

## Observations on the Seasonal Consistency in Germination Timing for *Scheelea zonensis*

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Seeds of palms are often reported to be difficult to store, presumably due to the lack of mechanisms for enforced dormancy (sensu Harper 1977; DeLeon 1958, Corner 1966, Dickie et al. 1993). However, many display innate dormancy (sensu Harper 1977; e.g., Braun 1968, Jordan 1970, Koebernik 1971, Basu and Mukherjee 1972, Broschat and Donselman 1988); delays to germination of over 6 months are not uncommon for seeds of palms (e.g., Braun 1968, Jordan 1970, Koebernik 1971).

Long delays to germination in palms has meant that little is known of the variation in germination timing for palms. Braun (1968)<sup>3</sup> stated that dramatic variation is commonplace for species of palm, but published data to support this generalization are few. We herein present relevant observations on the germination of seeds from *Scheelea zonensis* Bailey in seasonal moist forest of Panamá (Leigh et al. 1982).

*S. zonensis* fruits were collected in August, 1991 from along Old Gamboa Road near Summit Gardens, Panamá. Fruits with intact exocarps were found directly beneath adult palms, indicating that they had not been manipulated by fruit or seed eating animals prior to collection. All exocarp and mesocarp was removed from each of 400 seeds;

<sup>3</sup>"A most peculiar phenomenon and one typical for the palm family is the delayed germination of the seed at certain intervals. Early-germinating seeds, usually few in numbers, are followed at intervals by more groups of germinating seeds. Frequently, but depending on the species, the second batch represents the majority of seedlings. Delayed germination continues, but in reduced numbers. Often the last seedlings appear when the first seedlings have developed into strong young plants. There is an obvious benefit to the plant in delayed germination, especially in the natural habitat. Losses caused by climatic influences or herbivorous animals thus may be replaced by late-germinating seeds."

seeds were from 9 plants and the numbers collected from beneath each were: 22, 32, 33, 35, 40, 45, 50, 50, 63. These seeds were placed on the surface of the soil and were surrounded and covered by a hardware-cloth cage, to protect them from rodents, on Orchid Island in the Panama Canal. During September 1992 experiments were terminated on Orchid Island. 108 (27%) of the 400 seeds had germinated during the previous 5 months (April-August).

In order to follow subsequent germination of seeds remaining in the cage, a random sample of 184 of the ungerminated seeds were removed to nearby Barro Colorado Island (B.C.I.), Panamá in September 1992. These seeds were placed in seed-trays, on top of 3-cm soil, on the bottom shelves in a greenhouse. Over the course of the next year, seeds in the greenhouse experienced similar conditions of light to those they would have experienced had they been left in the understory on Orchid Island. However, trays were watered regularly during the dry season; therefore soil water was more evenly available than if the seeds had been left in the field. Seeds were inspected monthly for germination.

No further germination occurred until 8 months later, when in April 1993, 10 seeds germinated. An additional 2 seeds germinated during July of 1993. Again no further germination occurred until 1994, when 2 seeds germinated in April, 3 in May, 3 in June and 1 in July. A summary of the time to germination for these seeds is that most germinated after 10 months. However, small percentages of seeds germinated only after 2 or 3 years on the surface of soil.

It is striking that all seeds germinated at approximately the same time of year (the early wet season). In a community-wide study of germination strategies on B.C.I., Garwood (1983) found a sin-

gle peak in germination at the beginning of the wet season. Of 157 woody dicot species studied, 18% remained dormant for between 4 and 8 months between dispersal in one wet season and germination during the following. Therefore seasonal dormancy to prevent germination during the unfavorable dry season appears to be a common trait. Seasonal consistency over >1 yr for a single cohort of seeds was not reported by Garwood (1983), but seasonal germination after more than one year has been observed for the understory palm *Astrocaryum mexicanum* (N. Garwood and N. Smythe, pers. comm.). Similarly, seeds of the canopy tree *Vantanea occidentalis* (Humiriaceae) germinated in synchrony with those of *S. zonensis* after one, two, and three years in the greenhouse (Garwood and Dalling, unpubl. data).

Competition between seedlings may be the factor that selects for emergence during the early wet season among pioneer species (Garwood 1983). Non-pioneer and understory species may be selected to germinate during the wet season in order to grow sufficiently to survive the up-coming dry season and/or due to the availability of resources during that time (Garwood 1979, 1983 and references within). Wet season germination, but spread over several years within a seed-cohort, could increase plant fitness in species where the size of seed crops varies dramatically year to year, or under fluctuating pressure from herbivores that feed on reproductive structures (flowers, seeds, etc.). These conditions may apply to *S. zonensis*. DeSteven et al. (1987) reported that on average 19% of individuals of reproductive size failed to ripen fruit in any given year of their census. Of 12 reproductive individuals censused over 4 fruiting seasons, only 4 produced fruit in all 4 seasons (see Wright 1990). *S. zonensis* seeds are heavily attacked by larvae of a bruchid beetle once they reach the ground (Wright 1990) and a variety of vertebrates feed on and scatter-hoard these seeds (Smythe 1970, Giacalone-Madden et al. 1990). The combination of unpredictable reproduction and fluctuating seed-predation intensities suggests that there is a high degree of variation in viable seed output across years for individual adult palms.

The extent to which variability in the timing of germination for *S. zonensis* is genetically and environmentally determined is unknown. Differences in the time to germination may be the result of a genetic polymorphism since adults producing seeds which do not all germinate at the same time under identical immediate conditions are likely to

be favored by selection (Bradshaw 1965, Cohen 1966, Westoby 1981). However, delays to germination may be environmentally determined (Bradshaw 1965, Silvertown 1984, Schlichting 1986). Phenotypic plasticity may allow seeds of identical genotype to express alternative phenotypes (e.g., variation in germination delays); individual seeds found in unique circumstances may express unique phenotypes (e.g., different lengths of time to germination). The relative importance of these mechanisms on their own, or in concert, in producing variation in delays to germination deserve attention. Elucidating these mechanisms is necessary to understand the potential constraints on and adaptive significance of variation in germination timing for *S. zonensis* in particular and for palms in general.

There exists a gradient in rainfall and seasonality across the isthmus of Panamá (Croat 1978). Due to the occurrence of *S. zonensis* throughout the former Canal Zone (Croat 1978), this palm may serve as an appropriate species for evaluating the significance of variation in germination timing across sites of varying environmental conditions. We predict that seeds of individuals from less seasonal locations will show less seasonal tendency in germination timing.

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