






Review

# Chemical Element Concentrations of Cycad Leaves: Do We Know Enough?

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**Abstract:** The literature containing which chemical elements are found in cycad leaves was reviewed to determine the range in values of concentrations reported for essential and beneficial elements. We found 46 of the 358 described cycad species had at least one element reported to date. The only genus that was missing from the data was *Microcycas*. Many of the species reports contained concentrations of one to several macronutrients and no other elements. The cycad leaves contained greater nitrogen and phosphorus concentrations than the reported means for plants throughout the world. Magnesium was identified as the macronutrient that has been least studied. Only 14 of the species were represented by data from in situ locations, with most of the data obtained from managed plants in botanic gardens. Leaf element concentrations were influenced by biotic factors such as plant size, leaf age, and leaflet position on the rachis. Leaf element concentrations were influenced by environmental factors such as incident light and soil nutrient concentrations within the root zone. These influential factors were missing from many of the reports, rendering the results ambiguous and comparisons among studies difficult. Future research should include the addition of more taxa, more in situ locations, the influence of season, and the influence of herbivory to more fully understand leaf nutrition for cycads.

**Keywords:** *Bowenia*; *Ceratozamia*; Cycadaceae; *Cycas*; *Dioon*; *Encephalartos*; leaf element composition; leaf tissue analysis; *Lepidozamia*; *Macrozamia*; *Stangeria*; *Zamia*; *Zamiaceae*

## 1. Background

Effective horticultural management of economic crops or threatened plant taxa requires an adequate understanding of essential nutrient accumulation, partitioning among organs, and remobilization prior to organ senescence. These biological phenomena influence many issues such as attractiveness to herbivores, the speed of litter decomposition, and soil changes within the zone of root proliferation and leaf litterfall. Knowledge of the concentrations of essential elements in plant organs is useful for determining plant health, diagnosing the cause of an observable problem, and measuring the efficacy of a fertilizer program [1–3]. Therefore, plant tissue analysis has been part of the traditional toolbox to

meet management goals in agronomy, horticulture, and silviculture or to improve knowledge about the ecology of tree species.

In any testing procedure designed to determine the presence or absence of a measurable component from a sample, adherence to protocols that were developed through verifiable research is mandatory for achieving unambiguous results [4]. Moreover, recording and reporting the biological and environmental factors which are known to influence plant nutrient concentrations are necessary for methods to become standardized and repeatable, engender trust in the results, and to justify comparisons among studies.

The group of gymnosperm plants known as cycads is comprised of the mono-generic Cycadaceae family with 117 species and the Zamiaceae family with nine genera and 241 described species [5]. Research in applied sciences such as horticulture has been insufficient for members of this plant group [6,7]. For example, the global agenda of understanding how leaf element concentrations correlate with leaf functional traits has not sufficiently included cycad species [8]. This research agenda has expanded substantially in the past six years, and the subject has never been reviewed to date.

The aim of our review is to report which taxonomic groups have been most studied, to compile a listing of the published chemical element concentration data for cycad leaves, and to establish protocols for continued research to ensure the results are comparable among the various laboratories that contribute to the agenda in the future. Moreover, we conclude with a discussion of possible future research directions with the hope of inspiring more demanding protocols to better meet horticulture and conservation goals.

## 2. Species Studied

The literature search identified 18 publications in the primary literature in which the concentration of at least one chemical element was reported as a constituent of leaf tissue for at least one cycad species. Our primary focus was the essential nutrients, those chemical elements that are directly involved in plant function and are required by plants to complete the life cycle. Macronutrients are required in greater quantities, and micronutrients are required in small amounts. We also report beneficial nutrients, those chemical elements that may stimulate growth in some plants but do not meet the requirements of being essential. Other chemical elements which were reported in some studies were not included in this review. The numerical concentrations of elements which were presented in figures were estimated. Some reports used logarithmic data to meet parametric statistical requirements or to smooth regression modeling. In order to standardize our reported data into one format, we transformed these data to numerical concentrations. Misspelled species names were corrected and included if the mistake was easily diagnosed. Data were not included if misspelled species names could not be determined to be a currently accepted species. Synonyms or other obsolete names with an accepted binomial [5] were reported for the currently accepted binomial. These methods identified a total of 46 cycad species from the literature search (Table 1). In addition to the taxonomic authority, we also included the countries in which each species is considered endemic or indigenous. Leaf sampling from plants growing within natural habitat were considered “in situ” and leaf sampling from plants that were growing in managed gardens were considered “ex situ.”

**Table 1.** Forty-six cycad species with reported leaf element concentrations.

Species	Family	Taxonomic Authority	Native Range
<i>Bowenia serrulata</i>	Zamiaceae	(W. Bull) Chamb.	Australia
<i>Bowenia spectabilis</i>	Zamiaceae	Hook. ex Hook.f.	Australia
<i>Ceratozamia mexicana</i>	Zamiaceae	Brongn.	Mexico
<i>Cycas armstrongii</i>	Cycadaceae	Miq.	Australia
<i>Cycas debaoensis</i>	Cycadaceae	Y.C.Zhong & C.J.Chen	China
<i>Cycas diannanensis</i>	Cycadaceae	Z.T.Guan & G.D. Tao	China
<i>Cycas elongata</i>	Cycadaceae	(Leandri) D.Yue Wang	Vietnam
<i>Cycas fairylakea</i>	Cycadaceae	(Leandri) D.Yue Wang	China
<i>Cycas media</i>	Cycadaceae	R.Br.	Australia
<i>Cycas micholitzii</i>	Cycadaceae	Dyer	Laos, Vietnam

Table 1. Cont.

Species	Family	Taxonomic Authority	Native Range
<i>Cycas micronesica</i>	Cycadaceae	K.D. Hill	Guam, Rota, Palau, Yap
<i>Cycas nitida</i>	Cycadaceae	K.D.Hill & A.Lindstr.	Philippines
<i>Cycas nongnoochiae</i>	Cycadaceae	K.D.Hill	Thailand
<i>Cycas panzhihuaensis</i>	Cycadaceae	L.Zhou & S.Y.Yang	China
<i>Cycas revoluta</i>	Cycadaceae	Thunb.	China, Japan
<i>Cycas rumphii</i>	Cycadaceae	Miq.	Australia, Indonesia, Papua New Guinea
<i>Cycas sexseminifera</i>	Cycadaceae	F.N.Weii	China, Vietnam
<i>Cycas siamensis</i>	Cycadaceae	Miq.	Cambodia, Laos, Myanmar, Thailand, Vietnam
<i>Cycas szechuanensis</i>	Cycadaceae	W.C.Cheng & L.K.Fu	China
<i>Cycas thouarsii</i>	Cycadaceae	R.Br. ex Gaudich	Comoros, Kenya, Madagascar, Mozambique, Seychelles, Tanzania
<i>Cycas wadei</i>	Cycadaceae	Merr.	Philippines
<i>Dioon edule</i>	Zamiaceae	Lindl.	Mexico
<i>Dioon mejiae</i>	Zamiaceae	Standl. & L.O.Williams	Honduras
<i>Dioon sonorensis</i>	Zamiaceae	(De Luca, Sabato & Vázq.Torres) Chemnick, T.J.Greg. & Salas-Mor.	Mexico
<i>Dioon spinulosum</i>	Zamiaceae	Dyer ex Eichler	Mexico
<i>Encephalartos cupidus</i>	Zamiaceae	R.A.Dyer	South Africa
<i>Encephalartos ferox</i>	Zamiaceae	G.Bertol	Mozambique, South Africa
<i>Encephalartos gratus</i>	Zamiaceae	Prain	Malawi, Mozambique
<i>Lepidozamia hopei</i>	Zamiaceae	Regel	Australia
<i>Lepidozamia peroffskyana</i>	Zamiaceae	Regel	Australia
<i>Macrozamia communis</i>	Zamiaceae	L.A.S.Johnson	Australia
<i>Macrozamia lucida</i>	Zamiaceae	L.A.S.Johnson	Australia
<i>Macrozamia macleayi</i>	Zamiaceae	Miq.	Australia
<i>Macrozamia moorei</i>	Zamiaceae	F.Muell.	Australia
<i>Macrozamia mountperriensis</i>	Zamiaceae	F.M.Bailey	Australia
<i>Macrozamia parvifolia</i>	Zamiaceae	P.I.Forst. & D.L.Jones	Australia
<i>Macrozamia reidleyi</i>	Zamiaceae	(Gaudich.) C.A.Gardner	Australia
<i>Macrozamia serpentina</i>	Zamiaceae	D.L.Jones & P.I.Forst	Australia
<i>Stangeria eriopus</i>	Zamiaceae	(Kunze) Baill.	South Africa
<i>Zamia erosa</i>	Zamiaceae	O.F.Cook & G.N.Collins	Cuba, Jamaica, Puerto Rico
<i>Zamia fischeri</i>	Zamiaceae	Miq.	Mexico
<i>Zamia furfuracea</i>	Zamiaceae	L.f.	Mexico
<i>Zamia integrifolia</i>	Zamiaceae	L.f.	Bahamas, Cayman Islands, Cuba, United States
<i>Zamia portoricensis</i>	Zamiaceae	Urb.	Puerto Rico
<i>Zamia splendens</i>	Zamiaceae	Schutzman	Mexico
<i>Zamia standleyi</i>	Zamiaceae	Schutzman	Guatemala, Honduras
<i>Zamia vazquezii</i>	Zamiaceae	D.W.Stev., Sabato & De Luca	Mexico

### 3. Green Leaf Elements

#### 3.1. The Elements

Laboratory methods have varied among the years and among laboratories. The oldest articles in our review quantified nitrogen with Kjeldahl digestion, and most contemporary articles employ dry combustion approaches for nitrogen. The other minerals and metals are digested from the tissue, with nitric acid being used most often. Quantification is done with spectrometry most common in the earliest publications and spectroscopy being used more often in recent years. Macronutrient concentrations in cycad leaf tissue were highly variable among the elements. The total carbon found in cycad leaves was less variable than the other elements and ranged from 438–566 mg·g<sup>-1</sup> among taxa of nine genera (Table 2) [9–17]. The range in nitrogen concentration in the cycad leaf tissue was considerable, with a 6.9-fold difference among the species and studies and considerable overlap among the nine genera [9–23]. The phosphorus concentration of the cycad leaf tissue was less variable than nitrogen, with a 4.9-fold difference among the species and studies represented by nine genera [9–14,17–20]. Potassium concentration was highly variable with a 7.6-fold difference among the

nine genera studied [9–14,17–20,23,24]. Magnesium was determined for only two genera, yet the range in concentration was substantial with a 7.5-fold difference among the studies [11–14,17,18,20,22,24]. The calcium concentration of cycad leaf tissue was more variable than the other macronutrients, with a 19.8-fold difference among the nine genera and studies [9,11–14,17,18,20,23,24]. Sulfur concentration in cycad leaf tissue was also highly variable with a 22.8-fold difference among the nine genera and studies [9,17,19,20,23].

**Table 2.** Published ranges in green leaf concentrations of macronutrients, micronutrients, and beneficial elements for cycad plants.

Element	Genera	Species Studied	Species in Genus	Range	Reference
Aluminum	<i>Cycas</i>	1	117	22–60 mg·kg <sup>-1</sup>	[23]
Boron	<i>Cycas</i>	2	117	11.6–43.4 mg·kg <sup>-1</sup>	[11–14,20]
Calcium	<i>Bowenia</i>	2	2	5.0–6.1 mg·g <sup>-1</sup>	[9]
Calcium	<i>Ceratozamia</i>	1	32	7.1 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas</i>	14	117	1.2–23.7 mg·g <sup>-1</sup>	[9,11–14,17,18,20,24]
Calcium	<i>Dioon</i>	3	16	7.6–8.4 mg·g <sup>-1</sup>	[9]
Calcium	<i>Encephalartos</i>	3	65	4.5–14.3 mg·g <sup>-1</sup>	[9]
Calcium	<i>Lepidozamia</i>	2	2	3.6–5.0 mg·g <sup>-1</sup>	[9]
Calcium	<i>Macrozamia</i>	4	41	1.4–7.1 mg·g <sup>-1</sup>	[9,23]
Calcium	<i>Stangeria</i>	1	1	7.1 mg·g <sup>-1</sup>	[9]
Calcium	<i>Zamia</i>	5	81	3.0–7.7 mg·g <sup>-1</sup>	[9]
Carbon	<i>Bowenia</i>	2	2	508–519 mg·g <sup>-1</sup>	[9]
Carbon	<i>Ceratozamia</i>	1	32	514 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas</i>	13	117	463–509 mg·g <sup>-1</sup>	[9–14,17]
Carbon	<i>Dioon</i>	3	16	485–496 mg·g <sup>-1</sup>	[9]
Carbon	<i>Encephalartos</i>	3	65	490–505 mg·g <sup>-1</sup>	[9]
Carbon	<i>Lepidozamia</i>	2	2	438–566 mg·g <sup>-1</sup>	[9,16]
Carbon	<i>Macrozamia</i>	5	41	512–524 mg·g <sup>-1</sup>	[9,16]
Carbon	<i>Stangeria</i>	1	1	479 mg·g <sup>-1</sup>	[9]
Carbon	<i>Zamia</i>	7	81	477–491 mg·g <sup>-1</sup>	[9,15]
Chloride	<i>Cycas</i>	1	117	0.5–2.3 mg·g <sup>-1</sup>	[24]
Copper	<i>Cycas</i>	2	117	2.0–17.9 mg·kg <sup>-1</sup>	[11–14,18,20]
Copper	<i>Macrozamia</i>	1	41	2.1–2.8 mg·kg <sup>-1</sup>	[22]
Iron	<i>Bowenia</i>	2	2	189–207 mg·kg <sup>-1</sup>	[9]
Iron	<i>Ceratozamia</i>	1	32	106 mg·kg <sup>-1</sup>	[9]
Iron	<i>Cycas</i>	14	117	27–410 mg·kg <sup>-1</sup>	[9,11–14,18–20,24]
Iron	<i>Dioon</i>	3	16	117–163 mg·kg <sup>-1</sup>	[9]
Iron	<i>Encephalartos</i>	3	65	93–363 mg·kg <sup>-1</sup>	[9,19]
Iron	<i>Lepidozamia</i>	2	2	166–176 mg·kg <sup>-1</sup>	[9]
Iron	<i>Macrozamia</i>	3	41	83–253 mg·kg <sup>-1</sup>	[9]
Iron	<i>Stangeria</i>	1	1	228 mg·kg <sup>-1</sup>	[9]
Iron	<i>Zamia</i>	6	81	142–1700 mg·kg <sup>-1</sup>	[9,19]
Magnesium	<i>Cycas</i>	4	117	1.4–8.2 mg·g <sup>-1</sup>	[11–14,17,18,20,24]
Magnesium	<i>Macrozamia</i>	1	41	1.1–1.9 mg·g <sup>-1</sup>	[22]
Manganese	<i>Cycas</i>	3	117	20–152 mg·kg <sup>-1</sup>	[11–14,18,20,24]
Manganese	<i>Macrozamia</i>	1	41	6–57 mg·kg <sup>-1</sup>	[22]
Nitrogen	<i>Bowenia</i>	2	2	24–41 mg·g <sup>-1</sup>	[9,16]
Nitrogen	<i>Ceratozamia</i>	1	32	13 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas</i>	17	117	16–44 mg·g <sup>-1</sup>	[9–21]
Nitrogen	<i>Dioon</i>	4	16	14–17 mg·g <sup>-1</sup>	[9,22]
Nitrogen	<i>Encephalartos</i>	3	65	15–19 mg·g <sup>-1</sup>	[9,19]
Nitrogen	<i>Lepidozamia</i>	2	2	17–31 mg·g <sup>-1</sup>	[9,16]
Nitrogen	<i>Macrozamia</i>	8	41	8–55 mg·g <sup>-1</sup>	[9,16,21,23]
Nitrogen	<i>Stangeria</i>	1	1	22 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Zamia</i>	8	81	12–30 mg·g <sup>-1</sup>	[9,15,19]
Phosphorus	<i>Bowenia</i>	2	2	1.0–1.1 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Ceratozamia</i>	1	32	0.8 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas</i>	14	117	0.7–3.4 mg·g <sup>-1</sup>	[9–14,17–20]
Phosphorus	<i>Dioon</i>	3	16	0.8–1.5 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Encephalartos</i>	3	65	1.0–1.3 mg·g <sup>-1</sup>	[9,19]

Table 2. Cont.

Element	Genera	Species Studied	Species in Genus	Range	Reference
Phosphorus	<i>Lepidozamia</i>	2	2	0.8–1.2 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Macrozamia</i>	4	41	0.5–1.2 mg·g <sup>-1</sup>	[9,21]
Phosphorus	<i>Stangeria</i>	1	1	1.1 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Zamia</i>	6	81	0.7–1.3 mg·g <sup>-1</sup>	[9,19]
Potassium	<i>Bowenia</i>	2	2	5.5–6.2 mg·g <sup>-1</sup>	[9]
Potassium	<i>Ceratozamia</i>	1	32	4.9 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas</i>	15	117	3.1–23.7 mg·g <sup>-1</sup>	[9–14,17,18,20,24]
Potassium	<i>Dioon</i>	3	16	5.7–11.5 mg·g <sup>-1</sup>	[9,19]
Potassium	<i>Encephalartos</i>	3	65	6.2–8.9 mg·g <sup>-1</sup>	[9]
Potassium	<i>Lepidozamia</i>	2	2	9.5–10.6 mg·g <sup>-1</sup>	[9]
Potassium	<i>Macrozamia</i>	4	41	5.1–11.3 mg·g <sup>-1</sup>	[9,23]
Potassium	<i>Stangeria</i>	1	1	8.0 mg·g <sup>-1</sup>	[9]
Potassium	<i>Zamia</i>	6	81	4.6–18.0 mg·g <sup>-1</sup>	[9]
Selenium	<i>Cycas</i>	2	117	0.41–0.58 mg·kg <sup>-1</sup>	[11,12]
Sodium	<i>Cycas</i>	2	117	0.2–1.2 mg·g <sup>-1</sup>	[12,24]
Sodium	<i>Macrozamia</i>	1	41	0.3–1.0 mg·g <sup>-1</sup>	[23]
Sulfur	<i>Bowenia</i>	2	2	1.9 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Ceratozamia</i>	1	32	1.4 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Cycas</i>	12	117	0.8–2.6 mg·g <sup>-1</sup>	[9,17,19,20]
Sulfur	<i>Dioon</i>	3	16	1.1–1.4 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Encephalartos</i>	3	65	0.8–2.2 mg·g <sup>-1</sup>	[9,19]
Sulfur	<i>Lepidozamia</i>	2	2	1.4–1.6 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Macrozamia</i>	4	41	0.8–1.9 mg·g <sup>-1</sup>	[9,23]
Sulfur	<i>Stangeria</i>	1	1	2.3 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Zamia</i>	5	81	0.6–13.7 mg·g <sup>-1</sup>	[9,19]
Zinc	<i>Bowenia</i>	2	2	19–21 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Ceratoamia</i>	1	32	24 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas</i>	14	117	6–70 mg·kg <sup>-1</sup>	[9,11–14,18,20,24]
Zinc	<i>Dioon</i>	3	16	12–23 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Encephalartos</i>	3	65	11–22 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Lepidozamia</i>	2	2	23–25 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Macrozamia</i>	4	41	4–22 mg·kg <sup>-1</sup>	[9,22]
Zinc	<i>Stangeria</i>	1	1	53 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Zamia</i>	6	81	11–38 mg·kg <sup>-1</sup>	[9]

Micronutrient concentrations in cycad leaf tissue were also highly variable among the elements and studies. Iron and zinc were the only micronutrients included in numerous articles, with nine genera represented among the studies for each element (Table 2). Iron was also the only element exhibiting one extreme outlier species, with *Zamia fischeri* [9,18] exhibiting iron concentrations more than 4-fold greater than the range of the remaining 33 species that have been studied [9,11–14,18–20,24]. The remaining micronutrients have not been observed adequately. Leaf chloride concentrations were reported for a single *Cycas* species [24], boron concentrations were reported for only two species [11–14,20], copper concentrations were reported for three species [11–14,18,20,22], and manganese concentrations were reported for four species [11–14,18,20,22,24]. The cycad leaf content of the micronutrients molybdenum and nickel have not been reported for any cycad species.

Several beneficial elements have been reported from cycad leaf tissue (Table 2). Aluminum concentration has been reported for one species [23], selenium has been reported for two species [11,12], and sodium has been reported for three species [12,23,24]. The remaining beneficial nutrients have not been studied in the context of cycad leaf physiology.

### 3.2. The Taxa

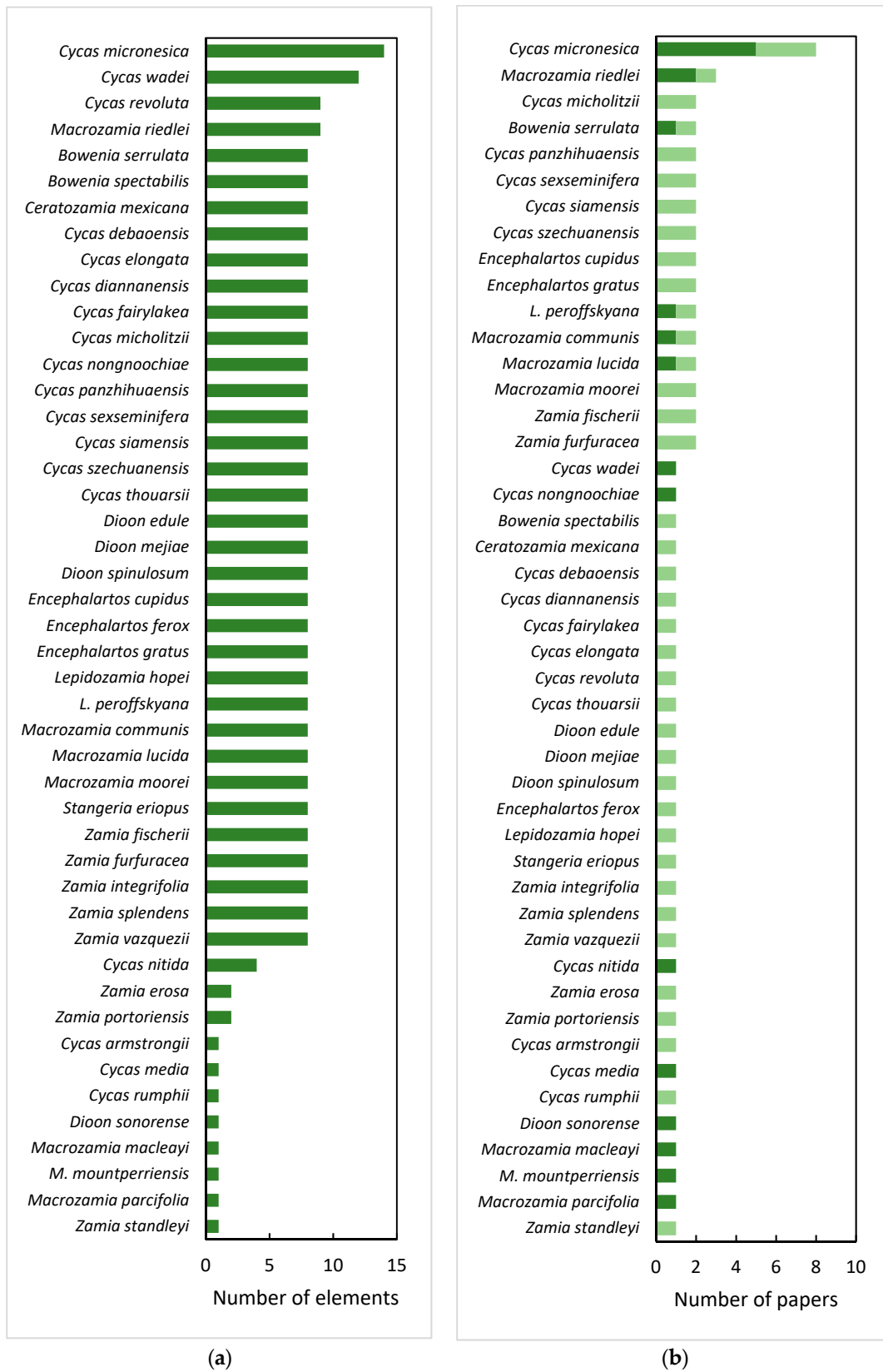
*Bowenia*, *Lepidozamia*, and *Stangeria* contain only one or two species each, and every one of these species was included in the literature review (Table 2, Table A1). *Cycas* contains more species than any other cycad genus and also is the genus with most species represented in this research agenda. However, on a percentage basis only 16% of *Cycas* species have been studied, compared with 20% of

*Macrozamia* species. Other speciose genera are *Encephalartos* with 5% of the species studied and *Zamia* with 10% of the species studied. The monotypic *Microcycas* was the only cycad genus that has not been included in this research agenda to date. The reported ranges in nutrient concentration did not appear to be constrained within each genus. For example, the least and greatest concentrations for some nutrients were reported within a single genus (Table 2).

The number of genera and species that have been studied for each element was greatest for most of the macronutrients, as would be expected. These are the chemical elements that are needed in greatest quantity by plants, and they comprise the core constituents of most commercial fertilizers that are manufactured to increase plant growth and productivity. Nitrogen was the most studied element with nine genera and 46 of the 358 described cycad species [5] being represented among 14 reports (Table 2). For unknown reasons, the inclusion of the macronutrient magnesium in cycad leaf tissue studies has been minimal, with only five species and two genera included. The micronutrients were much less represented in the literature. Iron and zinc were the only micronutrients that received considerable attention in this agenda. The remainder of the micronutrients have been mostly ignored during past research, with one to four *Cycas* and *Macrozamia* species included for each micronutrient. The leaf concentrations for only three of the six beneficial nutrients have been reported to date (Table 2), and each of these were represented by one or two *Cycas* or *Macrozamia* species.

Only two species have had more than 10 essential or beneficial elements reported, and both were *Cycas* species (Figure 1a). Ten of the 46 species had only one or two leaf elements reported. The most heavily studied species was *Cycas micronesica*, and five of the eight studies for this species included in situ data (Figure 1b). Only 14 of the 45 species were represented with in situ data. About two-thirds of the species were represented by only one study.

The original heavily cited description of the global leaf economic spectrum known as GLOPNET [21] compiled data from 2548 species and included nitrogen and potassium among the leaf traits that were built into the model. Their global average for leaf nitrogen was  $19.4 \text{ mg}\cdot\text{g}^{-1}$ . Our mean of leaf nitrogen concentration for cycad leaves was  $22.8 \text{ mg}\cdot\text{g}^{-1}$ , the greater value possibly occurring because of the nitrogen-fixing cyanobacteria endosymbionts for cycads [6]. The GLOPNET data included 155 species identified as having nitrogen-fixing endosymbionts, including one *Cycas* and one *Macrozamia* species [21]. The nitrogen mean for this subset was  $25.7 \text{ mg}\cdot\text{g}^{-1}$ , indicating cycad leaves contain less nitrogen on average than angiosperm plants that associate with nitrogen-fixing endosymbionts. The global average for leaf phosphorus was  $1.1 \text{ mg}\cdot\text{g}^{-1}$ , less than our mean of  $1.3 \text{ mg}\cdot\text{g}^{-1}$  for cycad species with reported phosphorus values. Overall, our findings indicated the reported values for nitrogen and phosphorus in cycad leaves were greater than the global average. However, this direct comparison suffers from procedural ambiguities. The compilers of the GLOPNET data were careful to restrict their methods to natural settings where the plants received no management of any type (Peter Reich, personal communication). Most of the published cycad reports included leaf data from managed plants in botanic gardens, and many of the studies failed to describe irrigation and fertilization protocols that preceded the sampling dates. Moreover, the explicit comparisons of cycads to leaf economic spectrum fundamentals [9,19,25] were based exclusively on managed botanic garden plants. Managed garden plants of two *Cycas* species were compared with in situ plants to indicate the managed plants produced leaves with macronutrient concentrations that were not similar to the unmanaged plants [20]. For example, *C. nongnoochiae* leaves from garden plants contained 2.6-fold greater phosphorus and 4.1-fold greater potassium than in situ plants. This species grows in one locality in central Thailand and exhibits an extreme small endemic range. Clearly, most published leaf element data from cycad species are not currently useful for comparison to GLOPNET.



**Figure 1.** Statistics of forty-six cycad species. (a) Number of essential and beneficial elements reported from leaves. (b) Number of papers containing leaf element data. Dark green portions of bars depict the number of papers with in situ data.

#### 4. Leaf Litter Elements

The elemental constituents of leaf litter interplay with many cascading ecosystem phenomena, such as plant soil feedback [26–29], the home field advantage in decomposition [30,31], and the soil food web [32–34]. Moreover, an understanding of leaf litter nitrogen is critically important for plant species in Fabaceae because these plants enter into symbiotic relationships with nitrogen-fixing bacteria (*Rhizobium*) and Cycadales because these plants enter into symbiotic relationships with nitrogen-fixing cyanobacteria (*Nostoc*) [35]. Therefore, some of the nitrogen released during litter decomposition for these plant groups represents new contributions to the bulk soil. Other plant groups that do not have nitrogen-fixing endosymbionts must absorb the required nitrogen from the edaphic substrates, then their litterfall contains that same nitrogen that is returned to the same edaphic substrates. Direct measurement of leaf litter chemistry is required for each species because translocation of green leaf elements back into the stem tissue occurs during the dismantling of a leaf's machinery as senescence commences. The percentage of resorption of each element is species-specific [36,37].

A literature review of cycad leaf litter chemistry reveals the definition of generalities is impossible because so few species have been studied. Leaf litter content of carbon and nitrogen has been determined for four *Cycas* [10,11,18,20,35,38] and two *Macrozamia* [16] species (Table 3). One to four *Cycas* species have been studied for other essential and beneficial elements (Table A2).

**Table 3.** Published ranges in leaf litter concentrations of macronutrients, micronutrients, and beneficial elements for cycad plants.

Element	Genera	Species Studied	Species in Genus	Range	Reference
Carbon	<i>Cycas</i>	3	117	475–534 mg·g <sup>-1</sup>	[10,11,18,35,38]
Carbon	<i>Macrozamia</i>	2	41	502–546 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Cycas</i>	4	117	15–22 mg·g <sup>-1</sup>	[10,11,18,35,38]
Nitrogen	<i>Macrozamia</i>	2	41	11–24 mg·g <sup>-1</sup>	[16]
Phosphorus	<i>Cycas</i>	4	117	0.3–2.0 mg·g <sup>-1</sup>	[10,11,18,38]
Potassium	<i>Cycas</i>	4	117	1.0–14.2 mg·g <sup>-1</sup>	[10,11,18,38]
Magnesium	<i>Cycas</i>	3	117	1.32–7.54 mg·g <sup>-1</sup>	[11,17,38]
Calcium	<i>Cycas</i>	3	117	2.5–32.3 mg·g <sup>-1</sup>	[11,18,38]
Sulfur	<i>Cycas</i>	1	117	1.20–1.38 mg·g <sup>-1</sup>	[38]
Iron	<i>Cycas</i>	2	117	28–547 mg·kg <sup>-1</sup>	[11,18,38]
Manganese	<i>Cycas</i>	2	117	25–141 mg·kg <sup>-1</sup>	[11,18,38]
Boron	<i>Cycas</i>	2	117	29.5–51.6 mg·kg <sup>-1</sup>	[11,38]
Copper	<i>Cycas</i>	2	117	1.3–5.9 mg·kg <sup>-1</sup>	[11,18,38]
Zinc	<i>Cycas</i>	2	117	4.48–31.21 mg·kg <sup>-1</sup>	[11,18,38]
Selenium	<i>Cycas</i>	1	117	0.48 mg·kg <sup>-1</sup>	[11]

#### 5. Biotic Factors

The direct influence of leaf age on nutrient concentration has been reported for three cycad species [13,16]. A 33% decline in leaf nitrogen occurred from youngest to oldest *C. micronesica* leaves [13], a 12% decline in leaf nitrogen occurred from youngest to oldest *M. communis* leaves [16], and a 13% increase in leaf nitrogen occurred from youngest to oldest *M. riedlei* leaves [16]. The leaf crown on a cycad plant is comprised of several cohorts of leaves with disparate age, each of which is separated by persisting cataphylls. The determination of the youngest cohort and the oldest cohort of leaves is unambiguous due to the persisting cataphylls. These contrasting results for three species were unexpected and point out the need to determine how leaf age influences leaf elements for more cycad species. The increase in nitrogen with leaf age for *M. riedlei* is in sharp contrast to the robust literature on the subject of nutrient resorption. Moreover, the description of which leaves were sampled from the plants in most cycad reports reviewed herein was not included. This oversight must be corrected in future studies. The persistence of cataphylls in cycad leaf crowns enables an unmistakable demarcation that separates the youngest leaf cohort from older leaves.



The influence of plant size on leaf nutrients has been reported for two cycad species [18,22]. Leaf nitrogen concentration declined with plant size for *C. micronesica* [18] and *D. sonorensis* [22]. The results point out the need to determine the influence of plant size on leaf nutrients for more cycad species. Both of these species produce arborescent stem growth. We suggest the results were under control of allometric relations rather than height per se. Therefore, cycad species which produce stem growth that is mostly subterranean may require a different variable to quantify stem growth, such as diameter of the stem clump or number of apices per plant.

The influence of leaflet sampling position along the leaf rachis has been reported for two cycad species [14,16]. *Cycas micronesica* leaf nitrogen concentration increased linearly for young leaves and non-linearly for old leaves with distance from the petiole [14]. A non-linear increase in leaf nitrogen concentration occurred for *M. riedlei* with distance from the petiole [16]. The leaf age was not reported. The majority of papers that we reviewed did not include a description of sampling location along the pinnately compound cycad leaf rachis. As with leaf age and plant size, this oversight must be corrected in future studies.

## 6. Environmental Factors

The direct influence of incident light on *C. micronesica* leaf element concentrations has been reported [13]. Nitrogen, phosphorus, and potassium concentrations were greater in shaded plants than in full sun plants. Differences in *C. micronesica* leaf element concentrations were reported between homogeneous shade conditions supplied by commercial shade cloth and heterogeneous shade conditions supplied by wood slats [17]. These results reveal the dangers in relying on data from managed gardens without augmenting the results with data from natural settings. A quantification of incident light or the general level of shade has not been reported for most of the cycad studies from the literature. A comparison of two *Cycas* species between garden and in situ settings revealed the nutrient concentrations of leaves from the garden plants were dissimilar from those of leaves from habitat [20]. The benign level of competition in the gardens versus robust competition with sympatric plants in habitat was considered a causal mechanism. The use of multiple sites with contrasting soil nutrient relations has revealed that cycad leaf concentrations of some leaf nutrients track with the differences soil concentrations [10,20]. Many of the cycad studies in this review did not include a description of soil nutrient concentrations accompanying the sampled plants. Other studies reported general soil characteristics but did not include measurements of the nutrients within soils subtending the sampled cycad plants. The differences of soil chemistry directly beneath cycad plants versus away from the plants [39,40] indicate soil nutrition within the root zone of the sampled cycad plants is a metric that should be determined in order to interpret leaf nutrient results accurately.

## 7. Future Directions

We consider three issues as the greatest needs within this agenda as more research accumulates. First, adherence to accepted binomials for every taxon included in this research is of paramount importance. Some reports included taxa names that did not conform to any known published species names, and these data were not included herein and should not be used in future meta-analyses and reviews. Careful adherence to accepted binomials [5] in future research would mitigate this ambiguity. Moreover, as changes in cycad classification and nomenclature will continue to occur, including specific provenance or pedigree data for samples included in studies, or preparing herbarium specimens representing these samples will help researchers compiling data for future meta-analyses and reviews.

Second, more species must be added to the data before large-scale generalities will become accurate for the Cycadales. Priority should be given to taxonomic groups that have not been studied adequately. The genus *Microcycas* is missing from the published data. However, the speciose genera are also not adequately represented in the literature. For example, only 3% of *Ceratozamia*, 5% of *Encephalartos*, 10% of *Zamia*, 16% of *Cycas*, and 20% of *Macrozamia* species have been studied to date.

Third, an increase in focus on natural habitats and reduction in focus on botanic garden settings is needed. The leaf nutrient relations of only 14 of the 358 described species [5] have been determined in situ, and most of those reports included a single locality. In situ leaf sampling of *Cycas micronesica* has occurred among numerous insular habitats across four geopolitical island groups. No other species has been studied with this level of focus on in situ sampling methods. This paucity of data from natural habitats renders the current cycad literature of little value for comparing to GLOPNET. Moreover, the genetic  $\times$  environmental control over leaf nutrient concentrations cannot be determined until multiple localities are included for indigenous species with an extensive native range.

Seasonal variation in leaf element concentrations may be considerable and modulated by biotic factors. For example, the influence of season on *Actinidia arguta* var. *arguta* (Siebold and Zucc.) Planch. ex Miq. leaf nutrient concentrations differed for male and female plants [41]. Moreover, the influence of season on *Olea europaea* L. leaves interacted with intraspecific genotypic variation [42]. These results indicate that research to determine the influence of season on cycad leaf nutrient relations should include multiple provenances and the distinction of male and female sampled plants. Until this is determined for numerous cycad species, the approach used by Marler and Lindström [20] is recommended for comparing more than one location, whereby one season is used to compare locations.

Zhang et al. [9,19] reported iron concentrations of *Zamia fischeri* leaves that were extreme outliers when compared with other species studied in two botanic garden locations. This observation should be confirmed in natural settings in Mexico and greater attention to iron variation among other closely related *Zamia* species may be warranted.

Marler and Lindström [20] reported that leaf magnesium concentration was constrained among *Cycas* plants from one provenance even when they were grown in different soils with substantial variation in soil magnesium concentrations. For example, *C. nongnoochiae* plants growing in Thailand habitat exhibited leaf magnesium concentration that did not differ from the plants growing in a managed cultivated garden, even though the garden soils contained magnesium that was only 14% of that in the habitat soils. Similarly, *C. micronesica* plants growing in Yap habitat exhibited leaf magnesium concentration that did not differ from the plants growing in a managed cultivated garden, even though the garden soils contained magnesium that was only 11% of that in the habitat soils. The maintenance of magnesium homeostasis in cycad leaves deserves further study. Some of the known roles of magnesium include maintenance of chlorophyll concentration, promotion of non-structural carbohydrate export from leaves, and control of ionic currents across membranes [43,44]. The observed homeostasis for two *Cycas* species is not unexpected, given this partial list of roles for this macronutrient. The observations need to be confirmed with other cycad species using multiple localities.

The nutrients which have been studied by more than one laboratory have revealed disparity in reported concentrations among the studies that may be explained by dissimilar methods. For example, green leaf nitrogen concentration reported by Kipp et al. [16] was more than double that reported by Grove et al. [23] for *Macrozamia riedlei* and almost double that reported by Zhang et al. [9] for *Bowenia serrulata*. Explanations for these differences among laboratories are difficult to consider because many of the co-varying factors discussed in Sections 5 and 6 were not reported. Effort should be made during every future study to record and report all sources of variation to improve our understanding of reported differences among studies.

Marler and Dongol [35] reported the only study that we are aware of which determined the influence of insect herbivory on cycad leaf nutrients. All three insects were invasive non-native pests. Many cycad taxa coevolved with folivorous insects, and these should be studied in a similar manner to determine how leaf nutrients are altered by the herbivory of these native sympatric insects.

The influence of *C. micronesica* leaf litter on decomposition speed, soil respiration, and mineralization dynamics has been reported [38]. This study revealed the speed of these leaf after-life phenomena was slower for the cycad leaves than for two Fabaceae species. The results indicated that the presence of cycad plants in biodiverse settings may influence community-level litter decomposition even if they are limited in incidence [45].

The long-term changes in soil nutrient concentrations beneath the canopy of cycad plants have been determined for *C. micronesica* and *Z. integrifolia* [39,40]. To our knowledge, the influences of cycad plants on the soils within the dripline of their canopy have not been studied for any other species. However, the two species that have been studied revealed that the presence of a cycad plant in unmanaged settings is valuable for introducing soil heterogeneity at the fine scale, potentially increasing biodiversity in soil organisms and increasing ecosystem health. We propose two phenomena that deserve direct study. First, rainfall rarely reaches the soil surface without first being intercepted by plant structures [46–51]. This intercepted rainfall is lost through evaporation or transferred to the soil as throughfall or stemflow. The relative proportions of these processes are affected by canopy and leaf traits, and strongly influence the spatial components of the hydrologic and chemical cycles beneath mixed stands of plants [46–50]. Throughfall is the precipitation component that drips from numerous plant surfaces, and stemflow is the precipitation component that drains along the plant stems to reach the soil. The percentage of precipitation that reaches the soil via stemflow and the concentration of solutes and suspensions of particulates in stemflow are strongly linked to leaf traits and canopy architecture traits [46–51]. Stemflow influences essential minerals and metals near the base of trees, but also influences soil carbon by the transfer of dissolved organic matter in the stem flow [51]. To our knowledge, no studies of stemflow have included a cycad representative. However, arborescent palm species exhibit stem and leaf shapes and orientations that are similar to cycads, and many palm trees are skilled at increasing soil nutrients in their root zone by maximizing stemflow [52–54]. The diameter of the *C. micronesica* leaf crown is up to 4 m for healthy trees, but the diameter of the *Z. integrifolia* leaf crown is less than 2 m, illuminating a highly contrasting ability to intercept rainfall for the individual plant. Projected canopy area is highly influential of stemflow volume [55]. The relative diameters of leaflets and rachis surfaces are also much greater for *C. micronesica* than for *Z. integrifolia*, and these organ traits directly influence how precipitation is intercepted by an individual plant. The inclusion of a range of cycad taxa in the stemflow research agenda would add greatly to our knowledge of how cycad plants directly affect soil chemistry, but would also improve our understanding of carbon, hydrologic, and nitrogen cycles by adding this unique gymnosperm plant group to the stemflow literature.

Second, some plants may influence the biogeochemical cycle by litter trapping. The leaf and stem traits of these plants increase the volume of litterfall that is trapped in the plant's canopy, and this trapped litter becomes a privatized slow compost pile that releases nutrients over time [56]. As with stemflow, we are not aware of any cycad taxa that have been studied for litter-trapping abilities. However, palm species [52,56–58] and fern species [56,59] are highly effective at trapping litter, and the plant traits that enable this ability for palms and ferns are similar to the plant traits of cycads. Trapped litter may further magnify nutrient accumulation by attracting animals which may bring food materials and add feces directly to the litter mass [52,56]. The need to study the litter trapping traits of cycad plants is clear, as this may explain the increases in carbon and nitrogen that we have documented beneath two cycad species. Two cycad leaf traits should be considered in this line of work. First, the size, shape, and insertion angle of spines and prickles on cycad petioles vary greatly among species [6,60], and these petiole traits may directly influence how much of the incoming litterfall is trapped. Second, some cycad species produce leaves that are replaced annually, while other species produce leaves that are retained for many years. Undoubtedly, the amount of trapped litter that can accumulate over time is under the direct influence of leaf longevity, and this leaf trait should be considered in future studies on litter trapping of cycad plants.

Plants employ multiple defensive strategies against herbivores that have been studied within the context of various models [61], and plant defensive strategies are generally classified as structural or chemical. Structural defenses include leaf toughness and the construction of modified organs such as thorns, spines, and prickles. Chemical defenses include metabolites that alter the taste of the tissues to deter herbivory or that act as animal toxins. Cycads employ both defensive strategies, and cycad plants have been the subject of myriad medical and biochemical studies because of the number of known toxins that are synthesized by the plants [6,62]. Structural defenses are important after leaf expansion

and maturation, but chemical defenses are important during leaf expansion [63]. The azoxyglycosides cycasin and macrozamin are among the most studied acute cycad toxins, and these nitrogenous compounds have been reported in all 10 genera and most species that have been studied [64,65]. These toxins may occur in greater concentrations in young cycad plants than in adult plants [66], which parallels the decline in leaf nitrogen concentration with plant size [18,22]. In general, elemental concentrations of plant tissues mediate defensive mechanisms [67]. These issues of secondary compounds in cycad biology suggest the individual plants with greater nutritive content are better protected with higher azoxyglycosides [66]. In consideration of the relevance of cycad toxins to human health research, continued research on element accumulation and partitioning in cycad plants may contribute substantially to toxicology research.

The elemental components of plant tissues cannot be studied in the absence of recognizing the contributions of root traits and symbionts. Cycad roots have not been adequately studied but these gymnosperms produce roots that appear typical of other seed-bearing plants, and although little is known about their general physiology, they are believed to function similarly to angiosperm roots [6 (p. 60)]. Seedlings initially produce a robust taproot which over time is augmented or replaced by similarly thick and fleshy branching secondary roots. Root hairs, which function in other plants to increase the volume of soil that plants are able to mine for nutrients, are rare in cycads and only irregularly formed in the thinnest of feeder roots. Cycads also produce specialized clusters of roots known as coralloid roots which typically grow upward above the soil surface and host nitrogen-fixing cyanobacteria which fix nitrogen for use by the plant [6,68–70]. Moreover, cycad roots are known to harbor arbuscular mycorrhizal fungi which enhance phosphorus uptake in low phosphorus soils and enhance water availability in seasonally dry habitats [71,72]. The incidence and diversity of these symbionts may contrast sharply between natural habitats where sympatric species of soil biota exist and botanic gardens where the soil biota that interacts with a cycad plant are novel to the plant. More studies are needed to understand cycad root traits and to tease apart the influences of these symbiotic relationships on leaf element concentrations in various cycad taxa.

Finally, many areas of occupancy for various cycad species are characterized by edaphic characteristics that most plant species would not consider as suitable for plant growth. We highlight three examples that deserve a dedicated look during future research on cycad plant nutrition. First, multiple cycad species thrive in littoral habitats where roots are exposed to saline substrates and leaves must contend with aerosol salt deposits. Second, some cycad species flourish on limestone mountain surfaces or karst outcrops where mineral soils are scarce and drought stress is extreme. Third, cycad populations also occur on either highly acidic volcanic substrates or ultramafic habitats, where the plants must cope between the spectrum of extreme acidity and high alkalinity compounded by calcium deficiencies and metal toxicities. This group of plants is ideal for studying the mechanisms that plants exploit to compete in these extreme habitats. Moreover, some species are endemic to one of these extreme habitat types while other species are indigenous and can be found in various ecological niche habitats. Comparing these two types of cycad species may tease apart the stress physiology mechanisms that indicate facultative versus obligate approaches for tolerating extreme edaphic conditions.

## 8. Conclusions

Cycad species are highly prized in the horticulture trade. We have reviewed the available literature on elemental concentrations in cycad leaves. A total of six gardens were included with two in China, one in Florida, one in Thailand, one in Philippines, and one in Guam. These results were discussed along with in situ data from Australia, Guam, Mexico, Palau, Philippines, Rota, Thailand, and Yap. The review illuminates the scant research landscape of this agenda. By highlighting the unexpected results that most papers reported data from botanic gardens and the authors failed to describe the irrigation and fertilization protocols of the managed plants, we aimed to inspire an adoption of more demanding protocols for expanding this research agenda. In part, this should include measurement

and reporting of plant size, leaf age, or position within the canopy, position of leaflets along the rachis, the shade level of the sampled leaves, and the soil element concentrations within the root zone of the sampled plants.

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## Appendix A

**Table A1.** Published ranges for green leaf element concentrations of cycad plants. Misspellings of species were corrected if identity was obvious, species that were misspelled were not included if identity was not obvious. Taxonomic synonyms were corrected. Data were estimated for reports displaying data as figures and transformed if data were presented in log format.

Element	Species	Range	Reference
Carbon	<i>Bowenia serrulata</i>	519 mg·g <sup>-1</sup>	[9]
Carbon	<i>Bowenia spectabilis</i>	508 mg·g <sup>-1</sup>	[9]
Carbon	<i>Ceratozamia Mexicana</i>	514 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas debaoensis</i>	485 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas diannanensis</i>	463 mg·g <sup>-1</sup>	[9] <sup>1</sup>
Carbon	<i>Cycas elongata</i>	483 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas fairylakea</i>	499 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas micholitzii</i>	475 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas micronesica</i>	479 mg·g <sup>-1</sup>	[12]
Carbon	<i>Cycas micronesica</i>	484–493 mg·g <sup>-1</sup>	[13]
Carbon	<i>Cycas micronesica</i>	480–505 mg·g <sup>-1</sup>	[14]
Carbon	<i>Cycas micronesica</i>	475–485 mg·g <sup>-1</sup>	[17]
Carbon	<i>Cycas nitida</i>	499–509 mg·g <sup>-1</sup>	[10]
Carbon	<i>Cycas panzhihuaensis</i>	466–504 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas sexseminifera</i>	467 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas siamensis</i>	469 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas szechuanensis</i>	475–498 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas thouarsii</i>	497 mg·g <sup>-1</sup>	[9]
Carbon	<i>Cycas wadei</i>	508 mg·g <sup>-1</sup>	[11]
Carbon	<i>Dioon edule</i>	496 mg·g <sup>-1</sup>	[9]
Carbon	<i>Dioon mejiae</i>	485 mg·g <sup>-1</sup>	[9]
Carbon	<i>Dioon spinulosum</i>	486 mg·g <sup>-1</sup>	[9]
Carbon	<i>Encephalartos cupidus</i>	490 mg·g <sup>-1</sup>	[9]
Carbon	<i>Encephalartos ferox</i>	494 mg·g <sup>-1</sup>	[9]
Carbon	<i>Encephalartos gratus</i>	497–505 mg·g <sup>-1</sup>	[9]
Carbon	<i>Lepidozamia hopei</i>	515 mg·g <sup>-1</sup>	[9]
Carbon	<i>Lepidozamia peroffskyana</i>	511 mg·g <sup>-1</sup>	[9]
Carbon	<i>Lepidozamia peroffskyana</i>	473–566 mg·g <sup>-1</sup>	[16]
Carbon	<i>Macrozamia communis</i>	512 mg·g <sup>-1</sup>	[9]
Carbon	<i>Macrozamia communis</i>	507–560 mg·g <sup>-1</sup>	[16]
Carbon	<i>Macrozamia lucida</i>	524 mg·g <sup>-1</sup>	[9]
Carbon	<i>Macrozamia lucida</i>	473–522 mg·g <sup>-1</sup>	[16]
Carbon	<i>Macrozamia macleaya</i>	438–508 mg·g <sup>-1</sup>	[16]
Carbon	<i>Macrozamia moorei</i>	519 mg·g <sup>-1</sup>	[9]

Table A1. Cont.

Element	Species	Range	Reference
Carbon	<i>Macrozamia riedlei</i>	455–525 mg·g <sup>-1</sup>	[16]
Carbon	<i>Stangeria eriopus</i>	479 mg·g <sup>-1</sup>	[9]
Carbon	<i>Zamia erosa</i>	495 mg·g <sup>-1</sup>	[9] <sup>2</sup>
Carbon	<i>Zamia erosa</i>	481 mg·g <sup>-1</sup>	[15]
Carbon	<i>Zamia fischeri</i>	458 mg·g <sup>-1</sup>	[9] <sup>3</sup>
Carbon	<i>Zamia furfuracea</i>	477–489 mg·g <sup>-1</sup>	[9]
Carbon	<i>Zamia integrifolia</i>	490–491 mg·g <sup>-1</sup>	[9]
Carbon	<i>Zamia portoricensis</i>	484 mg·g <sup>-1</sup>	[15]
Carbon	<i>Zamia splendens</i>	483 mg·g <sup>-1</sup>	[9]
Carbon	<i>Zamia vazquezii</i>	488 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Bowenia serrulata</i>	24 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Bowenia serrulata</i>	41 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Bowenia spectabilis</i>	24 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Ceratozamia mexicana</i>	13 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas armstrongii</i>	21 mg·g <sup>-1</sup>	[21]
Nitrogen	<i>Cycas debaoensis</i>	28 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas diannanensis</i>	26 mg·g <sup>-1</sup>	[9] <sup>1</sup>
Nitrogen	<i>Cycas diannanensis</i>	26 mg·g <sup>-1</sup>	[19] <sup>1</sup>
Nitrogen	<i>Cycas elongata</i>	28 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas fairylakea</i>	25 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas media</i>	44 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Cycas micholitzii</i>	25 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas micholitzii</i>	25 mg·g <sup>-1</sup>	[19]
Nitrogen	<i>Cycas micronesica</i>	29–30 mg·g <sup>-1</sup>	[15]
Nitrogen	<i>Cycas micronesica</i>	25 mg·g <sup>-1</sup>	[12]
Nitrogen	<i>Cycas micronesica</i>	14–30 mg·g <sup>-1</sup>	[18]
Nitrogen	<i>Cycas micronesica</i>	18–27 mg·g <sup>-1</sup>	[13]
Nitrogen	<i>Cycas micronesica</i>	18–29 mg·g <sup>-1</sup>	[14]
Nitrogen	<i>Cycas micronesica</i>	23–37 mg·g <sup>-1</sup>	[17]
Nitrogen	<i>Cycas micronesica</i>	17–30 mg·g <sup>-1</sup>	[20]
Nitrogen	<i>Cycas nitida</i>	24–28 mg·g <sup>-1</sup>	[10]
Nitrogen	<i>Cycas nongnoochiae</i>	26–30 mg·g <sup>-1</sup>	[20]
Nitrogen	<i>Cycas panhuhuaensis</i>	16–21 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas panhuhuaensis</i>	16 mg·g <sup>-1</sup>	[19]
Nitrogen	<i>Cycas rumphii</i>	30–31 mg·g <sup>-1</sup>	[15]
Nitrogen	<i>Cycas sexseminifera</i>	19 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas sexseminifera</i>	19 mg·g <sup>-1</sup>	[19] <sup>4</sup>
Nitrogen	<i>Cycas siamensis</i>	18 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas siamensis</i>	19 mg·g <sup>-1</sup>	[19]
Nitrogen	<i>Cycas szechuanensis</i>	21–25 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas szechuanensis</i>	21 mg·g <sup>-1</sup>	[19]
Nitrogen	<i>Cycas thouarsii</i>	23 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Cycas wadei</i>	21 mg·g <sup>-1</sup>	[11]
Nitrogen	<i>Dioon edule</i>	15 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Dioon mejiae</i>	14 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Dioon sonorensis</i>	14–17 mg·g <sup>-1</sup>	[22]
Nitrogen	<i>Dioon spinulosum</i>	15 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Encephalartos cupidus</i>	17 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Encephalartos cupidus</i>	18 mg·g <sup>-1</sup>	[19]
Nitrogen	<i>Encephalartos ferox</i>	15 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Encephalartos gratus</i>	18–19 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Encephalartos gratus</i>	18 mg·g <sup>-1</sup>	[19]
Nitrogen	<i>Lepidozamia hopei</i>	17 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Lepidozamia peroffskyana</i>	19 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Lepidozamia peroffskyana</i>	18–31 mg·g <sup>-1</sup>	[16]

Table A1. Cont.

Element	Species	Range	Reference
Nitrogen	<i>Macrozamia communis</i>	20 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Macrozamia communis</i>	10–38 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Macrozamia lucida</i>	21 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Macrozamia lucida</i>	14–22 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Macrozamia macleayi</i>	8–43 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Macrozamia moorei</i>	20 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Macrozamia mountperriensis</i>	54–55 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Macrozamia parcifolia</i>	47–49 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Macrozamia riedlei</i>	14 mg·g <sup>-1</sup>	[21]
Nitrogen	<i>Macrozamia riedlei</i>	11–15 mg·g <sup>-1</sup>	[23]
Nitrogen	<i>Macrozamia riedlei</i>	8–38 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Macrozamia serpentina</i>	28–31 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Stangeria eriopus</i>	22 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Zamia erosa</i>	18 mg·g <sup>-1</sup>	[9] <sup>2</sup>
Nitrogen	<i>Zamia erosa</i>	26 mg·g <sup>-1</sup>	[15]
Nitrogen	<i>Zamia fischeri</i>	28 mg·g <sup>-1</sup>	[9] <sup>3</sup>
Nitrogen	<i>Zamia fischeri</i>	28 mg·g <sup>-1</sup>	[19] <sup>3</sup>
Nitrogen	<i>Zamia furfuracea</i>	12–14 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Zamia furfuracea</i>	13 mg·g <sup>-1</sup>	[19]
Nitrogen	<i>Zamia integrifolia</i>	18–21 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Zamia portoricensis</i>	18 mg·g <sup>-1</sup>	[15]
Nitrogen	<i>Zamia splendens</i>	15 mg·g <sup>-1</sup>	[9]
Nitrogen	<i>Zamia standleyi</i>	19 mg·g <sup>-1</sup>	[15]
Nitrogen	<i>Zamia vazquezii</i>	30 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Bowenia serrulata</i>	1.0 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Bowenia spectabilis</i>	1.1 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Ceratozamia mexicana</i>	0.8 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas debaoensis</i>	1.4 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas diannanensis</i>	2.4 mg·g <sup>-1</sup>	[9] <sup>1</sup>
Phosphorus	<i>Cycas diannanensis</i>	2.4 mg·g <sup>-1</sup>	[19] <sup>1</sup>
Phosphorus	<i>Cycas elongata</i>	1.2 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas fairylakea</i>	1.1 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas micholitzii</i>	1.5 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas micholitzii</i>	1.5 mg·g <sup>-1</sup>	[19]
Phosphorus	<i>Cycas micronesica</i>	2.9 mg·g <sup>-1</sup>	[12]
Phosphorus	<i>Cycas micronesica</i>	1.2–2.7 mg·g <sup>-1</sup>	[18]
Phosphorus	<i>Cycas micronesica</i>	0.9–2.5 mg·g <sup>-1</sup>	[13]
Phosphorus	<i>Cycas micronesica</i>	0.8–2.8 mg·g <sup>-1</sup>	[14]
Phosphorus	<i>Cycas micronesica</i>	2.6–2.9 mg·g <sup>-1</sup>	[17]
Phosphorus	<i>Cycas micronesica</i>	1.5–2.9 mg·g <sup>-1</sup>	[20]
Phosphorus	<i>Cycas nitida</i>	1.1–1.9 mg·g <sup>-1</sup>	[10]
Phosphorus	<i>Cycas nongnoochiae</i>	1.3–3.4 mg·g <sup>-1</sup>	[20]
Phosphorus	<i>Cycas panzhihuaensis</i>	1.0–1.1 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas panzhihuaensis</i>	1.1 mg·g <sup>-1</sup>	[19]
Phosphorus	<i>Cycas sexseminifera</i>	1.5 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas sexseminifera</i>	1.2–1.5 mg·g <sup>-1</sup>	[19] <sup>4</sup>
Phosphorus	<i>Cycas siamensis</i>	1.2 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas siamensis</i>	1.2 mg·g <sup>-1</sup>	[19]
Phosphorus	<i>Cycas szechuanensis</i>	1.0–1.2 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas thouarsii</i>	1.2 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Cycas wadei</i>	1.1 mg·g <sup>-1</sup>	[11]
Phosphorus	<i>Dioon edule</i>	0.8 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Dioon mejiae</i>	1.5 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Dioon spinulosum</i>	0.8 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Encephalartos cupidus</i>	1.2 mg·g <sup>-1</sup>	[9]

Table A1. Cont.

Element	Species	Range	Reference
Phosphorus	<i>Encephalartos cupidus</i>	1.2 mg·g <sup>-1</sup>	[19]
Phosphorus	<i>Encephalartos ferox</i>	1.0 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Encephalartos gratus</i>	1.1–1.3 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Encephalartos gratus</i>	1.1 mg·g <sup>-1</sup>	[19]
Phosphorus	<i>Lepidozamia hopei</i>	0.8 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Lepidozamia peroffskyana</i>	1.2 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Macrozamia communis</i>	1.0 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Macrozamia lucida</i>	1.2 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Macrozamia moorei</i>	0.9 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Macrozamia riedlei</i>	0.5 mg·g <sup>-1</sup>	[21]
Phosphorus	<i>Stangeria eriopus</i>	1.1 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Zamia erosa</i>	1.0 mg·g <sup>-1</sup>	[9] <sup>2</sup>
Phosphorus	<i>Zamia fischeri</i>	1.7 mg·g <sup>-1</sup>	[9] <sup>3</sup>
Phosphorus	<i>Zamia fischeri</i>	1.7 mg·g <sup>-1</sup>	[19] <sup>3</sup>
Phosphorus	<i>Zamia furfuracea</i>	0.7–0.8 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Zamia furfuracea</i>	0.7 mg·g <sup>-1</sup>	[19]
Phosphorus	<i>Zamia integrifolia</i>	1.3 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Zamia splendens</i>	0.8 mg·g <sup>-1</sup>	[9]
Phosphorus	<i>Zamia vazquezii</i>	0.7 mg·g <sup>-1</sup>	[9]
Potassium	<i>Bowenia serrulata</i>	5.5 mg·g <sup>-1</sup>	[9]
Potassium	<i>Bowenia spectabilis</i>	6.2 mg·g <sup>-1</sup>	[9]
Potassium	<i>Ceratozamia mexicana</i>	4.9 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas debaoensis</i>	4.4 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas diannanensis</i>	9.9 mg·g <sup>-1</sup>	[9] <sup>1</sup>
Potassium	<i>Cycas elongata</i>	9.8 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas fairylakea</i>	5.8 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas micholitzii</i>	7.0 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas micronesica</i>	15.3 mg·g <sup>-1</sup>	[12]
Potassium	<i>Cycas micronesica</i>	6.9–23.0 mg·g <sup>-1</sup>	[18]
Potassium	<i>Cycas micronesica</i>	3.8–22.1 mg·g <sup>-1</sup>	[13]
Potassium	<i>Cycas micronesica</i>	3.1–23.7 mg·g <sup>-1</sup>	[14]
Potassium	<i>Cycas micronesica</i>	14.9–16.4 mg·g <sup>-1</sup>	[17]
Potassium	<i>Cycas micronesica</i>	10.5–18.9 mg·g <sup>-1</sup>	[20]
Potassium	<i>Cycas nitida</i>	6.4–16.6 mg·g <sup>-1</sup>	[10]
Potassium	<i>Cycas nongnoochiae</i>	4.4–18.3 mg·g <sup>-1</sup>	[20]
Potassium	<i>Cycas panzhihuaensis</i>	5.8–7.7 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas revoluta</i>	4.9–11.9 mg·g <sup>-1</sup>	[24]
Potassium	<i>Cycas sexsemifera</i>	4.3 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas siamensis</i>	10.2 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas szechuanensis</i>	3.7–5.7 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas thouarsii</i>	8.8 mg·g <sup>-1</sup>	[9]
Potassium	<i>Cycas wadei</i>	7.4 mg·g <sup>-1</sup>	[11]
Potassium	<i>Dioon edule</i>	5.7 mg·g <sup>-1</sup>	[9]
Potassium	<i>Dioon mejiae</i>	11.5 mg·g <sup>-1</sup>	[9]
Potassium	<i>Dioon spinulosum</i>	7.9 mg·g <sup>-1</sup>	[9]
Potassium	<i>Encephalartos cupidus</i>	6.2 mg·g <sup>-1</sup>	[9]
Potassium	<i>Encephalartos ferox</i>	6.7 mg·g <sup>-1</sup>	[9]
Potassium	<i>Encephalartos gratus</i>	7.2–8.9 mg·g <sup>-1</sup>	[9]
Potassium	<i>Lepidozamia hopei</i>	9.5 mg·g <sup>-1</sup>	[9]
Potassium	<i>Lepidozamia peroffskyana</i>	10.6 mg·g <sup>-1</sup>	[9]
Potassium	<i>Macrozamia communis</i>	9.8 mg·g <sup>-1</sup>	[9]
Potassium	<i>Macrozamia lucida</i>	11.3 mg·g <sup>-1</sup>	[9]
Potassium	<i>Macrozamia moorei</i>	5.1 mg·g <sup>-1</sup>	[9]
Potassium	<i>Macrozamia riedlei</i>	6.5–9.2 mg·g <sup>-1</sup>	[23]
Potassium	<i>Stangeria eriopus</i>	8.0 mg·g <sup>-1</sup>	[9]



Table A1. Cont.

Element	Species	Range	Reference
Potassium	<i>Zamia erosa</i>	10.0 mg·g <sup>-1</sup>	[9] <sup>2</sup>
Potassium	<i>Zamia fischeri</i>	6.6 mg·g <sup>-1</sup>	[9] <sup>3</sup>
Potassium	<i>Zamia furfuracea</i>	4.6–10.2 mg·g <sup>-1</sup>	[9]
Potassium	<i>Zamia integrifolia</i>	9.3–9.5 mg·g <sup>-1</sup>	[9]
Potassium	<i>Zamia splendens</i>	8.1 mg·g <sup>-1</sup>	[9]
Potassium	<i>Zamia vazquezii</i>	18.0 mg·g <sup>-1</sup>	[9]
Magnesium	<i>Cycas micronesica</i>	2.3 mg·g <sup>-1</sup>	[12]
Magnesium	<i>Cycas micronesica</i>	1.7–8.2 mg·g <sup>-1</sup>	[18]
Magnesium	<i>Cycas micronesica</i>	2.5–4.8 mg·g <sup>-1</sup>	[13]
Magnesium	<i>Cycas micronesica</i>	2.9–5.1 mg·g <sup>-1</sup>	[14]
Magnesium	<i>Cycas micronesica</i>	2.2–2.4 mg·g <sup>-1</sup>	[17]
Magnesium	<i>Cycas micronesica</i>	3.1–7.0 mg·g <sup>-1</sup>	[20]
Magnesium	<i>Cycas nongnoochiae</i>	2.4–2.6 mg·g <sup>-1</sup>	[20]
Magnesium	<i>Cycas revoluta</i>	1.9–3.1 mg·g <sup>-1</sup>	[24]
Magnesium	<i>Cycas wadei</i>	1.4 mg·g <sup>-1</sup>	[11]
Magnesium	<i>Macrozamia reidlei</i>	1.1–1.9 mg·g <sup>-1</sup>	[23]
Calcium	<i>Bowenia serrulata</i>	6.1 mg·g <sup>-1</sup>	[9]
Calcium	<i>Bowenia spectabilis</i>	5.0 mg·g <sup>-1</sup>	[9]
Calcium	<i>Ceratozamia mexicana</i>	7.1 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas debaoensis</i>	11.8 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas diannanensis</i>	11.4 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas elongata</i>	11.6 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas fairylakea</i>	3.9 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas micholitzii</i>	2.7 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas micronesica</i>	2.8 mg·g <sup>-1</sup>	[12]
Calcium	<i>Cycas micronesica</i>	7.1–23.7 mg·g <sup>-1</sup>	[18]
Calcium	<i>Cycas micronesica</i>	1.2–8.6 mg·g <sup>-1</sup>	[13]
Calcium	<i>Cycas micronesica</i>	7.8–10.6 mg·g <sup>-1</sup>	[14]
Calcium	<i>Cycas micronesica</i>	2.5–3.1 mg·g <sup>-1</sup>	[17]
Calcium	<i>Cycas micronesica</i>	3.1–19.9 mg·g <sup>-1</sup>	[20]
Calcium	<i>Cycas nongnoochiae</i>	3.2–7.0 mg·g <sup>-1</sup>	[20]
Calcium	<i>Cycas panzhihuaensis</i>	6.6–7.0 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas revoluta</i>	7.7–15.6 mg·g <sup>-1</sup>	[24]
Calcium	<i>Cycas sexseminifera</i>	8.6 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas siamensis</i>	9.9 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas szechuanensis</i>	1.4–2.8 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas thouarsii</i>	6.3 mg·g <sup>-1</sup>	[9]
Calcium	<i>Cycas wadei</i>	2.51 mg·g <sup>-1</sup>	[11]
Calcium	<i>Dioon edule</i>	7.7 mg·g <sup>-1</sup>	[9]
Calcium	<i>Dioon mejiae</i>	8.4 mg·g <sup>-1</sup>	[9]
Calcium	<i>Dioon spinulosum</i>	7.6 mg·g <sup>-1</sup>	[9]
Calcium	<i>Encephalartos cupidus</i>	4.5 mg·g <sup>-1</sup>	[9]
Calcium	<i>Encephalartos ferox</i>	14.3 mg·g <sup>-1</sup>	[9]
Calcium	<i>Encephalartos gratus</i>	4.7–6.2 mg·g <sup>-1</sup>	[9]
Calcium	<i>Lepidozamia hopei</i>	5.0 mg·g <sup>-1</sup>	[9]
Calcium	<i>Lepidozamia peroffskyana</i>	3.6 mg·g <sup>-1</sup>	[9]
Calcium	<i>Macrozamia communis</i>	1.4 mg·g <sup>-1</sup>	[9]
Calcium	<i>Macrozamia lucida</i>	2.8 mg·g <sup>-1</sup>	[9]
Calcium	<i>Macrozamia moorei</i>	4.7 mg·g <sup>-1</sup>	[9]
Calcium	<i>Macrozamia reidlei</i>	3.1–7.1 mg·g <sup>-1</sup>	[23]
Calcium	<i>Stangeria eriopus</i>	7.1 mg·g <sup>-1</sup>	[9]
Calcium	<i>Zamia erosa</i>	3.0 mg·g <sup>-1</sup>	[9] <sup>2</sup>
Calcium	<i>Zamia fischeri</i>	7.7 mg·g <sup>-1</sup>	[9] <sup>3</sup>
Calcium	<i>Zamia furfuracea</i>	4.9–7.0 mg·g <sup>-1</sup>	[9]
Calcium	<i>Zamia integrifolia</i>	4.2–4.3 mg·g <sup>-1</sup>	[9]

Table A1. Cont.

Element	Species	Range	Reference
Calcium	<i>Zamia splendens</i>	4.4 mg·g <sup>-1</sup>	[9]
Calcium	<i>Zamia vazquezii</i>	6.7 mg·g <sup>-1</sup>	[9]
Chloride	<i>Cycas revoluta</i>	0.5–2.3 mg·g <sup>-1</sup>	[24]
Sodium	<i>Cycas micronesica</i>	0.5 mg·g <sup>-1</sup>	[12]
Sodium	<i>Cycas revoluta</i>	0.2–1.2 mg·g <sup>-1</sup>	[24]
Sodium	<i>Macrozamia reidlei</i>	0.3–1.0 mg·g <sup>-1</sup>	[23]
Sulfur	<i>Bowenia serrulata</i>	1.9 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Bowenia spectabilis</i>	1.9 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Ceratozamia mexicana</i>	1.4 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Cycas debaoensis</i>	2.6 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Cycas diannanensis</i>	1.6 mg·g <sup>-1</sup>	[9] <sup>1</sup>
Sulfur	<i>Cycas diannanensis</i>	1.6 mg·g <sup>-1</sup>	[19] <sup>1</sup>
Sulfur	<i>Cycas elongata</i>	2.0 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Cycas fairylakea</i>	1.7 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Cycas micholitzii</i>	1.4 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Cycas micholitzii</i>	1.4 mg·g <sup>-1</sup>	[19]
Sulfur	<i>Cycas micronesica</i>	1.2–1.6 mg·g <sup>-1</sup>	[17]
Sulfur	<i>Cycas micronesica</i>	1.1 mg·g <sup>-1</sup>	[20]
Sulfur	<i>Cycas nongnoochiae</i>	1.4 mg·g <sup>-1</sup>	[20]
Sulfur	<i>Cycas panzhihuaensis</i>	0.9–1.4 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Cycas panzhihuaensis</i>	0.8 mg·g <sup>-1</sup>	[19]
Sulfur	<i>Cycas sexseminifera</i>	1.0 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Cycas sexseminifera</i>	0.9 mg·g <sup>-1</sup>	[19] <sup>4</sup>
Sulfur	<i>Cycas siamensis</i>	1.3 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Cycas siamensis</i>	1.3 mg·g <sup>-1</sup>	[19]
Sulfur	<i>Cycas szechuanensis</i>	1.1–1.4 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Cycas szechuanensis</i>	1.1 mg·g <sup>-1</sup>	[19]
Sulfur	<i>Cycas thourarsii</i>	1.4 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Dioon edule</i>	1.4 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Dioon mejiae</i>	1.4 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Dioon spinulosum</i>	1.1 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Encephalartos cupidus</i>	1.2 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Encephalartos cupidus</i>	1.2 mg·g <sup>-1</sup>	[19]
Sulfur	<i>Encephalartos ferox</i>	1.3 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Encephalartos gratus</i>	0.9–2.2 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Encephalartos gratus</i>	0.8 mg·g <sup>-1</sup>	[19]
Sulfur	<i>Lepidozamia hopei</i>	1.6 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Lepidozamia peroffskyana</i>	1.4 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Macrozamia communis</i>	1.2 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Macrozamia lucida</i>	1.9 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Macrozamia moorei</i>	1.0 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Macrozamia riedlei</i>	0.8–1.2 mg·kg <sup>-1</sup>	[23]
Sulfur	<i>Stangeria eriopus</i>	2.3 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Zamia erosa</i>	1.0 mg·g <sup>-1</sup>	[9] <sup>2</sup>
Sulfur	<i>Zamia fischeri</i>	2.7 mg·g <sup>-1</sup>	[9] <sup>3</sup>
Sulfur	<i>Zamia fischeri</i>	2.7 mg·g <sup>-1</sup>	[19] <sup>3</sup>
Sulfur	<i>Zamia furfuracea</i>	0.6–1.5 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Zamia furfuracea</i>	0.6 mg·g <sup>-1</sup>	[19]
Sulfur	<i>Zamia integrifolia</i>	13.6–13.7 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Zamia splendens</i>	1.1 mg·g <sup>-1</sup>	[9]
Sulfur	<i>Zamia vazquezii</i>	2.9 mg·g <sup>-1</sup>	[9]
Iron	<i>Bowenia serrulata</i>	189 mg·kg <sup>-1</sup>	[9]
Iron	<i>Bowenia spectabilis</i>	207 mg·kg <sup>-1</sup>	[9]
Iron	<i>Ceratozamia mexicana</i>	106 mg·kg <sup>-1</sup>	[9]
Iron	<i>Cycas debaoensis</i>	114 mg·kg <sup>-1</sup>	[9]

Table A1. Cont.

Element	Species	Range	Reference
Iron	<i>Cycas diannanensis</i>	406 mg·kg <sup>-1</sup>	[9] <sup>1</sup>
Iron	<i>Cycas diannanensis</i>	406 mg·kg <sup>-1</sup>	[19] <sup>1</sup>
Iron	<i>Cycas elongata</i>	149 mg·kg <sup>-1</sup>	[9]
Iron	<i>Cycas fairylakea</i>	98 mg·kg <sup>-1</sup>	[9]
Iron	<i>Cycas micholitzii</i>	340 mg·kg <sup>-1</sup>	[9]
Iron	<i>Cycas micholitzii</i>	345 mg·kg <sup>-1</sup>	[19]
Iron	<i>Cycas micronesica</i>	43.5 mg·kg <sup>-1</sup>	[12]
Iron	<i>Cycas micronesica</i>	38.5–88.6 mg·kg <sup>-1</sup>	[18]
Iron	<i>Cycas micronesica</i>	39.6–46.8 mg·kg <sup>-1</sup>	[13]
Iron	<i>Cycas micronesica</i>	26.8–56.9 mg·kg <sup>-1</sup>	[14]
Iron	<i>Cycas micronesica</i>	71.4 mg·kg <sup>-1</sup>	[20]
Iron	<i>Cycas nongnoochiae</i>	76.4 mg·kg <sup>-1</sup>	[20]
Iron	<i>Cycas panzhihuaensis</i>	134–215 mg·kg <sup>-1</sup>	[9]
Iron	<i>Cycas panzhihuaensis</i>	225 mg·kg <sup>-1</sup>	[19]
Iron	<i>Cycas revoluta</i>	31 mg·kg <sup>-1</sup>	[24]
Iron	<i>Cycas sexseminifera</i>	311 mg·kg <sup>-1</sup>	[9]
Iron	<i>Cycas sexseminifera</i>	300 mg·kg <sup>-1</sup>	[19] <sup>4</sup>
Iron	<i>Cycas siamensis</i>	218 mg·kg <sup>-1</sup>	[9]
Iron	<i>Cycas siamensis</i>	225 mg·kg <sup>-1</sup>	[19]
Iron	<i>Cycas szechuanensis</i>	234–304 mg·kg <sup>-1</sup>	[9]
Iron	<i>Cycas szechuanensis</i>	300 mg·kg <sup>-1</sup>	[19]
Iron	<i>Cycas thouarsii</i>	166 mg·kg <sup>-1</sup>	[9]
Iron	<i>Cycas wadei</i>	71.3 mg·kg <sup>-1</sup>	[11]
Iron	<i>Dioon edule</i>	163 mg·kg <sup>-1</sup>	[9]
Iron	<i>Dioon mejiae</i>	117 mg·kg <sup>-1</sup>	[9]
Iron	<i>Dioon spinulosum</i>	123 mg·kg <sup>-1</sup>	[9]
Iron	<i>Encephalartos cupidus</i>	363 mg·kg <sup>-1</sup>	[9]
Iron	<i>Encephalartos cupidus</i>	355 mg·kg <sup>-1</sup>	[19]
Iron	<i>Encephalartos ferox</i>	93 mg·kg <sup>-1</sup>	[9]
Iron	<i>Encephalartos gratus</i>	121–339 mg·kg <sup>-1</sup>	[9]
Iron	<i>Encephalartos gratus</i>	340 mg·kg <sup>-1</sup>	[19]
Iron	<i>Lepidozamia hopei</i>	176 mg·kg <sup>-1</sup>	[9]
Iron	<i>Lepidozamia peroffskeyana</i>	166 mg·kg <sup>-1</sup>	[9]
Iron	<i>Macrozamia communis</i>	83 mg·kg <sup>-1</sup>	[9]
Iron	<i>Macrozamia lucida</i>	197 mg·kg <sup>-1</sup>	[9]
Iron	<i>Macrozamia moorei</i>	253 mg·kg <sup>-1</sup>	[9]
Iron	<i>Stangeria eriopus</i>	228 mg·kg <sup>-1</sup>	[9]
Iron	<i>Zamia erosa</i>	142 mg·kg <sup>-1</sup>	[9] <sup>2</sup>
Iron	<i>Zamia fischeri</i>	1697 mg·kg <sup>-1</sup>	[9] <sup>3</sup>
Iron	<i>Zamia fischeri</i>	1700 mg·kg <sup>-1</sup>	[19] <sup>3</sup>
Iron	<i>Zamia furfuracea</i>	194–272 mg·kg <sup>-1</sup>	[9]
Iron	<i>Zamia furfuracea</i>	260 mg·kg <sup>-1</sup>	[19]
Iron	<i>Zamia integrifolia</i>	211–270 mg·kg <sup>-1</sup>	[9]
Iron	<i>Zamia splendens</i>	160 mg·kg <sup>-1</sup>	[9]
Iron	<i>Zamia vazquezii</i>	478 mg·kg <sup>-1</sup>	[9]
Manganese	<i>Cycas micronesica</i>	23.8 mg·kg <sup>-1</sup>	[12]
Manganese	<i>Cycas micronesica</i>	19.5–44.7 mg·kg <sup>-1</sup>	[18]
Manganese	<i>Cycas micronesica</i>	26.1–77.5 mg·kg <sup>-1</sup>	[13]
Manganese	<i>Cycas micronesica</i>	25.4–95.6 mg·kg <sup>-1</sup>	[14]
Manganese	<i>Cycas micronesica</i>	36.6 mg·kg <sup>-1</sup>	[20]
Manganese	<i>Cycas micronesica</i>	68.6 mg·kg <sup>-1</sup>	[20]
Manganese	<i>Cycas revoluta</i>	27.1–73.7 mg·kg <sup>-1</sup>	[24]
Manganese	<i>Cycas wadei</i>	152 mg·kg <sup>-1</sup>	[11]
Manganese	<i>Macrozamia riedlei</i>	6–57 mg·kg <sup>-1</sup>	[22]
Boron	<i>Cycas micronesica</i>	13.6 mg·kg <sup>-1</sup>	[12]

Table A1. Cont.

Element	Species	Range	Reference
Boron	<i>Cycas micronesica</i>	11.6–14.3 mg·kg <sup>-1</sup>	[13]
Boron	<i>Cycas micronesica</i>	13.6–15.9 mg·kg <sup>-1</sup>	[14]
Boron	<i>Cycas micronesica</i>	43.4 mg·kg <sup>-1</sup>	[20]
Boron	<i>Cycas micronesica</i>	25.6 mg·kg <sup>-1</sup>	[20]
Boron	<i>Cycas wadei</i>	17.2 mg·kg <sup>-1</sup>	[11]
Copper	<i>Cycas micronesica</i>	4.2 mg·kg <sup>-1</sup>	[12]
Copper	<i>Cycas micronesica</i>	6.5–17.9 mg·kg <sup>-1</sup>	[18]
Copper	<i>Cycas micronesica</i>	3.1 mg·kg <sup>-1</sup>	[13]
Copper	<i>Cycas micronesica</i>	2.0–4.0 mg·kg <sup>-1</sup>	[14]
Copper	<i>Cycas micronesica</i>	7.7 mg·kg <sup>-1</sup>	[20]
Copper	<i>Cycas micronesica</i>	9.7 mg·kg <sup>-1</sup>	[20]
Copper	<i>Cycas wadei</i>	3.9 mg·kg <sup>-1</sup>	[11]
Copper	<i>Macrozamia riedlei</i>	2.1–2.8 mg·kg <sup>-1</sup>	[23]
Zinc	<i>Bowenia serrulata</i>	19.2 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Bowenia spectabilis</i>	21.4 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Ceratozamia mexicana</i>	24.4 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas debaoensis</i>	18.6 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas diannanensis</i>	18.9 mg·kg <sup>-1</sup>	[9] <sup>1</sup>
Zinc	<i>Cycas elongata</i>	19.8 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas fairylakea</i>	26.6 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas micholitzii</i>	14.1 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas micronesica</i>	19.0 mg·kg <sup>-1</sup>	[12]
Zinc	<i>Cycas micronesica</i>	15.2–70.2 mg·kg <sup>-1</sup>	[18]
Zinc	<i>Cycas micronesica</i>	20.4–45.7 mg·kg <sup>-1</sup>	[13]
Zinc	<i>Cycas micronesica</i>	18.1–59.8 mg·kg <sup>-1</sup>	[14]
Zinc	<i>Cycas micronesica</i>	32.5 mg·kg <sup>-1</sup>	[20]
Zinc	<i>Cycas nongnoochiae</i>	28.0 mg·kg <sup>-1</sup>	[20]
Zinc	<i>Cycas panzhihuaensis</i>	13.1–15.1 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas revoluta</i>	5.7–68.5 mg·kg <sup>-1</sup>	[24]
Zinc	<i>Cycas sexseminifera</i>	13.6 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas siamensis</i>	11.1 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas szechuanensis</i>	13.6–18.3 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas thouarsii</i>	14.2 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Cycas wadei</i>	10.3 mg·kg <sup>-1</sup>	[11]
Zinc	<i>Dioon edule</i>	22.6 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Dioon mejiae</i>	12.3 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Dioon spinulosum</i>	16.4 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Encephalartos cupidus</i>	10.5 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Encephalartos ferox</i>	17.8 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Encephalartos gratus</i>	14.9–22.2 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Lepidozamia hopei</i>	23.2 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Lepidozamia peroffskyana</i>	25.2 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Macrozamia communis</i>	21.5 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Macrozamia lucida</i>	21.0 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Macrozamia moorei</i>	18.2 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Macrozamia riedlei</i>	3.6–6.6 mg·kg <sup>-1</sup>	[23]
Zinc	<i>Stangeria eriopus</i>	53.3 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Zamia erosa</i>	13.9 mg·kg <sup>-1</sup>	[9] <sup>2</sup>
Zinc	<i>Zamia fischeri</i>	20.0 mg·kg <sup>-1</sup>	[9] <sup>3</sup>
Zinc	<i>Zamia furfuracea</i>	10.5–13.7 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Zamia integrifolia</i>	15.5–16.1 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Zamia splendens</i>	13.8 mg·kg <sup>-1</sup>	[9]
Zinc	<i>Zamia vazquezii</i>	38.4 mg·kg <sup>-1</sup>	[9]
Aluminum	<i>Cycas revoluta</i>	22.0–59.6 mg·kg <sup>-1</sup>	[24]

Table A1. Cont.

Element	Species	Range	Reference
Selenium	<i>Cycas micronesica</i>	0.58 mg·kg <sup>-1</sup>	[12]
Selenium	<i>Cycas wadei</i>	0.41 mg·kg <sup>-1</sup>	[11]

<sup>1</sup> Reported as *Cycas parvula* S.L. Yang ex D.Y. Wang; <sup>2</sup> Reported as *Zamia amblyphyllidia* D.W. Stev.; <sup>3</sup> The name *Z. fischeri* is widely misapplied to the species *Z. vazquezii* in cultivation. The real *Z. fischeri* is extremely rare in cultivation, and it is probable that the taxon sampled was *Z. vazquezii*; <sup>4</sup> Reported as *Cycas miquelii* Warb.

**Table A2.** Published ranges for leaf litter element concentrations of cycad plants. Misspellings of species were corrected if identity was obvious, species that were misspelled were not included if identity was not obvious. Taxonomic synonyms were corrected. Data were estimated for reports displaying data as figures and transformed if data were presented as log.

Element	Species	Range	Reference
Carbon	<i>Cycas micronesica</i>	475–486 mg·g <sup>-1</sup>	[35]
Carbon	<i>Cycas micronesica</i>	501–534 mg·g <sup>-1</sup>	[18]
Carbon	<i>Cycas micronesica</i>	509 mg·g <sup>-1</sup>	[36]
Carbon	<i>Cycas nitida</i>	494–519 mg·g <sup>-1</sup>	[10]
Carbon	<i>Cycas wadei</i>	513 mg·g <sup>-1</sup>	[11]
Carbon	<i>Macrozamia communis</i>	515–546 mg·g <sup>-1</sup>	[16]
Carbon	<i>Macrozamia riedlei</i>	502–534 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Cycas micronesica</i>	16–22 mg·g <sup>-1</sup>	[35]
Nitrogen	<i>Cycas micronesica</i>	21–22 mg·g <sup>-1</sup>	[18]
Nitrogen	<i>Cycas micronesica</i>	20 mg·g <sup>-1</sup>	[36]
Nitrogen	<i>Cycas nitida</i>	17–22 mg·g <sup>-1</sup>	[10]
Nitrogen	<i>Cycas wadei</i>	19 mg·g <sup>-1</sup>	[11]
Nitrogen	<i>Macrozamia communis</i>	11–24 mg·g <sup>-1</sup>	[16]
Nitrogen	<i>Macrozamia riedlei</i>	11–20 mg·g <sup>-1</sup>	[16]
Phosphorus	<i>Cycas micronesica</i>	0.5–0.9 mg·g <sup>-1</sup>	[18]
Phosphorus	<i>Cycas micronesica</i>	1.3–2.0 mg·g <sup>-1</sup>	[35]
Phosphorus	<i>Cycas nitida</i>	0.3–0.9 mg·g <sup>-1</sup>	[10]
Phosphorus	<i>Cycas wadei</i>	0.5 mg·g <sup>-1</sup>	[11]
Potassium	<i>Cycas micronesica</i>	1.0–1.9 mg·g <sup>-1</sup>	[18]
Potassium	<i>Cycas micronesica</i>	2.2–14.2 mg·g <sup>-1</sup>	[35]
Potassium	<i>Cycas nitida</i>	1.2–4.5 mg·g <sup>-1</sup>	[10]
Potassium	<i>Cycas wadei</i>	3.2 mg·g <sup>-1</sup>	[11]
Magnesium	<i>Cycas micronesica</i>	3.39–6.52 mg·g <sup>-1</sup>	[18]
Magnesium	<i>Cycas micronesica</i>	3.38–5.82 mg·g <sup>-1</sup>	[35]
Magnesium	<i>Cycas wadei</i>	1.32 mg·g <sup>-1</sup>	[11]
Calcium	<i>Cycas micronesica</i>	4.2–15.1 mg·g <sup>-1</sup>	[18]
Calcium	<i>Cycas micronesica</i>	11.9–32.3 mg·g <sup>-1</sup>	[35]
Calcium	<i>Cycas wadei</i>	2.5 mg·g <sup>-1</sup>	[11]
Sulfur	<i>Cycas micronesica</i>	1.20–1.38 mg·g <sup>-1</sup>	[35]
Iron	<i>Cycas micronesica</i>	64–272 mg·kg <sup>-1</sup>	[35]
Iron	<i>Cycas micronesica</i>	28–547 mg·kg <sup>-1</sup>	[18]
Iron	<i>Cycas wadei</i>	37 mg·kg <sup>-1</sup>	[11]
Manganese	<i>Cycas micronesica</i>	24.5–86.1 mg·kg <sup>-1</sup>	[18]
Manganese	<i>Cycas micronesica</i>	23.0–37.3 mg·kg <sup>-1</sup>	[35]
Manganese	<i>Cycas wadei</i>	141 mg·kg <sup>-1</sup>	[11]
Boron	<i>Cycas micronesica</i>	29.5–51.6 mg·kg <sup>-1</sup>	[35]
Boron	<i>Cycas wadei</i>	9.9 mg·kg <sup>-1</sup>	[11]
Copper	<i>Cycas micronesica</i>	2.4–4.4 mg·kg <sup>-1</sup>	[35]
Copper	<i>Cycas micronesica</i>	1.3–5.9 mg·kg <sup>-1</sup>	[18]
Copper	<i>Cycas wadei</i>	3.3 mg·kg <sup>-1</sup>	[11]
Zinc	<i>Cycas micronesica</i>	4.5–31.2 mg·kg <sup>-1</sup>	[18]
Zinc	<i>Cycas micronesica</i>	11.0–23.8 mg·kg <sup>-1</sup>	[35]
Zinc	<i>Cycas wadei</i>	5.9 mg·kg <sup>-1</sup>	[11]
Selenium	<i>Cycas wadei</i>	0.48 mg·kg <sup>-1</sup>	[11]

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