

Comparative Demography of a Clonal Palm (*Oenocarpus mapora* subsp. *mapora*) in Panama

DIANE DE STEVEN

*Department of Biological Sciences,
University of Wisconsin-Milwaukee,
Milwaukee, WI 53201*

As one facet of palm ecology, demographic studies are useful in providing information about the status and performance of species populations in a community. Palms are attractive subjects for studies of demographic processes (e.g., Bannister 1970, Bullock 1980, Piñero et al. 1984). Because they are widespread, and abundant in tropical forests, palms are important food sources for tropical animal communities. They also have a relatively fixed pattern of morphological development that provides convenient features for population analysis. In 1980, I started a demographic study of a colonial or vegetatively-reproducing palm, *Oenocarpus mapora* subsp. *mapora* (syn. *O. panamanus*), in central Panama, in order to evaluate the contribution of the clonal habit to the palm's overall population dynamics.

The ecological and evolutionary significance of clonal reproduction in plants is a subject of recent theoretical interest, and at least two potential, though not mutually exclusive, benefits have been suggested (Cook 1979, Abrahamson 1980). The first is that clonal spread allows an individual plant to exploit new "resources," whether in the form of more space, a new area of soil and its associated nutrients, or a different light environment. The second is that the vegetative production of identical plant units (shoots or ramets) reduces the probability of ecological extinction of the genetic individual (genet), since the risk

of mortality is "spread" among the ramets within a genet or clone. These hypotheses are frequently difficult to evaluate in field populations because the form of clonal proliferation in many plant species makes it nearly impossible to distinguish different genetic individuals in a population. The clustering palm *Oenocarpus mapora* subsp. *mapora* provides two aspects useful for evaluating the importance of some hypothesized benefits of clonal growth. First, the clustering of stems resulting from limited lateral spread allows genetic individuals to be identified easily, and thus it is possible to study both the dynamics of the "population" of vegetative ramets and the contribution of ramet dynamics to the population dynamics of genets or clones. Second, since the growth of any palm stem is dependent upon a single terminal meristem, loss of the meristem results in death of the stem and, for a non-clonal palm, in death of the individual genet. Thus, for palms, the potential benefit of clonal growth in reducing mortality risk to the genet may be particularly pertinent.

Here I present an overview of the *Oenocarpus* study system and objectives. Current population monitoring is designed to examine the consequences of clonal growth for genet demography and for variation in genet demography in different forest types on Barro Colorado Island, Panama, a tropical moist forest where the palm is abundant.

Natural History

Oenocarpus mapora subsp. *mapora* is a member of an arecoid genus whose distribution is centered in South America, although this particular species occurs primarily in Costa Rica and Panama. It is found in all forest types on Barro Colorado Island. Clones consist of clumps of vegetative shoots of various ages that are produced from lateral buds at the base of other shoots. Clumps remain distinct from each other because there is very little rhizome extension of the buds prior to rooting. Basal diameter of adult clones ranges from 0.5–3.0 m, depending on the number of stems in the clone.

Shoot growth follows a typical palm pattern and allows the delineation of developmental phases for use in demographic analysis. There is initially a seedling phase characterized by distinctive leaf morphology with crowded, almost palmate leaflets. After several years the pinnate leaf morphology develops, and the palm enters a long juvenile phase of establishment growth during which the shoot axis increases in diameter with little or no stem elongation between nodes. As nodes accumulate on the shoot, a juvenile grows from a height of about 0.1 m to about 1.0 m (measured to a standard point on the juvenile shoot axis) before rapid stem elongation begins due to increased internode length. This change signals an immature phase in which the palm undergoes rapid growth in height to reproductive size. The adult or reproductive phase begins when the palm reaches a height of about 8 m (the shortest palm which I have observed flowering) and continues as the palm grows to a mature height of 16–20 m. Sexual reproduction is seasonal, with an average of 50% of adult-sized stems flowering each year, producing an average of 1–3 inflorescences per stem each year. About 36% of the inflorescences consist of staminate flowers only, while the remaining 64% have both staminate and pistillate flowers.

Table 1. Functional stages assigned to *Oenocarpus clones*.

Seedling
Non-clonal juvenile
Small (<0.5 m)
Large (0.5–1 m)
Clonal juvenile (largest ramet 0.5–1 m)
Immature (largest ramet 1–8 m)
Adult (largest ramet >8 m)

An inflorescence may produce about 400 mature single-seeded fruits, but fruit production varies as a consequence of losses from abortion and predation. There appears to be no seed dormancy, and seeds germinate 1–2 months after fruit fall.

A vegetatively-produced shoot (ramet) starts out as a small "juvenile" with pinnate leaf morphology; the "seedling" morphology stage is bypassed. An individual palm begins producing ramets in the late juvenile phase; over a three year period, less than 1% of juveniles <0.5 m tall produced ramets while 18% of juveniles >0.5 m produced new ramets. Only about 12% of small (1–3 m) immature palms lack one or more ramets and all large immature individuals have them; thus, in a developing *Oenocarpus* genet, the primary shoot tends to become clonal before it enters the immature phase of rapid height growth. Presumably a shoot axis has a limited number of basal buds available for ramet production; however, the ramets in turn begin producing their own ramets as they reach the appropriate size. This leads to the development of the large clump of varying-aged shoots that constitutes an *Oenocarpus* clone.

Demographic Analysis

Instead of evaluating clones according to their size (number of ramets), I classify individual genets or clones by the developmental stage of the largest (oldest) ramet, since this defines the *functional* status of the individual in the population

Table 2. Three-year stage-specific survivorship of *Oenocarpus* genets.

Stage Class	Genet Survival	Survival of Ramets Within Genets
Seedling	.27	—
Non-clonal juvenile		
Small	.76	—
Large	.98	—
Clonal juvenile	1.00	.87
Immature	.98	.78
Adult	.99	.78

(Table 1). Ramets within clones can be classified into the same developmental stages, e.g., an immature clone may have juvenile ramets in addition to the one or more immature stems that define its functional stage.

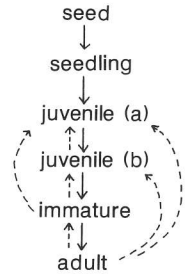
A significant consequence of clonal growth is evident from the survival rates of genets at specific stages (Table 2). Seedlings suffer high mortality due largely to debris fall and herbivory, while mortality from the same causes declines somewhat for small juveniles. Continued increase in size is associated with decreased mortality, as large non-clonal juveniles have high survival. Clones have extremely high survival, although individual ramets within these clones appear to suffer higher rates of mortality than do the clones themselves, particularly the stemmed ramets within the immature and adult clones. Most mortality in the larger stages is due to treefall damage. These patterns of survival suggest that clonal proliferation reduces the probability of genet extinction.

The classification of clones by developmental stage (Table 1) allows me to focus upon the demographic behavior of genets rather than just on the vegetative ramets. While ramet births and deaths may affect clone size, the functional behavior of the clone as a genetic individ-

A. NON-CLONAL



B. CLONAL



1. Developmental transitions in the life histories of a non-clonal (A) and clonal (B) palm. See text for explanation.

ual in the population is determined by the oldest ramet(s); consequently, addition of new ramets to a clone does not alter its functional status in the population. However, death of ramets can change a clone's functional status if the oldest ramet(s) dies, since the clone's developmental stage will be redefined by that of the oldest *surviving* ramet. This produces the qualitative difference between non-clonal and clonal life histories illustrated in Figure 1. Individuals in a non-clonal population (1A) grow through a fixed sequence of developmental stages, with mortality removing individuals from the population and thus reducing recruitment to subsequent stages. In a clonal plant (1B), individual development initially may resemble the non-clonal pattern (solid arrows) for the phases that lack vegetative reproduction (seedling and juvenile "a") and for the cases where entire clones die. However, with initiation of clonal reproduction by larger individuals (juvenile "b" and older), attainment of subsequent stages may be assured if clones die infrequently; instead, death of ramets, depending upon which ones die, may simply "push back" the functional status of the genetic individual to an earlier point in the developmental sequence (broken arrows). This obviously creates a more complex demographic pattern than in a

non-clonal species, since there are a number of possible "regressive" pathways that ramet mortality can generate for different clones.

Comparative Demography

Barro Colorado Island has a mixture of forest types (see Foster and Brokaw 1982 for a detailed description). I am monitoring *Oenocarpus* populations in three areas. Old forest (OF) is estimated to have been free of major disturbance for at least 200 years; it has a tall heterogeneous canopy with many old trees and a fairly high degree of canopy turnover from branch and tree falls. Secondary forest represents advanced regrowth from old clearings and is probably at least 100 years old; it has a shorter canopy and higher stem density than the old forest. A third area (disturbed forest, DF) is located near the site of a several-hectare canopy blow-down that occurred in 1973. The forest canopy near this blowdown site is composed of short, young trees and appears to have been repeatedly windthrown. *Oenocarpus* is a subcanopy species in the old forest, is more frequently near the canopy in the shorter secondary forest, and is a dominant canopy-level species in the disturbed forest.

Oenocarpus population density and structure differ considerably between forest types (Table 3). Population density varies widely, with very low density in the old forest and extremely high density in the disturbed forest. Excluding seedlings, which are a highly variable fraction of the population from year to year, the most striking difference among sites is that the old forest population has a high proportion of adult clones and a low seedling/adult ratio in comparison with the other two sites, which suggests that regeneration is poor in mature forest. That the mature forest population is an old, persistent population is also suggested by the presence of more large, many-stemmed adult clones

Table 3. *Oenocarpus* population structure in three Barro Colorado Island forest types.

Genet Stage Class	% of Population in Stage Class		
	Old Forest	Secondary Forest	Disturbed Forest
Non-clonal juvenile	38	66	70
Clonal juvenile	6	8	7
Immature	14	16	9
Adult	42	10	14
Estimated palm density per ha (excluding seedlings)	109	244	1,744
Plot size sampled (ha)	1	.7	.16
Average seedling/adult ratio	2.5	8.5	11.8

there than in the other two sites. Overall, the high population densities and high seedling occurrence in the disturbed forest site suggest that the palm is favored in windthrown areas, perhaps because clones can survive canopy fall despite some ramet death and subsequently show strong growth response to increased light levels.

Long-range Objectives

Detailed monitoring of the growth and survival of both genets and ramets in all three *Oenocarpus* populations will allow me to estimate the demographic status of genet populations in each of the three contrasting forest types, and to evaluate the contribution of ramet dynamics to the status of each. The importance of vegetative reproduction to genet population dynamics is likely to vary under different regeneration conditions. Where ramet mortality is low, clonal growth may provide little additional advantage over a solitary growth habit; however, clonal growth would allow longer genet persistence under conditions of high ramet mortality. Fur-

ther analysis, including projection matrix techniques in which both genet and ramet values are utilized to estimate population status, will explore these questions.

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