SYSTEMATICS
CHAPTER 32

Variability of Natural Populations and Conservation Issues Facing Plicate-Leaved Zamia Species in Central and Western Panama

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Abstract

The Isthmus of Panama is host to at least 12 described *Zamia* taxa, some of which occupy a very wide swath of western Panama. Many natural populations have been extensively and intensively studied for both vegetative and reproductive variability, taking into account such parameters as position, size, and relationship of stems, leaves, and cones; coning period; and reproductive mechanism. We obtained and analyzed data for seven population groups, and the results are given herein, with the aim of clarifying population dynamics, species plasticity, and the development of a coherent postulate of population structure of the species implied.

Resumen

El Istmo de Panamá es sede de por lo menos 12 taxa descritos del género *Zamia,* algunos de los cuales ocupan una extensión muy considerable del oeste de Panamá. Muchas poblaciones naturales han sido estudiadas en forma extensiva e intensiva tanto por sus características vegetativas como por su variabilidad reproductiva, tomando en cuenta parámetros tales como la posición, tamaño y la interrelación de tallos, hojas y conos; período de formación de conos; y mecanismo reproductor. Se han obtenido y analizado datos de siete grupos poblacionales y los resultados se presentan aquí, con la finalidad de esclarecer la dinámica poblacional, plasticidad específica, y el desarrollo de un postulado coherente sobre la estructura poblacional de las especies implicadas.

Introduction

The genus *Zamia* in the Isthmus of Panama (Stevenson, 1990; Schutzman et al., 1998; Jones, 2002; Whitelock, 2002; Hill et al., 2003) represents the highest concentration of species in the neotropics (Stevenson, 1993). The distribution of *Zamia* in Panama extends from the border with Colombia in the east to Costa Rica in the west (Stevenson, 1993, 2001). With at least 13 known species (Stevenson, 1993; Schutzman et al., 1998), there is considerable debate on species limits and relationships. There are notable works, both morphological and molecular, dealing with the subject (Hill et al., 2003; Caputo et al., 2004; Schutzman, 2004;). Populations of taxonomically misunderstood plicate-leaved species of *Zamia,* referable to both *Z. skinneri* and *Z.neurophyllidia* D. W.Stevenson, exist

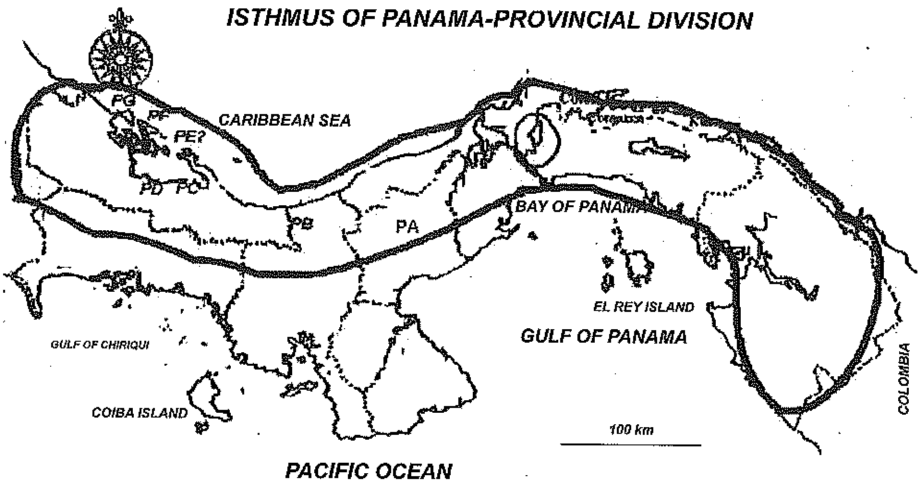


Figure 32-1. Distribution of plicate-leaved populations of Zamia in north-central to western Panama between 1982 and 2005.

mostly in western Panama, and are here considered as the *Zamia skinneri–Zamia neurophyllidia* complex.

The Isthmus of Panama was formed from a series of oceanic islands of volcanic origin, and the eastern part is only 3 million years old; hence, the introduction and colonization of plants and animals have been quite rapid (Coates, 1997). This process, of course, includes species of *Zamia* that are from northern or southern sources, as well as others that have evolved on the Isthmus itself, where they have formed localized endemics (Stevenson, 1993).

Population studies in cycads have addressed numerous issues, including herbivory and postfire events (Negrón-Ortiz et al., 2000), hurricane damage (Hirsch & Marier, 2002), gender performance in a cultivated cohort (Ornduff, 1996), among others discussed by Pérez-Farrera et al. (2004). The *Z. skinneri–Z. neurophyllidia* complex has been referred to before and attention has ensued, in both written (Stevenson, 1993; Whitelock, 2002; and Schutzman, 2004) and oral (D. Wm. Stevenson, pers. comm.) formats.

We conducted an extensive and intensive study on seven population of this species complex, which occupies a large swath of the isthmus from the central northeast, near the boundary of the Canal enclave, to the extreme northwest, impinging on the Costa Rican border (Fig. 32-1). The prime objective of this research was to amass a large database of vegetative and reproductive characteristics that could be used to compare populations within the complex to arrive at a better understanding of species delimitations. This research represents the most extensive population-level study conducted to date on this group, and the results presented herein will diminish some of the confusion surrounding this controversial species complex.

Materials and Methods

Every population represented in Table 32-1 and Figures 32-1 to 32-7 was studied by one or more of the authors, beginning with a general plant survey in early February 1982 by faculty and students of the Botany Department of the University of Panama. This initial survey benefited from the contribution of the systematist Dr. Robert Dressler. Dressler later wrote an unpublished manuscript, which he gave to Dr. Dennis Stevenson to carry

Table 32-1 Emergent leaf color and averages with standard deviation for variability of vegetative structures in populations of plicate-leaved *Zamia* species in central and western Panama.

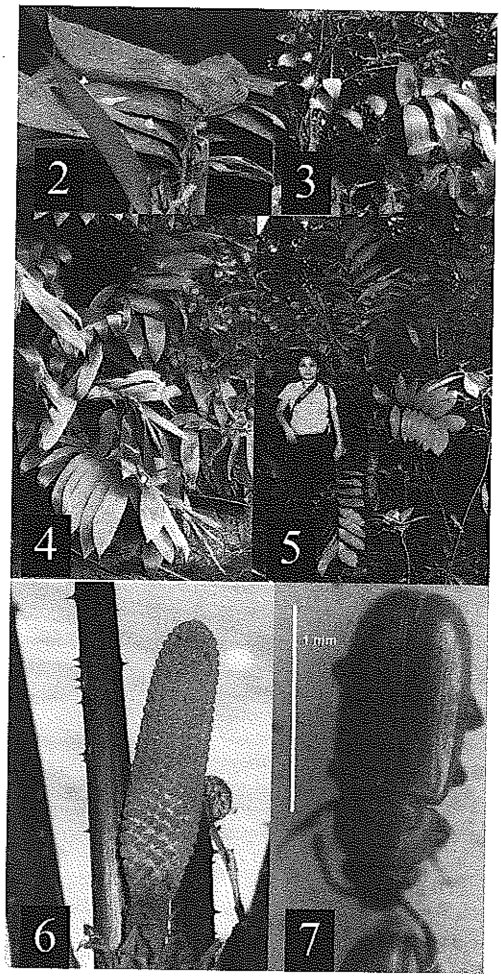
Population	**A**	**B**	**C**	**D**	**E**	**F**	**G**
Plant structure							
Color of new leaf	Red	Red	Red	Green	Reddish	Green	Green
No. of leaves	3 1	3 2	5	5 2	12 5	11 5	10 4
Petiole length	101 (16)	96 (25)	67 (12)	68 (13)	75 (13)	62 (10)	77 (15)
Rachis length	51 (17)	62 (25)	71 (12)	49 (21)	80 (15)	84 (21)	74 (17)
Leaf length	150 (32)	156 (49)	137 (20)	117 (30)	154 (25)	146 (23)	151 (27)
Ratio P/R	2.1 (0.6)	2 (1)	1 (0.2)	2 (1)	1 (0.2)	0.8 (0.3)	1 (0.3)
No. of leaflets	9 (2)	10 (3)	11 (3)	10 (2)	16 (2)	19 (5)	16 (4)
Width apical l ft	14 (2)	12 (2)	13 (1)	12 (2)	10 (2)	9 (1)	10 (1)
Length apical l ft	44 (5)	48 (8)	45 (2)	35 (6)	39 (5)	29 (4)	30 (4)
Ratio W/L	0.3 (0.04)	0.26 (0.04)	0.3 (0.02)	0.3 (0.05)	0.3 (0.04)	0.3 (0.04)	0.3 (0.05)
Width median l ft	15 (2)	13 (2)	14 (2)	11 (2)	10 (1)	9 (1)	9 (1)
Length median l ft	47 (6)	50 (8)	46 (3)	35 (7)	41 (6)	29 (3)	30 (3)
Ratio W/L	0.3 (0.04)	0.25 (0.04)	0.3 (0.02)	0.3 (0.05)	0.23 (0.03)	0.28 (0.02)	0.3 (0.03)
Width basal l ft	14 (2)	11 (2)	10 (2)	10 (2)	9 (2)	7 (2)	8 (1)
Length basal l ft	45 (6)	47 (9)	45 (4)	32 (6)	37 (6)	27 (4)	27 (3)
Ratio W/L	0.3 (0.05)	0.5 (0.05)	0.2 (0.05)	0.3 (0.05)	0.2 (0.05)	0.3 (0.04)	0.3 (0.04)

Measurements are in cm and only healthy-looking leaves at least 100 cm in length are measured. Numbers in parentheses stand for 1 standard deviation.

on the work on the systematics of *Zamia* in Panama (Stevenson, 1993). The first author, fortunately, participated in field work with Stevenson, Russell Adams, and others, and embarked on investigating the Panamanian zamias, principally focused on ecology and reproductive biology.

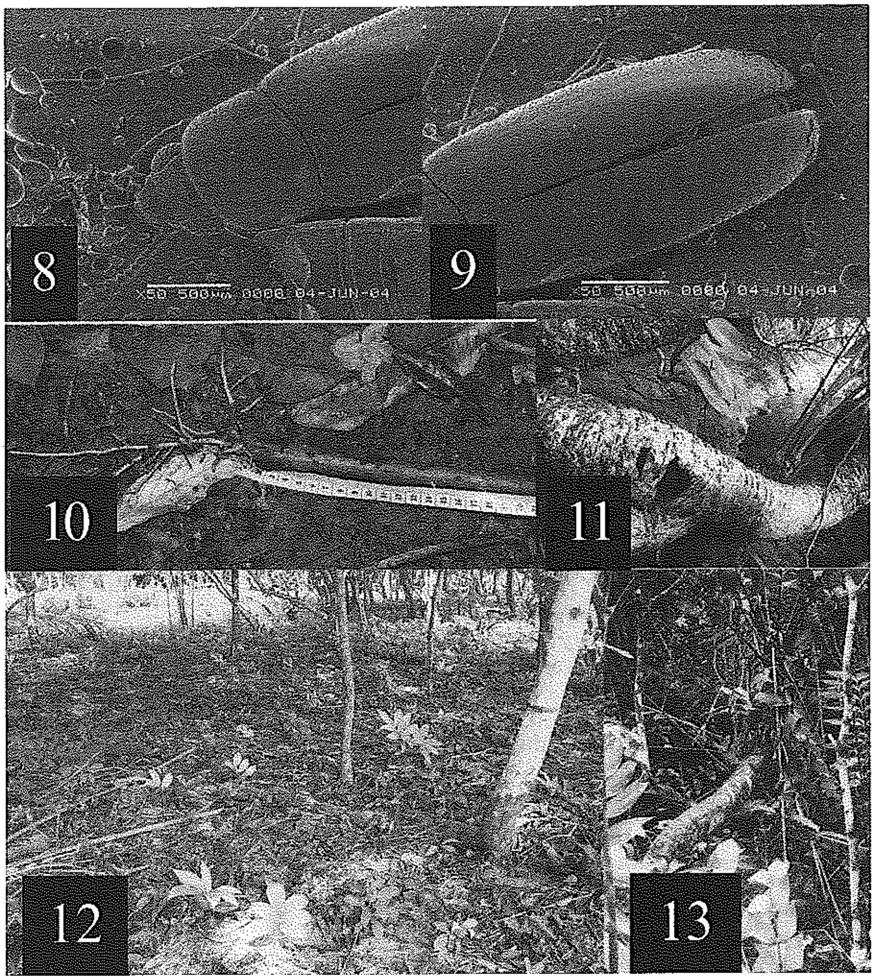
We surveyed 7 populations of the *Zamia skinneri–Z. neurophyllidia* complex , and 31 morphological variables for vegetative and reproductive structures were recorded. Four of the populations had more than 50 mature individuals (coning specimens and non-coning plants).

Although the age of zamias cannot be accurately determined in the field, any plant with leaf size comparable to that of reproductive specimens in the population was considered an adult. Three populations (C, D, and F) were less intensively surveyed, due to highly dispersed individuals, or plants having been cut down, but measurements were taken in these populations for purposes of comparison.



Figures 32-2 to 32-7. Habit, leaf shape and reproduction of plicate-leaved *Zamia* species in Central and Western Panama. 2. Plants in population A. 3. Plant in population B. 4. Plants in population E. 5. Plant in population G. 6. Dehiscing pollen cone in island population E. 7. Clavicorn beetle *Pharaxonotha*, collected from dehiscing pollen cones in every population. Figure shown is from population E.

Vegetative data included the number of leaves and leaflets pairs, stem length and diameter, petiole length, rachis length, entire leaf length, and width and length of apical, median, and basal leaflets. Petiole to rachis length and leaflet width-to-length ratios were calculated. Annotations were made on the maturity and sex of cones when present. Dehiscing pollen cones were considered mature and so were seed cones with visibly ripe seeds.



Figures 32-8 to 32-13. Reproduction, growth and regeneration in plicate-leaved *Zamia* populations in western Panama. **8, 9.** Scanning electron micrograph of *Pharaxnotha* beetle. Proximal and distal, respectively. **10.** Close-up view of apparent root regeneration from detached petiole base. **11.** Old plant in population E, growing over and quite near the surface of the sea. **12.** Regeneration in population F. **13.** Giant plant in population F, destroyed between 2002 and 2004.

Other data included cone length and diameter, length of peduncle or stipe, and maximum diameter of the same near the base of the cone. Number of sporophyll columns and rows were counted, and the ratio of peduncle diameter to length for both seed and pollen cones was calculated. The data in Table 32.1 are simple statistics for values of average (Avg) and standard deviation (SD), and the color of emergent leaves, a very conspicuous and stable characteristic in four of the populations studied, was included. A statistical analysis between populations A, B, E, and G, making use of the SAS ANOVA procedure for Duncan's multiple range test, was made because more data based on adult size of individuals were available (Table 32-2). All populations, with more inclusive data including reproductive organs, will be addressed in a future publication dealing with the systematics of the of this species complex.

We collected pollinator beetles from pollen cones in all populations over the years, one population having been subjected to exclusion experiments by the last author (population G), as described elsewhere (Norstog and Nicholls, 1997; Stevenson, pers. comm.).

Scanning electron micrographs were made at the University of Panama (Universidad de Panamá) scanning microscope facility. Uncoated beetles were used (Figs. 32-8 and 32-9).

Results and Discussion

POPULATION STRUCTURE AND VARIABILITY

Population A occurs at about 600 or more m.a.s.l., while population B, considered to be conspecific, is found from sea level up to about 200 m. Populations C and D are also land forms near sea level and in shaded rain forest, in contrast with populations E, F, and G, which are found at sea level and near the sea, receiving on some occasions salt spray from the water, and being lightly shaded to barely shaded in many places.

Populations A and B are here considered as representatives of *Zamia skinneri*, and F and G are somewhat similar to the description of *Z. neurophyllidia* D. W. Stevenson, although some differences have been observed. Population E appears to be a new taxon with intermediate features between populations A/B and F/G. Adequate data for populations C and D were not available at the time of this writing, and neither were there enough samples of population F. These will be included in the future systematic assessment of the species complex.

Table 32-1 shows that there is much variability in every parameter measured for all populations, based on simple statistics of means and standard deviations. It should be noted that the color of emergent leaves in adult plants and in most plantlets of the same population is a reliable measure of variability.

Table 32-2 Results of the SAS ANOVA procedure for Duncan's multiple-range test for comparison of select vegetative variables of plicate-leaved populations of Zamia in central and western Panama.

	Variables									
	Nleaf	**Pet**	**rac**	**pet/rac**	**Tleaf**	**Nfol 1**	**nfol r**	**wmdfol**	**lmdfol**	**wmdfol/lmdfol**
F value	86.17	41.06	32.25	83.05	3.77	124.35	114.93	95.73	111.36	73.00
Duncan Grouping	A PopE	A PopB	A PopE	A PopA	A PopB	A PopE	A PopE	A PopA	A PopB	A PopG
	B PopG	A PopA	A PogG	B PopB	B PopE	A PopG	A PopG	B PopB	B PopA	A PopA
	C PopA	B PopG	B PopB	C PopG	B PopG	B PopB	B PopB	C PopE	C PopE	B PopB
	C PopB	B PopE	C PopA	C PopE	B PopA	C PopA	C PopA	C PopG	D PopG	C PopE

	Wapfol	**lapful**	**wapfol/ lapfol**	**wbslfol**	**Lbslfol**	**wbslfol/ lbslfol**
F value	60.66	109.76	48.95	68.82	105.67	27.48
Duncan Grouping	A PopA	A PopB	A PopG	A PopA	A PopB	A PopA
	B PopB	B PopA	B PopA	B PopB	A PopA	A PopG
	C PopG	C PopE	C PopB	C PopE	B PopE	B PopB
	C PopE	D PopG	C PopE	C PopG	C PopG	B PopE

nleaf=number of leaf on plant; pet=petiole length; rac=rachis length; tleaf=leaf length; nfoll=number of left side leaflets; nfolr=number of right side leaflets; wmdfol=width median leaflets; lmdfol=length median leaflet; wapfol=width apical leaflet; lapfol=length apical leaflet; wbslfol=width basal leaflet; lbslfol=length basal leaflet.pr > *F* < 0.0001. Populations with the same letter at the left in each column are not significantly different for the characteristic.

Table 32-2 gives the result of the SAS ANOVA of vegetative characteristics of populations A, B, E, and G. Populations A and B, although occurring in separate habitats, are similar in the number of leaves on trunk, petiole length, and length of basal leaflets. Populations E and G share a large number of size features of the leaves, including petiole length, rachis length, ratio of petiole length to rachis length, total leaf length, number of leaflets, and maximum widths of leaflets (apical, median, and basal). Populations A and E share same value for total leaf length; populations A and G also share similar values for total leaf length, and the width-to-length ratio of median and basal leaflets. Populations B and E share the same values for the width-to-length ratio of apical leaflets and basal leaflets. The data show quite a number of similarities in size of vegetative characteristics of leaves among the four populations analyzed, and some of this may be due to ecological differences. Although the results show many size differences of leaf features between populations A and B, both considered conspecific, the differences could be due to ecological and habitat differences, because both populations appear to be the same in leaf number, petiole size, emergent leaf color, and reproductive organs characteristics, the latter to be dealt with in a future publication on the systematics of the group.

Although it has been stressed that size and even form differences in leaf characteristics do not always mean specific differences among populations growing in different habitats (Newell, 1986), when these differences are many, the interpretation for considering species differences might vary among different workers. This has been the case in the research of Newell (1986), while studying the variations of leaflet morphology among populations of *Zamia* in Porto Rico and in which differences in leaflet morphology were found in three populations of the genus. The "narrow leaflet" form has been ascribed to *Zamia portoricensis* Urban, while the "wide leaflet" form has been considered to be *Zamia latifoliolata* Prenl. or *Zamia debilis* L. f. Some workers, such as Eckenwalder (1980), argue for synonymy based on a presumptive continuous variation or frequency distribution in leaflet widths throughout the Caribbean, but Stevenson and others argue for at least five or more valid species among Caribbean zamias (Norstog & Nicholls, 1997).

Much research on the value of leaf characteristic variations in cycads has been carried out by workers at La Selva Biological Station in Costa Rica, Central America (Clark & Clark, 1987, 1988; Clark et al., 1992) with populations of a species considered to be *Zamia skinneri* but which has since come to be considered by others as *Z. neurophyllidia* D. W. Stevenson, citing the same works (Norstog & Nicholls, 1997). However, there is some doubt as to the real specific entity of the tax on, and future research, including both the Costa Rica and Panama forms, will be undertaken to clear up matters. According to Clark and Clark (1987), the result of their 6-year research on the aforementioned species shows correlation between reproductive performance and plant size, given as number of leaves per plant or as number of leaflets in the largest leaf. This study was circumscribed to temporal and environmental patterns of reproduction. Light availability in primary and secondary forests also had an influence on reproductive growth. More light in open canopy of secondary forest meant a higher degree of sex organs formation and function. This result was the outcome of a 6-year study in a guarded biological station in a tropical rain forest. In contrast, all the populations in the present work are of free access to the public and are being continually degraded by human actions (building of fences for cattle, cutting down of plants to make pathways through the forest, etc.). Even population A, within a national park, is vulnerable to poaching and destruction, albeit on a smaller scale. This means that population values tend to change on a yearly basis. Even so, enough data have been gathered to make more than preliminary assumptions on a population scale, with four populations under analysis and two to study the effect of plant size on reproductive growth.

Tables 32-3 and 32-4 contain data correlating plant size, measured by number of leaves and number of leaflets on largest leaf, respectively, with cone production. Usually, more pollen plants than ovulate plants are present, although the highest percentage of coning was intermediate, considering the lower and the higher measures of plant size and coning activity. In other words, the highest values for plant size did not correlate with more coning activity than lower values. More data during additional years are warranted here to be comparable with the 6-year study at La Selva in Costa Rica for estimating the so-called operational sex ratio, and the "adult" or cumulative sex ratio. The former refers to pollen dehiscence correlated with ovule receptivity in seed cones, and the second to cumulative data on coning in the populations during many years of observation (Clark & Clark, 1987). However, coning sex ratios are given for the years of observation in many of the populations (Table 32-5), and it can be clearly seen that they change from year to year, that coning, per se, is very low in all populations and that in some years no seed cones were observed. In every case, when a ratio of unity was not obtained, the population was definitely male biased. This reinforces the fact that ovulate plants are more resource dependent than pollen plants, as has been seen elsewhere (Clark & Clark, 1987, 1988), although

Table 32-3 Maximum plant size by number of leaves and leaflets respectively correlated with reproductive activity in a *Zamia skinneri* population in northwestern Panama during 2004–2005.

Number of Leaves	Vegetative Plants	Pollen Plants	Seed Plants
2–4	(22) 67	(9) 27	(2) 6
5–7	(6) 35	(9) 53	(2) 12
8–10	(2) 50	(1) 25	(1) 25
Leaflets on largest leaf			
8–11	(13) 72	(3) 17	(2) 11
12–15	(10) 48	(9) 43	(2) 9
16–18	(5) 50	(4) 40	(1) 10

Sample size is given in parentheses with percentages in the population at right.

Table 32-4 Maximum plant size by number of leaves and leaflets respectively correlated with reproductive activity in a *Zamia* sp. nov. in western Panama in 2004.

Number of Leaves	Vegetative Plants	Pollen Plants	Seed Plants
6–12	(26) 81	(2) 6	(4) 13
13–19	(11) 69	(2) 12	(3) 19
20–28	(3) 67	(0) 0	(1) 33
Leaflets on largest leaf			
10–14	(18) 95	(0) 0	(1) 5
15–17	(10) 63	(4) 25	(2) 12
18–20	(12) 71	(0) 0	(5) 29

Sample size is given in parentheses with percentages in population at right.

Table 32-5 Estimated population size, time of cone dehiscence, and coning sex ratios of plicate-leaved *Zamia* populations in central and western Panama.

Population	*N*	DT	Sex Ratio (Male:Female)	*n*	Year
A	>100	Nov	2 : 0	(2)	2003
	>100	Nov	1 : 1	(4)	2004
	>100	Nov	1 : 3	(8)	2005
B	<100	Nov	1 : 1	(2)[a]	2003
	<100	Nov	1 : 1	(2)	2004
	<100	Oct	8 : 1***	(26)	2005
C	<50	Sept	1 : 0	(1)	2004
	<50	Sept	5 : 1	(6)	2005
D	17	Oct	1 : 0	(1)	2000
	> 40	Sept	7 : 1	(8)	2005
E	>200	Sept–Oct	4.3 : 1	(7)	2004
F	<100	Apr–May	1 : 1	(4)	2000
	>500	June	1 : 0	(1)	2001
	>1000[b]	Oct	2 : 1	(3)[c]	2004
	>1000[b]	Sept	2 : 1	(26)[d]	2005
G	>400	Apr–June,	2 : 1	(6)	2000
	>400	Sept–Dec			
	>400	Sept–Oct	1 : 1	(2)	2001
	<100	Sept	1 : 1	(15)	2005

N = number of plants seen or estimated; *n* = number of coning plants seen in a given year; DT = time of observed cone dehiscence. \

[a] Seed cone not seen but existence based on cone with ripe seeds in 2004.

[b] > 1000 with estimates > 5000.

[c] One male plant had 4 cones and another was 7-branched with 4 cones on each of four of the apices.

[d] More cones were seen but only a random selection was made. Sex ratios were tested for departure from 1:1 with significance by a binomial test. *** $p<0.001$.

pollen plants can form up to seven cones on the same plant in a coning cycle. There was a higher tendency toward unity in coning sex ratio in population G, even with a higher output of cones. But it must be mentioned that population G has been severely destroyed and the remaining individuals are growing in minimal shade and very near the sea shore. This fact, perhaps, is reminiscent of a population of *Zamia neurophyllidia* (Clark & Clark, 1987), reported as *Z. skinneri* in the original publication, at La Selva Biological Station in Costa Rica, growing under higher canopy openness.

REPRODUCTIVE BIOLOGY

Phenology

During the study of the various populations of the *Zamia skinneri–Zamia neurophyllidias*–complex, notes were made of certain aspects of reproductive biology. Pollen cone reproductive cycle for populations A and B is from about late July to early November, with dehiscing cones in late October to November. Data for the other populations were extrapolated from the time of cone dehiscence, and previous knowledge for almost all the known Panamanian Zamias. In these groups, with the exception of *Zamia elegantissima* Schutzman, Vovides and Adams, coning events take 3.5–4 months, from the time of first sight of cone emergence between the bracts, to time in which a pollen cone is seen dehiscing or an ovulate cone is seen receptive (usually later than the pollen cones) with dehiscence occurring over a 1- to 2-month period. Spent pollen cones were observed in population G in April, September, and November, and new cone formation was observed in June and September. In this case, it appears that pollen cones are produced many times during the year, instead of during a single coning cycle. This also has been observed in population F, while populations A, B, and E appear to maintain an annual cycle. In populations C and D, both receptive seed cones and dehiscing pollen cones have been found in September, and it appears that this maturing of cones would proceed into early or mid-October. The same was found for population E. Seed cones take more than 14 months to mature after pollination in population G, but only a year in population E. In both populations A and B seed mature in the cones about a year after pollination. In previous unpublished reports, it has been noted that certain *Zamia* populations do indeed form mature seed cones at different times, even within the same population.

Pollination Biology

Pollinators (Figs. 32-7 to 32-9) have been recovered from dehiscing pollen cones (Fig. 32-6) in all populations and, in every case, they have turned out to be one or more species of the clavicorn beetle *Pharaxonotha*, which has also been found in other zamias, such as *Zamia pumila* and *Z. furfuracea* (Norstog et al., 1986; Tang, 1987; Norstog & Fawcett, 1989; Stevenson et al., 1998). *Pharaxonotha*, accompanied sometimes by the weevil *Rhopalotria*, has also been found as the major pollinator in all the Panamanian zamias that have been studied in this respect (Taylor, unpubl. data). The importance of insect pollination for the survival of cycads cannot be underestimated, considering the wide-ranging data for such in different genera and species (Norstog & Fawcett, 1989; Ornduff, 1991, 1992; Donaldson, 1997; Vovides et al., 1997; Stevenson et al., 1998; Mound & Terry, 2001; Schneider, 2002; Wilson, 2002; Hall et al., 2004). For effective conservation of cycads in the wild, their pollinators must also be conserved (Norstog & Fawcett, 1989).

Considering the aforementioned factors, pollination by the same species of insect could be additional evidence for close phylogenetic relationships of this species complex in western Panama.

Conservation Status and Threats

Many of the *Zamia* populations of western Panama are threatened by agricultural expansion, and changes in land use and some sites have been under intense pressure (Fig. 32-12). Other localities under less pressure have had plants recover naturally, even after being exposed to seawater (Fig. 32-11). Many plants, or parts thereof, whether in the wild or under cultivation, have grown new apices from detached trunks, and, in two occasions, from what appears to be roots growing out of a petiole base. In both cases, the petioles with roots were found in population B. (Fig. 32-10). It has been suggested that this might have been a case of roots growing out of small pieces of trunk attached to the petiole (Vovides, pers. comm.) so the matter remains open to further research. Given the opportunity, new apices can reform new plants.

The threats to the cycads arise from a complex of circumstances based on many factors. The Atlantic side of Panama lacks an extensive road system and, because of this, populations are relatively difficult to access. This has been quite advantageous in allowing undisturbed cycad habitats to remain intact. Many of the populations are accessible only by boat, which is a major source of transportation in the area. Many people who live in the cycad sites do not know anything about them or have very little use for them in their daily living, yet others have medicinal uses for the cycads or employ the mucilage in the assembly of guitar or other local musical instruments. Where the cycads are used, a certain amount of destruction from harvesting can hamper a population's recruitment ability for a very long time. Because of this, all cycads in western Panama that are part of this study are vulnerable to habitat destruction, the inability to reproduce, or to the possible depletion from over-collecting.

Population A might survive for many years, unless an adequate road is made available to people living near the site; however, population B is practically decimated to the extent that almost half of the mature plants observed in November 2004 had been cut down by October 2005.

At the present time, habitat destruction is a threat to each of the populations studied, except population E. The plants in populations F and G live in beach strand habitat and are being exploited for their perceived medicinal value by the local people, resulting in a sustained harvest of trunks. Because of the very large cycad populations, the harvest of trunks at the sites has not had a pronounced adverse effect on regeneration, but perhaps the tallest *Zamia* in the region, measuring greater than 3 m (Fig. 32-13), is now gone. Regrown damaged trunks are commonplace, and the plants are typically in full reproductive capacity within a 10-year period. The fact that many plants were observed with multiple trunk scars in succession is evidence that the harvest is a long-standing tradition. Habitat destruction from development of beach house lots is more of a threat on the island sites in which these plants grow. Fortunately, a national park, created for the protection of sea turtle nesting sites on one of the islands, has, for the moment, provided the nearby cycad population a sanctuary. However, another large population in the area is under threat from ongoing development.

Population E is one of the few populations without large-scale habitat destruction, which appears to be due to its isolation and human population expansion. The real threat here comes in the form of future development of a resort or exploitation by collectors, because of its relatively small area. The uses of the trunks by humans in this area are unknown at this time, but are most likely of medicinal origin.

In population C, cycads are being wiped out by slash-and-burn agricultural practices. The plants grow on steep hillsides that are rocky and unsuitable for crops, but the forest has been largely cut down to make it easier to hunt a large rodent, similar to the capybara of South America. The animal burrows into the hills and the hunters find it easier to capture without the thick vegetation. People of the area know the plants but have no use for them. The cycads are seen as being beautiful, and, after the landowners were informed of their botanical value, they became interested in helping preserve what remained of the hillside population. It is our belief that education is very helpful in the preservation of these plants, but the habitat will be preserved only if alternative sources of revenue are secured for the local people. Aboriginal people living in the area have no uses for the plants. These were found far from human settlements along creeks in rain forest. Many of the creeks are used as water sources, and the water is piped to distant villages. The cycads are neither used nor appreciated as being special, and, because of the spines on the petioles, they are cut with machetes (as are all spiny plants growing along the pathways). In this area, more cycads were observed cut down than standing, and the main reason for this was their simply being in the way. Interestingly, the cut pieces readily regenerate new growth, even the decapitated apices. Because the population consisted of very few individuals of low reproductive rate, no seedlings were found. Undoubtedly, there are other undisturbed populations within the same general area, and further study might yield healthy populations. However, the lack of human uses and their spiny nature put these plants in peril. The aboriginal people in this area are very aware of the area's vulnerability and limited resources. Again, education will be a key factor in conservation, and the few people familiar with the plants immediately appreciated their beauty when informed of their botanical significance. In fact, following a brief "on-the-spot" history lesson, some were seen looking in botanical texts under candlelight with their children to learn more about the plants.

Conclusions and Recommendations

SUMMARY OF MORPHOMETRIC AND POLLINATION BIOLOGY RESULTS

The populations assessed in this study can be distinguished based on general features of leaf size, petiole length-to-rachis length ratios, and emergent leaf color. Stem height and diameter were not taken into account, as most plants in almost every population had been repeatedly cut.

The data delimit at least three distinct species, two of which have been described and at least one that is new. Plants of populations A and B can be ascribed to *Z. skinneri*, and those of populations F and G have been ascribed by many workers to *Z. neurophyllidia*. Population C needs further study, because the plants appear to represent different taxa, some being similar to *Z skinneri* and some of dubious affinity. Population E is very interesting because the plants appear in some ways to be intermediate between populations A/B and F/G but in other ways are distinct from them both. The data herein suggest that population E might represent a species lacking description, and that will be studied in detail in an upcoming systematic treatment.

The data shed light on either an incomplete circumscription of *Z. neurophyllidia*, according to Stevenson or the existence of a distinct species represented by population F and possibly G. The future systematic publication will take up this issue in detail. .

In contrast to Stevenson's (1993) report of *Z. neurophyllidia* being somewhat small in stature (Fig. 32-5), when left undisturbed for decades these plants attain a very large size indeed (Fig. 32-13). In fact, Stevenson's (1993) description of *Z. neurophyllidia* and reassessment of *Z. skinneri* appear to include a mixed bag of representative specimens, including plants that are more like those in populations A/B and others that are more like those in populations F/G. Accordingly, it is thought that the taxa represented by populations E and F/G are in need of description and this study can aid in achieving that goal.

SUGGESTIONS FOR CONSERVING THE *Z. Skinneri*–*Z. neurophyllidia* COMPLEX

1. Information on populations, number of individuals, and present and future threats should be supplied to the country's environmental institutions.
2. The owners of lands on which the plants grow should be informed of their importance, made aware of the threats against their survival, and convinced to participate in their conservation within the framework of ongoing developments, so that certain areas are preserved for these plants.
3. In some cases, arrangements should be made for transplantation of a certain number of individual plants to educational institutions, especially to the University of Panama, where there is already a functional cycad garden, albeit very modest in scope and with hardly any financial assets of its own.
4. The environmental authorities, with the assistance of cycad workers at the university level and growers if these exist, should organize seminars at the grass-roots level and also at higher levels to make the lay public aware of the importance of

> preserving these plants. This recommendation was put into practice by three of the authors in western Panama in a rural village elementary school, with the attendance of the environmental authorities, education representatives, teachers, and schoolchildren.

The National Environmental Authority (ANAM Spanish acronym) has been informed of potential and ongoing threats and destructions of plants, especially in populations E, F, and G, but the institution is understaffed and underfinanced, so the problem also needs to be addressed by the private sector (nongovernmental organizations) and international cooperative efforts.

ASSIGNMENT/REASSIGNMENT OF POPULATION GROUPS (TAXA) TO THE IUCN RED LIST OF THREATENED SPECIES

According to the 2004 IUCN Red List of Threatened Species (IUCN, 2004), only *Z. skinneri* among the plicate-leaved populations of central and western Panama is considered threatened, being assigned the following codes, according to the 2001 Red List Categories and Criteria (ver. 3.1): EN A2acd; C1.However, in view of the destruction of *Zamia* sites observed during this study, and taking into consideration the 2001 Red List Categories and Criteria (ver. 3.1), we propose a reassignment of this species (i.e., the mainland red-emergent leaved populations) to critically endangered status (CR B2abc). Our population E, at the moment considered as *Zamia* sp. nov, should be assigned as CR B1ab(ii,iii,v)+2ab(ii,iii,v). Our populations F and G, tentatively considered as being similar to *Z. neurophyllidia* D.W. Stevenson, until further treatment in an upcoming publication, should be assigned the codes CR B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v). For the present assessment, the following issues were considered: geographic range, comprising extent of occurrence of each population being less than 100 km^2, estimates indicating severely fragmented, continuing decline observed in extent of occurrence, area of occupancy and area /extent and / or quality of habitat (rapidly being destroyed by human activities).

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