journal of Botany*, **45**, 545-563.
- Kirch, P.V. and Hunt, T.L. 1988. The spatial and temporal boundaries of Lapita. In: *Archaeology of the Lapita cultural complex: a critical review*. P.V. Kirch and T.L. Hunt (Eds), Thomas Burke Memorial Washington State Museum, Research Report No.5. Burke Museum, Seattle, USA, 9-31.
- Kirch, P.V. and Yen, D.E. 1982. Tikopia. The prehistory and ecology of a Polynesian outlier. *Bernice P. Bishop Museum Bulletin*, **238**(complete).
- Knoll, J. 2001. Berthold Seemann. *Aus den Herrenhäuser Gärten*, **3/2001**, 2-11.
- Kornerup, A. and Wanscher J.H. 1967. *Methuen Handbook of Colour*. Methuen, London, UK.
- Laubenfels, J.D. de 1972. Gymnospermes. In: *Flore de la Nouvelle-Calédonie et Dépendances*, A. Aubréville and J.F. Leroy (Eds), Muséum National D'Histoire Naturelle, Paris, France.
- Laubenfels, J.D. de and Adema, F. 1998. A taxonomic revision of the genera *Cycas* and *Epicycas* gen.nov. (Cycadaceae). *Blumea*, **43**, 351-400.
- Linden, L. 1881. Plantes introduites et mises pour la première fois dans de commerce. *Illustrationes Horticole*, **28**, 32.
- Lindström, A. 2004. Morphological characters useful in determining species boundaries in *Cycas* (Cycadaceae). In: *Cycad Classification. Concepts and Recommendations*, T. Walters and R. Osborne (Eds). CAB International Publishing, Wallingford, Oxfordshire, UK, 23-44.

- Mueller-Dombois, D. and Fosberg, F.R. 1998. *Vegetation of the Tropical Pacific Islands*. Springer-Verlag, New York, USA.
- Massal, E. and J. Barrau. 1956. *Food Plants of the South Sea Islands*. South Pacific Commission Technical Paper No.94. South Pacific Commission, Noumea, New Caledonia.
- Nei, M. 1972. Genetic distance between populations. *The American Naturalist*, **106**, 283-292.
- Newell, S.J. 1985. Intrapopulational variation in leaflet morphology of *Zamia pumila* L. in relation microenvironment and sex. *American Journal of Botany*, **72**, 217-221.
- Newell, S.J. 1989. Variation in leaflet morphology among populations of Caribbean cycads (*Zamia*). *American Journal of Botany*, **76**, 1518-1523.
- Norstog, K.J. and Nicholls, T.J. 1997. *The Biology of the Cycads*. Cornell University Press, New York, USA.
- Pant, D.D. 1973. *Cycas and the Cycadales*. Central Book Depot, Allahbad, Pakistan.
- Parham, J.W. 1948. The botanical gardens, Suva. *Fiji Agricultural Journal*, **19**: 88-105.
- SAS Institute Inc. 1988. *SAS/STAT® User's Guide, Release 6.03 Edition*. SAS Institute Inc. Cary, North Carolina, USA.
- Schuster, J. 1932. Cycadaceae. *Das Pflanzenreich* **99**, 1-168.
- Seemann, B. 1865-73. *Flora Vitiensis: A Description of the Plants of the Viti or Fiji Islands with an Account of their History, Uses, and Properties*. L. Reeve and Co., London, UK.
- Smith, A.C. 1979. *Flora Vitiensis Nova. A New Flora of Fiji (Spermatophytes only). Volume 1 – Introduction. Gymnospermae, Families 1-6. Angiospermae: Monocotyledones, Families 7-43 (except Family 32. Orchidaceae)*. Pacific Tropical Botanical Garden, Lawai, Kauai, Hawaii, USA.
- Smith, W.K. and Nobel, P.S. 1977. Influences of seasonal changes in leaf morphology on water-use efficiency for three desert broadleaf shrubs. *Ecology*, **58**, 1033-1043.
- Smith, W.K. and Nobel, P.S. 1978. Influence of irradiation, soil water potential, and leaf temperature on leaf morphology of a desert broadleaf, *Encelia farinosa* Gray (Compositae). *American Journal of Botany*, **65**, 429-432.
- Spencer, P.S., Nunn, P.B., Hugon, J., Ludolph, A.C., Ross, S.M., Roy D.W. and Robertson, R.C. 1987. Guam amyotrophic lateral sclerosis-parkinsonism-dementia linked to plant excitant neurotoxin. *Science*, **237**, 517-522.
- Stearns, S.C. 1989. The evolutionary significance of phenotypic plasticity. *BioScience*, **39**, 436-445.
- Sultan, S.E. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evolutionary Biology* **21**: 127-176.
- Sultan S.E. and Bazzaz, F.A. 1993a. Phenotypic plasticity in *Polygonum persicaria*. I. Diversity and uniformity in genotypic norms of reaction to light. *Evolution*, **47**, 1009-1031.
- Sultan S.E. and Bazzaz, F.A. 1993b. Phenotypic plasticity in *Polygonum persicaria*. II. Norms of reaction to soil moisture, ecological breadth, and the maintenance of genetic diversity. *Evolution*, **47**, 1032-1049.
- Thaman, R.R. 1992. Batiri kei Baravi: The ethnobotany of Pacific island coastal plants. *Atoll Research Bulletin*, **361**, 1-62.
- UNEP. 2008. *Convention on International Trade in Endangered Species of Wild Flora and Fauna*. <http://www.cites.org/eng/app/appendices.shtml> (accessed March 2009).
- Whiting, M.G. 1963. Toxicity of cycads. *Economic Botany*, **17**, 270-302.
- Whitmore, T.C. 1980. A monograph of *Agathis*. *Plant Systematics and Evolution*, **135**, 41-69.
- Yuncker, T.G. 1959. *Plants of Tonga*. Bernice P. Bishop Museum Bulletin 220. Honolulu, Hawaii, USA.

Correspondence to: Gunnar Keppel
(gunnar.keppel@gmail.com)