



The Population Dynamics of Columnar and Other Cacti: A Review

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Abstract

In this article, we review the population cycles of cacti, with an emphasis on the large, often keystone columnar cacti of the North American deserts. These and many other cacti often experience dramatic increases and declines in their numbers. Seeds that germinate in years that provide favourable conditions for regeneration and subsequently survive establish a cohort. We first review the limitations to estimating the age of any given individual; without this information, we cannot reconstruct the age of a population and reconstruct its age structure and demography. We then discuss the techniques for so doing, the data that are available, and the work that has been carried out on a few limited and isolated populations, primarily of *Carnegiea gigantea*. We then link century-scale population fluctuations with micro, local, regional and global climate factors, which include nurse-plant relationships, periodic freezing and El Niño events, and proceed to elaborate on the factors that influence cactus demographics, such as dispersal, pollination, human impacts and climate change.

Introduction and Distribution

The cactus family (Cactaceae) is widely distributed from Canada, across the USA, and south to Mexico, Central and South America, including the Galápagos Islands and the West Indies (Anderson 2001; Benson 1982; Kearney and Peebles 1960). With the exception of *Rhipsalis baccifera*, which is found in Africa, Sri Lanka and Madagascar, cacti are native exclusively to the Americas; this one epiphytic species was likely carried by birds to the Old World (Anderson 2001; Barthlott 1983). In addition to being prominent dwellers of the desert, to which many species are well adapted (Nobel and Loik 1999), members of the cactus family are found over a wide range of habitats, from cold continental climates, to Patagonia, to tropical rain forests (Anderson 2001; Benson 1982; Mauseth 2006; Robichaux 1999). The *Opuntia* genus alone can be found, both introduced and naturally, in diverse habitats (Rebman and Pinkava 2001), including South America and the Galápagos Islands (Hicks and Mauchamp 2000; Wiggins and Porter 1971), Mexico (Bravo-Hollis 1978; Soberon et al. 2001), Canada

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Fig. 1. A very large *Carnegiea gigantea*, about 12 m tall. Photo by T. D. Drezner.

(Benson 1982; Loik and Nobel 1993), Africa (Hoffman et al. 1998) and Europe (Gimeno and Vila 2002).

At the local scale, the distribution of cacti is affected by many environmental factors. Cacti require favourable climate (Steenbergh and Lowe 1983; Whitford 2002), nurse cover (Franco and Nobel 1989; Nobel 1984; Rojas-Arechiga et al. 1998), adequate pollination and seed dispersal (Fleming and Valiente-Banuet 2002; Suzan et al. 1996), proper drainage (Rebman and Pinkava 2001) and soil conditions (Bashan et al. 2000; Despain 1974), and often, mycorrhizae (Camargo-Ricalde et al. 2003; Cui and Nobel 1992; McAuliffe 1994; Parker 1991; Pimienta-Barrios et al. 2002).

Many cacti are keystone (Paine 1969) species or are at least critical for the survival of many other plant and animal species in their communities. Among these keystone species are several of the columnar cacti of the Pachycereae tribe, such as the massive *Pachycereus pringlei* (cardon), *Lophocereus schottii* (senita), *Carnegiea gigantea* (saguaro; Figures 1 and 2), and *Stenocereus thurberi* (organ pipe cactus; Figure 3) (Bashan 2000; Fleming 2002), which



Fig. 2. Examples of both *Opuntia* (segmented cacti) groups, the chollas with rounded stem segments (cylindropuntias, front right) and the prickly pears with flattened stem segments (pads) (platyopuntias, middle view on left and right, the flat round pads of the distinctive plants are visible). See also Figure 4. Many of the tall *Carnegiea gigantea* are also visible. Photo by T. D. Drezner taken at Saguaro National Park West, Arizona, USA.

may reach heights of greater than 10 m. Other cactus species such as *Pterocereus gaudieri* (Mendez et al. 2004), *Stenocereus eruca* (Niklas et al. 2003), *Peniocereus striatus* (Suzan et al. 1994), *Coryphantha robbinsorum* (Schmalzel et al. 1995), *Mammillaria crucigera* (Contreras and Valverde 2002) and others (Campbell 1983, 1984) are endangered or rare, sometimes due to higher habitat specificity (Esparza-Olguin et al. 2002; Ruedas et al. 2006).

Population Cycles

THE PEAKS AND TROUGHS

The population cycles of many species of cacti, particularly some of the longer-lived columnar cacti such as *S. thurberi* (Parker 1987, 1993), *C. gigantea* (Brum 1973; Drezner 2006a; Turner 1990), *P. pringlei* (Bullock et al. 2005; Medel-Narvaez et al. 2006), as well as *Ferocactus* (Jordan and Nobel 1982) and *Opuntia* (Bowers 2005), are characterized by a peak and trough pattern. Many columnar cacti have very high, sometimes near 100%, mortality during the first year of life, such as *Neobuxbaumia* spp. (Flores-Martinez et al. 1994; Godinez-Alvarez and Valiente-Banuet 2004; Valiente-Banuet and Ezcurra 1991), *C. gigantea* (Steenbergh and Lowe 1977) and *L. schottii* (Parker 1989a). Mortality then declines dramatically over time. Specific favourable climate conditions, which can include mild summers and winters, and ample rainfall (Steenbergh and Lowe 1983; Turner et al. 1995; though, see Pierson and Turner 1998) during any given year (or a few years) promote seedling survival during the crucial

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Fig. 3. A small *Stenocereus thurberi* (= *Lemaireocereus thurberi*) taken at Organ Pipe Cactus National Monument, Arizona, USA. Photo by T. D. Drezner.

establishment period (Steenbergh and Lowe 1983). When all conditions are met, a successful period of regeneration occurs (Shreve 1929). In the years that follow, most individuals will survive in the long term, even with less than ideal conditions. Thus, favourable conditions promote a period of intensified regeneration, creating a peak (cohort). During other periods, conditions will not be ideal for establishment and only a few or no new individuals establish. Superimposed on this pattern are some post-establishment environmental events that reduce established populations, namely periodic freezes (Niering et al. 1963; Parker 1989a). Drought (Jordan and Nobel 1981) also reduces populations, and in some locales hurricanes cause wind throw and premature mortality, particularly of large and tall cacti (Clark and Ward 2000).

The best-studied columnar cactus, *Carnegiea gigantea*, has long been known to exhibit tremendous variability in both space and time. Dense populations are found in the vicinity of Saguaro National Park near Tucson, Arizona, USA (Figures 2 and 4), where they are near their environmental optimum (Niering et al. 1963). Because the species is limited by different

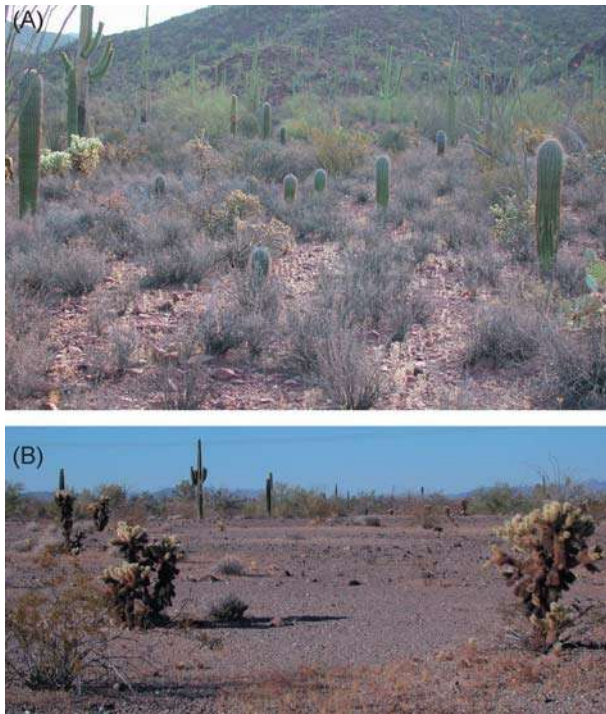


Fig. 4. (A) The high density of *Carnegiea gigantea* young at Saguaro National Park West, Arizona, USA. In the front, far right a platyopuntia is visible, as are a couple of different species of cylindropuntias (middle left of image; also the whitish-brown plant on the far left of the image between the two taller *Carnegiea*). (B) At a western, dry, marginal site, sparse *C. gigantea* can be seen, along with several *Opuntia bigelovii* (segmented cacti, cholla, cylindropuntia) individuals, white near their tops and the lower portion of the plant is brown. See also Figure 2. Both photos by T. D. Drezner.

environmental factors over its range (e.g. periodic freezes in the north, lack of summer precipitation in the west), as well as locally, one population may be growing while another is in equilibrium and yet another is in decline.

These ups and downs are typically temporary relative to the life span of an individual. For example, the *Carnegiea* population at Tumamoc Hill, Arizona, declined over many decades starting around the mid-1800s, though populations have since increased at that locale and are now viable and healthy (Pierson and Turner 1998; Shreve 1910). MacDougal Crater, Mexico, experienced three major periods of establishment between 1800 and 1960, most notably during the period around the late 1800s to early 1900s (Turner 1990). This peak was similarly observed at two other locales in Arizona (Drezner 2006a), and possibly at another site near Saguaro National Park West. The record is unclear at the latter site as high mortality may have followed the establishment period, thus ‘erasing’ the record by killing individuals from a possible cohort (Drezner 2006a). Similarly, in the

Tumamoc Hill study, Pierson and Turner (1998) suggest that while a peak was not observed during this same period, a subsequent drought may have resulted in post-establishment mortality that similarly erased that record. In another study, *Carnegiea* sampled from thirty populations throughout Arizona were merged to produce one region-wide regeneration curve (Drezner 2006b). That curve showed a peak during this same period (late 1800s to early 1900s).

Overall, there are overlapping peaks and troughs in the different populations, but their extent (e.g. amplitude) varies from site to site. Drezner (2006a) found that a statistically significant regional trend could be observed in the peak and trough pattern of *Carnegiea* at different sites in the northern Sonoran Desert; however, local variability was also evident. The *Carnegiea* site with the greatest summer rain and the coolest summer temperatures (the period when they establish) had greater regeneration (more frequent peaks) than the other sites, but as this was the coolest site, it also appeared to have been more adversely affected by cold season freezes (Drezner 2006a). The hot, marginal site not only had less favourable establishment opportunities overall, but also appeared to be less susceptible to post-establishment mortality (Drezner 2006a), as freezing events are the single greatest threat to established populations (Steenbergh and Lowe 1983). Local variability has also been observed in *P. pringlei* populations that result from variable summer rains (Bullock et al. 2005).

Unfortunately, these peaks, and in particular the troughs, have been poorly understood in the past. A freeze during the mid-20th century resulted in great concern about the future of the beloved *C. gigantea* and studies predicted its demise (Alcorn and May 1962). McAuliffe (1996) and Steenbergh and Lowe (1983) provide excellent reviews of the scare, the subsequent management and funding efforts, and the poor conclusions drawn from studies that were then followed by the destruction of individuals at Saguaro National Park. It was later determined that the cause of the die-off was subfreezing temperatures, and not the 'pathogenic' *Erwinia carnegiana* bacterium originally blamed (Lightle et al. 1942; McAuliffe 1996). Thus, natural post-mortem decomposition was interpreted as a pathogenic assault on *Carnegiea* populations at Saguaro National Park. It is not likely that this species will face extinction in the near future (e.g. Parker 1993; Steenbergh and Lowe 1983; Turner et al. 1969). As Steenbergh and Lowe (1983, VII) state:

Dramatic fluctuations in certain of its [the saguaro] populations, witnessed during this century, are a critically important, wholly natural, and widely misunderstood part of this dynamic process. Numerous journalists dedicated to the philosophy that 'bad news makes good copy' have enthusiastically promoted and perpetuated the widespread popular belief that the saguaro is doomed to early extinction.

Today, we have a much clearer understanding of these population cycles, and the temporal scale at which they operate.

Other related columnar cacti of the Sonoran Desert are more poorly studied, and researchers often assume *Carnegiea* patterns can be extended to them. For example, in an article on the giant columnar cactus *P. pringlei* (cardon), Moran (1968, 1998) refers the reader to growth data on *C. gigantea*, instead. Shreve (1935) suggests that during their early years, *S. thurberi* grow faster than *Carnegiea* but at about 1 m in height, growth rate slows to less than that of *Carnegiea*. He also suggests that *L. schottii* grows faster than *S. thurberi* and that early growth in *Ferocactus wislizeni* is faster than for any of the aforementioned columnar cacti (Shreve 1935). Shreve provides some description of growth, but seems to be limited to the Tucson, Arizona region, and does not consider variations in growth in different populations or under different environmental conditions. Even with new techniques and models, data are still limited geographically and temporally. We are not aware of even a crude estimate (e.g. order of magnitude) of the number of *C. gigantea* individuals in the wild. It is not clear whether the species range-wide is presently stable, increasing or in decline.

AGE ESTIMATION

Many cactus species are long-lived, particularly the columnar cacti, with some species exceeding 250 years of age. Cacti do not produce tree rings and thus their age cannot be determined through use of dendrochronological techniques, although Otis and Buskirk (1986) observed annual waxy bands in the tropical *Lemaireocereus argonii*. A few studies have estimated the age of *Opuntia* spp. individuals by counting the number of pads or quantifying the general size of the plant (Bowers 2005; Figures 2 and 4). Stem height and/or branch length have been used to date columnar cacti, which grow apically upwards over time. Some studies have used long-term repeat photography that documents changes in height over time (Martin and Turner 1977; Turner et al. 2003). Total stem length and growth have been used to estimate age for *S. thurberi* (Parker 1993; Figure 3). Age of individuals of *L. schottii* (Parker 1989a) and *C. gigantea* (Hastings 1961; Hastings and Alcorn 1961; Pierson and Turner 1998; Steenbergh and Lowe 1983) has been estimated by height and growth. All of these approaches are fundamentally limited as, unlike tree rings that for some species are reasonably reliable, all of these approaches for cacti provide estimates, which are sometimes fairly crude, more so for some species than others. While plants do tend to get larger with age, some variation exists. These techniques do provide estimates for data about species (and individuals) that are otherwise unavailable (either due to temporal requirements to collect the data or other limitations), and do provide reasonable baseline estimates.

In the studies mentioned above about columnar cacti, the age-height relationships established were specific to the population sampled and were not transferable to other locales. This is because growth rates (e.g. in *C. gigantea*) are highly variable over space (Drezner 2005, 2006a; Steenbergh

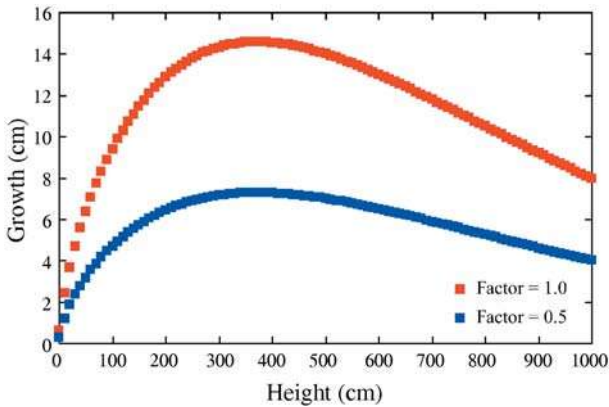


Fig. 5. Estimated growth (cm) by height (cm) of *Carnegiea gigantea* with a growth adjustment (factor) of 1.0 (at Saguaro National Park West, red line), and with a growth rate that is half as fast, as is common in drier portions of the species' range (growth adjustment of 0.5, blue line), from Drezner's (2003a) growth model.

and Lowe 1983), as growth at one locale may be more than twice as fast as at another site (Drezner 2005). A general model for estimating *Carnegiea* age from height and growth was recently developed that is not site-specific (Drezner 2003a). A site-specific adjustment factor is computed from local measurements of individuals, and this adjustment (or correction) factor (Figure 5) is then applied to a general model of individual growth (Drezner 2003a). Thus, individual age and local population structure can be estimated (Drezner 2006a,b) using an index value, which also allows relative growth to be compared across populations and sites (Drezner 2005; Figure 5). For example, growth rate is highly correlated to mean July rainfall in the northern Sonoran Desert where they were studied (Drezner 2005). This new method provides new approaches and a base for comparing populations and for estimating age without having to wait decades or longer for the same data; like all the other approaches, however, this only provides age estimates. Projection matrices have been used to understand the limiting factors and demographics of columnar cacti such as *Neobuxbaumia* (Esparza-Olguin et al. 2002; Godinez-Alvarez and Valiente-Banuet 2004), *Carnegiea* (Silvertown et al. 1993) and *Pterocereus* (Mendez et al. 2004), as well as of *Mammillaria crucigera* (Contreras and Valverde 2002) and *Mammillaria magnimamma* (Valverde et al. 2004). Godinez-Alvarez et al. (2003) review population dynamics using these projection models.

The only established way to definitively determine an individual's age is with long-term data, documenting the year of establishment. Such data are generally not available, and the few long-term records that do exist are geographically limited. In addition, columnar cacti typically establish under the often dense canopy of a nurse and it may take several years until the plant reaches a height of 1 cm (Steenbergh and Lowe 1983), further

limiting our ability to determine year of establishment. There are many limitations to estimating age and, thus, understanding the population cycles and structure of those species, but such data are nevertheless critical, particularly in the face of environmental change. Without understanding the demographics of cacti, we are severely handicapping our ability to understand not only the ecology and future of those species (whether common, rare or invasive), but also the ecology and future health of the biomes in which many are keystone species.

Species Interactions, Mutualisms and Reproduction

POLLINATION

Many species of columnar cacti rely on bats for pollination services in part or exclusively (Fleming et al. 2001; Valiente-Banuet et al. 1997a,b). Despite apparent pollinator scarcity, the bat-pollinated *Pachycereus weberi* and *Pilosocereus chrysacanthus* are not successfully pollinated by non-bat species (Valiente-Banuet et al. 1997b). *Pachycereus pecten-aboriginum* relies on bats in the southern portion of its range, becoming more of a generalist in the northern part of its range where bats are migratory (Molina-Freaner et al. 2004; Valiente-Banuet et al. 2004). *Stenocereus queretaroensis*, *Neobuxbaumia tetetzo* and *Pachycereus pringlei* are pollinated by bats, as well as by insects and birds (Fleming et al. 1996, 2001; Ibarra-Cerdena et al. 2005; Valiente-Banuet et al. 1996). Other species do not rely on bats such as some *Opuntia* that are bee pollinated (Grant and Hurd 1979), and some tropical cacti that are hummingbird pollinated (Gibson and Nobel 1986). *Lophocereus* is moth pollinated in an obligate, mutualistic relationship (Hartmann et al. 2002; Holland and Fleming 1999).

Many columnar cacti are self-incompatible (or nearly so), including *S. thurberi*, *Pachycereus pecten-aboriginum*, *C. gigantea* and *Ferocactus* spp. (Alcorn et al. 1961, 1962; Grant and Grant 1979; McGregor et al. 1962; McIntosh 2002; Valiente-Banuet et al. 1996, 1997b, 2004). Some species such as *P. pringlei* are both gynodioecious and trioecious in different parts of their range (Fleming et al. 1994, 1998), although the sex-frequency distribution is not related to the presence of their pollinator (Molina-Freaner et al. 2003). Fleming and Valiente-Banuet (2002) provide an excellent reference on the pollination biology and the mutualisms of cacti.

SEEDS AND DISPERSAL

Some cacti are hydrochorous (dispersal through transport by water) and a few are anemochorous (dispersal by wind), but most species are zoochorous (dispersal by animals) (Rojas-Arechiga and Vasquez-Yanes 2000; van Rheede van Oudtshoorn and van Rooyen 1999). Synzoochory (intentional transport by animals) is common, including in species of *Opuntia*, *Strombocactus* and

others (Rojas-Arechiga and Vasquez-Yanes 2000). Unintentional dispersal of seeds by birds expelling their young's fecal sacs has also been documented (Simons and Simons 1993). Species of *Pachycereus*, *Pilosocereus*, *Neobuxbaumia*, *Ferocactus*, *Carnegiea*, *Stenocereus* and others are endozoochorous (internal consumption by animals followed by regurgitation or defecation) (Rojas-Arechiga and Vasquez-Yanes 2000; Ruedas et al. 2006; Wendelken and Martin 1988).

A host of animals disperse seeds, including numerous species of reptiles (Cortes Figueira et al. 1994), mammals (volent and non-volent), birds and insects (Arizmendi and Espinosa de los Monteros 1996; Godinez-Alvarez et al. 2002; Olin et al. 1989; Rojas-Martinez and Valiente-Banuet 1996; Steenbergh and Lowe 1977). In some cases, dispersal is ineffective or the animal destroys the seeds, and thus is predatory (Olin et al. 1989; Silvius 1995). Because many cacti are associated with nurse plants, particularly in desert environments, endozoochory is an effective strategy for reaching suitable microsites (Suzan et al. 1996). Without proper dispersal to suitable microsites, many species will have substantially reduced survivorship and successful establishment (Turner et al. 1966). *Opuntia maxima* seedlings grow under olive plants or other *Opuntia* adults in Spain likely due to the preferred perching sites of seed dispersing birds (Gimeno and Vila 2002). Nurse plant relationships are discussed below.

Many studies have looked at the conditions required for seeds to germinate such as solar radiation and light (Benitez-Rodriguez et al. 2004; Nolasco et al. 1997; Rojas-Arechiga et al. 1997), temperature (De la Barrera and Nobel 2003; Fearn 1974; McDonough 1964), salinity and acidity (Nolasco et al. 1996), and scarification and passage through a faunal disperser (Godinez-Alvarez and Valiente-Banuet (1998). All of these play a role in germination, with conditions varying by species. Other studies have considered variability in self shading patterns of individual cacti with varying size and the resulting trade-off between growth and reproduction (Martorell et al. 2006). Some studies have also considered vegetative propagation (Godinez-Alvarez et al. 2005). Excellent reviews of seed dispersal and germination are available (Bregman 1988; Bregman and Bouman 1983; Rojas-Arechiga and Vasquez-Yanes 2000).

NURSE PLANTS AND FACILITATION

Young cacti face many obstacles to their survival during their first year of life. During their first summer, plants are very small (e.g. *C. gigantea* is perhaps 3 mm tall by the end of its first year; Steenbergh and Lowe 1983) and in desert environments they must overcome temperatures in excess of 45 °C, extended periods without any or adequate rainfall (Drezner 2004a; Turner et al. 1966), as well as detrimental faunal activity and seed predation (Steenbergh and Lowe 1969). During the winter, subfreezing temperatures can result in high seedling mortality (Nobel 1980a,b; Parker 1989a).

It has been estimated that fewer than five in one million *Carnegiea* seeds survive through their first year of life (Steenbergh and Lowe 1977). In arid regions, facilitative relationships [Callaway (1995) defines these as 'positive interactions', such as among plants; for example, plants that benefit from the presence of another plant in their vicinity that provides some resource or advantage] can be seen in nurse plant associations. Nurse plants are typically perennial plants that impart some benefit to the nursed individual (of a different species) in close proximity to or beneath their protective canopy (Drezner 2004b; Niering et al. 1963).

Nurse plant associations have been documented in many ecosystems worldwide (Arriaga et al. 1993; Callaway and Walker 1997; de Viana et al. 2001; Gass and Barnes 1998; Reay and Norton 1999), but they are particularly well documented in the desert (e.g. Castellanos et al. 1999; Drezner 2004b; Nabhan and Suzan 1994; Withgott 2000). While nurse shading can slow seedling growth and alter branching patterns (Drezner 2003b), nurse plants also ameliorate local environmental conditions and promote survivorship. It has been observed that facilitation between species may overshadow competition under extreme environmental conditions (Bertness and Callaway 1994; Holmgren et al. 1997).

Benefits provided by a nurse include increased water availability (Dawson 1993), protection from browsing animals and from wind (Parker 1989b), presence of fertile soil islands (Carrillo-Garcia et al. 2000; Franco-Pizana et al. 1996; Garner and Steinberger 1989; Reyes-Olivas et al. 2002), and a wide variety of climatic benefits. These include providing shade and protection from excessive sun, which reduces mortality from desiccation (Evans et al. 1994a; Turner et al. 1966). Regeneration of *C. gigantea* has been more successful in sites with cooler summer temperatures (Drezner 2004a). Other climatic benefits include reduction of ambient air temperatures and evapotranspiration losses (Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991), and elevated minimum temperatures during the cold season (Drezner 2007; Drezner and Garrity 2003; Nobel 1980c), to which many species are sensitive (Nobel 1982; Shreve 1911; Steenbergh and Lowe 1976; Turnage and Hinckley 1938; Turner et al. 1995), and thus are range limited (Parker 1987; Turner et al. 1995). Nurses actually extend the range of some cactus species northwards in North America (Nobel 1980c). Freezes are so limiting that Nobel (1980c) suggested individuals in cold northern populations have thicker stems to slow the freezing of the plant and its apical meristem. However, recent work suggests that increased stem thickness is primarily a function of greater rainfall from orographic lift in the northern mountains, though protection from cold is a secondary benefit (Drezner 2003c).

Nurse plants are typically woody (Mandujano et al. 2002), although grasses and other herbs have been known to act as nurses (Cody 1993; Franco and Nobel 1988). In Wisconsin, *Opuntia fragilis* has been observed growing in association with lichen (Bennett et al. 2003). A cactus may

also act as a nurse for other species, such as cylindropuntia cacti with their spiny, detachable stem segments that painfully attach to passing animals; these act as a deterrent and keep animals at a distance, thus protecting other plants growing near the cylindropuntia cactus (McAuliffe 1984a; Figures 2 and 4B). Many cacti such as *Pachycereus*, *Ferocactus*, *Stenocereus*, *Carnegiea*, *Opuntia*, *Trichocereus*, *Machaerocereus* and *Mammillaria* are associated with nurse plants (Arriaga et al. 1993; Carrillo-Garcia et al. 1999; Cody 1993; de Viana et al. 1990; Drezner 2004b, 2006c; Leirana-Alcocer and Parra-Tabla 1999; Martinez et al. 2001). *Carnegiea* (Drezner 2006c), *Ferocactus* (Arriaga et al. 1993), *Opuntia* (Reyes-Olivas et al. 2002), *Trichocereus* (de Viana et al. 1990), *Stenocereus* (Arriaga et al. 1993; Figure 3), and *Mammillaria* (Martinez et al. 2001) display a clumped pattern, although this may result in competition for water, and thus thinner individuals, resulting in an increased occurrence of premature freezing mortality (McAuliffe and Janzen 1986). In some cases, the regional distribution and density of cacti are related to the distribution of their preferred nurses (Drezner 2003d, 2006d). Some species are preferred over others as potential nurse plants (e.g. the cactus successfully establishes disproportionately more under some species than others) likely resulting from differences in canopy density and architecture (Drezner 2006c; Parker 1989b). Survivorship without a nurse can vary for different species by seed and seedling characteristics such as size (Bowers and Pierson 2001).

Microhabitat and the availability of nurse plants have been shown to impact the population dynamics of many cacti. Recruitment success of *Opuntia rastrera* in scrublands and grasslands of the Chihuahuan Desert was influenced by the presence of rodents, and differential seed availability (Mandujano et al. 2001). Seeds are disproportionately found under nurse canopies (Hutto et al. 1986) and evidence suggests that establishment and survival are more successful at superior microsites (Drezner 2006c). The proportion of seeds of *Opuntia rastrera* that establish is related to availability of nurse plants and reduced herbivory (Mandujano et al. 1998; Montiel and Montana 2003). Some *Opuntia* species decrease in response to dense grass (Dougherty 1986; Hyder et al. 1975). For example, the number and size of *Opuntia fragilis* cladodes (stem segments) and population size increased after grassland vegetation was removed (Burger and Louda 1995). This was attributed to competition for light and to increased herbivorous insects associated with the grasses (Burger and Louda 1995).

Local interactions contribute to observed regional scale population cycles of cacti and nurses. For example, adult *C. gigantea* have shallower roots than their nurses, which enable them to outcompete their nurse for water, in turn leading to the premature death of the nurse (McAuliffe 1984b). As a result, nurse populations decline, causing *Carnegiea* populations to decline with more limited nurse subcanopy habitat, which then results in increased nurse presence, promoting *Carnegiea* establishment. This has been likened to the predator (cactus)–prey (nurse) cycles observed in animals

(Vandermeer 1980). This replacement cycle and competitive effect have also been reported for *Neobuxbaumia tetetzo* and *Cephalocereus hoppenstedtii* (Flores-Martinez et al. 1994, 1998; Valiente-Banuet et al. 1991a), although not for the smaller globose cacti *Coryphanta pallida* and two *Mammillaria* species, presumably due to the lower impact these have on the nurse's ability to obtain water (Valiente-Banuet et al. 1991a,b). Sonoran Desert cycles have been observed in other studies as well (e.g. Martin and Turner 1977). McAuliffe's (1988) dynamic view of Sonoran Desert ecosystems further develops these observations and expands these ideas to community-wide patterns of establishment and replacement, including the shrub *Ambrosia dumosa*, which can establish on bare ground and subsequently nurses a variety of other plants, including other future nurse individuals (for cacti and other species), such as *Larrea tridentata*. Succession (changes in plant community composition over time) is also discussed in Turner et al. (2003), who discuss vegetation change and replacement in the Sonoran Desert using repeat photography. By returning to sites for which there is a photographic history, these locales could then be described as having increases and decreases in certain species (Turner et al. 2003), and physiognomic (structure of a plant community) changes. In extreme environments, facilitation may overshadow competition (Bertness and Callaway 1994; Holmgren et al. 1997). Several reviews of nurse plant associations have been published (Callaway 1995; Withgott 2000), including one emphasizing cacti (Drezner 2004b).

Reproductive Investment

Investment in reproduction is geographically variable over species' ranges and is related to variations in climatic and environmental characteristics of different regions. Reproductive output and seed production are variable across individual cacti and their stems (Schmidt and Buchmann 1986). Bowers (1996a) found that *Carnegiea* flowering is partly triggered by winter rain, and Drezner (2003e, 2004c) related branch production to winter rain as well. Branching is a strong predictor of reproductive output as *Carnegiea* and other cacti produce flowers and fruits at the tips of each of their branches and stems (Johnson 1924; Steenbergh and Lowe 1977). A study (30 populations over the northern Sonoran Desert) that considered *C. gigantea* population density and the density of stems and branches (reproductive effort), compared hot and dry sites, northern cold-limited (cold) sites, and cool, high summer rain (wet) sites (that promote successful establishment), using ANOVA. Population density is, not surprisingly, the highest in the cool, wet sites (Drezner 2003d, 2006d; Figures 2 and 4). Cold-limited populations have the low densities of hot and dry locales, but cold sites invest intensely in reproduction, having high reproductive densities that are not found in hot and dry locales (Drezner 2006d). The hot, dry locales appear to be less affected by periodic freezes in the long term,

and this likely contributes to their continued survival, despite their lower reproductive investment (Drezner 2006d). Cold northern populations also become reproductive at a younger age (and at a shorter height) than in the hot and dry marginal populations, further exaggerating cold population investment in reproduction (Drezner 2008).

Establishment and Survival – Global and Local Influences

TOPOGRAPHY AND SLOPE

Slopes are generally drier than flat areas, and south facing slopes in the northern hemisphere tend to be hotter and drier than north facing slopes. In addition, in many desert areas, cold air drainage is common during the winter (Parker 1988). Thus, slopes may sometimes be warmer than the valleys below during winter nights.

In Tumamoc Hill, Tucson, Arizona, USA, a relatively cool and wet Sonoran Desert site, *C. gigantea* were more abundant on south and east facing slopes than on north and west facing slopes, which was attributed to higher recruitment and survivorship (Pierson and Turner 1998). Between 1908 and 1964, fatal freezes declined while drought increased on Tumamoc Hill (Pierson and Turner 1998). At nearby Saguaro National Park West, regeneration was much more successful than at the hotter and drier South Mountain Park site in Phoenix, Arizona (Drezner 2004d). North facing slopes at Saguaro National Park West had fewer short (i.e. young) individuals than south facing slopes or flat areas, while in South Mountain, nearly all small individuals were in flat areas (Drezner 2004d). Because South Mountain is a hotter and drier locale, the typically drier slopes were more likely limiting for establishment and regeneration (Drezner 2004d). *Carnegiea* may also have higher survival rates on slopes at Saguaro National Park West than at South Mountain as the valleys are susceptible to cold air drainage, which may be more limiting at the cooler Saguaro National Park West than at South Mountain (Drezner 2004d). Seed production is reduced on slopes as *Carnegiea* are underbranched there (Yeaton et al. 1980), although the implications for successful establishment are unclear.

Bowers' (2005) study of *Opuntia engelmannii* showed that although populations peaked overall in response to increased moisture, the north-slope population declined between 1996 and 2003, while the northwest slope remained stable. *Opuntia echios* had higher densities at the less shaded lower elevations (Hicks and Mauchamp 2000), while *Opuntia microdasys* has been shown to have higher survival in the shade (Palleiro et al. 2006).

EL NIÑO AND GLOBAL SCALE CLIMATE

Cactus recruitment, mortality and demography have been linked with El Niño and the Southern Oscillation, such as in *Carnegiea* (Drezner and

Balling 2002), *Mammillaria* (Valverde et al. 2004), *Opuntia* (Bowers et al. 1995; Hamann 2001), *Ferocactus* (Bowers 1997; Bowers et al. 1995; Goldberg and Turner 1986) and *Echinocactus* (Jordan and Nobel 1981).

In the Galápagos Islands, *Opuntia echios* var. *gigantea* had high recruitment during the very wet 1982–1983 El Niño event (Hicks and Mauchamp 1996). However, Hamann (2001) found that mortality events among *Opuntia echios* var. *barringtonensis* occurred in association with El Niños and the associated increase in water availability. The large *Opuntia* became top-heavy from water stored in their pads, and the soil became water-logged, which lead to root rot, and ultimately led to the large *Opuntia* falling over and dying (Hamann 2001). El Niño had a negative effect on the survival of younger individuals, although no impact on the emergence of seedlings was observed (Hamann 2001).

El Niño-related recruitment events have been associated with higher rainfall and soil moisture. Higher recruitment in *Opuntia acanthocarpa*, *Opuntia basilaris* and *Opuntia erinacea* has been linked with increased rain associated with El Niño in northern Arizona (Bowers et al. 1995). At Tumamoc Hill in southern Arizona, all *Opuntia engelmannii* establishment peaks since 1975 coincided with El Niño periods (Bowers 2005). El Niño events and the increased moisture yield favourable conditions for fruit production, seed germination and seedling survival (Bowers 1996b, 2005).

Drezner and Balling (2002) linked *Carnegieia gigantea* regeneration surges from 1895 to 1980 with relatively warm temperatures and greater soil moisture in winter in the USA, associated with El Niño. *Mammillaria magnimamma* had improved seedling survival in Mexico during the 1997/1998 El Niño event (Valverde et al. 2004). More recent work (Drezner and Balling 2008) shows a significant relationship between successful *C. gigantea* establishment, and volcanic activity at a global scale from 1870 to 1980. Volcanic eruptions (e.g. Krakatau) produce milder summer and winter temperatures, which promote seedling survival during the first year or two of life when climatic effects are most important (Drezner and Balling 2008; Robock and Mao 1992). For example, the late 1800s to early 1900s (described earlier as a time when many populations exhibited peaks) was a period of unusually high volcanic activity (Lindzen and Giannitsis 1998).

HUMAN IMPACTS AND INVASION

Stiling et al. (2004) found extremely high mortality rates for *Opuntia corallicola*, an endangered species in Florida, caused by *Cactoblastis cactorum*, a cactus moth introduced to control other *Opuntia* species (Stiling et al. 2004). This moth, native to central South America, has been introduced in many parts of the world, including in the Caribbean, from where it likely reached southern Florida either on its own powers from Cuba or through Miami where cacti are imported (Stiling et al. 2004). There is now a serious threat to the 79 native species of *Opuntia* in Mexico that

are vulnerable to attack by this moth, and will be difficult to protect if the moth becomes naturalized in the area (Perez-Sandi 2001).

Human disturbance was a major factor in the decline of *Opuntia fragilis* in Kaladar, eastern Ontario, Canada (Staniforth and Frego 2000). A massive collection by vandals caused the population to drop from 300 individuals to as few as six (Beschel 1967; Klinkenberg 1987; Staniforth and Frego 2000). Human impact is of concern for many other species, including the rare columnar *Pterocereus gaumeri* (Mendez et al. 2004), as well as *Peniocereus striatus*, which has high habitat specificity and nurse reliance; people are removing nurse species from the cacti's natural habitat (Suzan et al. 1994).

Many cacti are also highly restricted in their distributional range, and are at risk from anthropogenically driven habitat loss (Esparza-Olguin et al. 2002). Seedling survival of *M. magnimamma* in Valverde et al.'s (2004) study was higher in a preserved site than in a disturbed site. Unfortunately, cacti are particularly sensitive to human disturbances because of their slow growth rates and their vulnerability to environmental factors during the early stages of their development (Hernandez and Godinez-Alvarez 1994).

Saguaro National Park is one of the most vulnerable (for vascular plants) of the US National Parks to pollution, specifically SO₂ and ozone (Bennett et al. 1986). However, Kolberrg and Lajtha (1997) found that trace metal pollution was not responsible for premature cactus death at Saguaro National Park. Other concerns include fire (Rogers 1985; Thomas 2006; Thomas and Goodson 1992) and the premature death of cacti (such as *Carnegiea*) from epidermal browning (Evans et al. 1992; Evans and Fehling 1994), which was once thought to be related to human activities. Epidermal browning has been observed on several North and South American cacti (Evans and Fehling 1994). However, research suggests that it is natural, resulting from exposure to the sun (Evans et al. 1992, 1994a). Epidermal browning occurs disproportionately more on the south (sun-facing) side of North American cacti, and more on the north side of South American cacti such as *Trichocereus pasacana*, *Trichocereus terscheckii*, *Echinopsis chilensis* and *Echinopsis scotsbergii* (Evans et al. 1994b). There is also concern about *Pachycereus pringlei* populations in Mexico, where branch tips, entire branches or entire plants are dying prematurely, although the causes are uncertain (Bashan et al. 1995; Holguin et al. 1993). The cause of malformations found over many populations of *P. pringlei* are also uncertain, although these do not appear to have impacted population fitness (Dubrovsky and Leon de la Luz 1996).

In contrast, *Opuntia* spp. have invaded different vegetation communities around the world (Cronk and Fuller 1995; Gimeno and Vila 2002) with the help of people. *Opuntia* were introduced to Europe from Central America by Spanish conquerors between the end of the 15th century and the beginning of the 16th century (Barbera et al. 1992) and have since been introduced in Australia (Stiling et al. 2004) and the Mediterranean basin (Ellenberg 1989; Inglese et al. 1995; Nerd et al. 1993) for ornamental

use, fencing and human food (Ellenberg 1989; Inglese et al. 1995; Stiling et al. 2004). Exotic species can cause changes to the structure of the ecosystems and communities they invade (Chaplin et al. 1995; Parker et al. 1999) and therefore some now consider some *Opuntia* species to be pests (Hoffman et al. 1998; Humphrey 1960). However, in their native range, *Opuntia* are an important part of the ecosystem and food web (Bowers 2005). Some species provide feed for livestock and reduce livestock pressures on other species that may be endangered or impacted by grazing (Vega-Villasante et al. 1997).

GLOBAL WARMING, CARBON DIOXIDE AND THE FUTURE

The impacts of global warming and rising carbon dioxide levels on the future of cacti are unclear. Little research has been done on climate change and its impact on the future of cacti, leaving many unanswered questions about the future of these species. It is safe to say that the impacts on different species will be varied. Global warming relates not only to temperature, but also to changes in rainfall, and climate change also involves predicted increases in atmospheric CO₂, and these and other changes will all impact the potential success or failure of cacti.

Photosynthesis is carried out by one of three (C₃, C₄, CAM) chemical processes in plants; cacti are CAM (Crassulacean acid metabolism) photosynthesizers. See Nobel (1988) and Gibson and Nobel (1986) for a complete description. Driven by solar radiation, photosynthesis always occurs during the day. In C₃ photosynthesis (the most common photosynthetic pathway), plants open their stomata during the day while photosynthesizing. However, when stomata are open, water is also lost into the atmosphere. In the desert, with high temperatures and low humidity, water loss would be great and survival would be compromised for many species if stomata were open during the day. Thus, plants have also evolved the CAM pathway for photosynthesis (although they sometimes revert to C₃ early in the morning or during other favourable conditions). CAM plants store the oxygen normally expelled during photosynthesis. At night, when temperatures are cooler and relative humidity is higher, they open their stomata, release oxygen and take in CO₂, which they store until the sun rises when they can begin photosynthesizing again. CAM photosynthesis, however, has its drawbacks, including limited photosynthesis from 'storage' and thus slower growth rates, among others (Jordan and Nobel 1982; Niering et al. 1963).

Changing carbon dioxide concentrations in the atmosphere can have a profound impact on cacti and many other arid land species. So how would increased CO₂ affect cacti and CAM plants? Park Nobel and his colleagues have done several studies on the impact of increased CO₂ and climate change on *Opuntia ficus-indica*. Like other cacti, this species is a CAM photosynthesizer. With increased atmospheric CO₂, gas exchange would be more efficient, thus resulting in reduced water loss during the

gas exchange process (e.g. Drennan and Nobel 2000; Nobel 1999), and enhanced root growth (Drennan and Nobel 1998). In the case of *Opuntia ficus-indica*, an invasive species, its range could extend to much larger areas, including in other parts of the world (e.g. Africa, Australia) where it is invasive (Nobel 1988; Nobel and Israel 1994). Nobel (1996) predicted that with a doubling of atmospheric CO₂, the western Mexican endemic *Stenocereus queretaroensis* (e.g. Ibarra-Cerdena et al. 2005) and other species would also show increased biomass productivity and expand their range, as well as with the increasing temperatures associated with global warming (Nobel 1996). The ranges of many cacti are limited by freezing temperatures, and with increasing global temperatures, coupled with improved photosynthetic efficiency, which also promotes survival during drought, many species may potentially extend their range (Drennan and Nobel 2000).

In contrast, Tellez-Valdes and Davila-Aranda (2003), who did not incorporate carbon dioxide changes in their model, suggest that a 2 °C temperature increase and a 15% decrease in precipitation would cause the extinction of *Cephalocereus columna-trajani*, *Mammillaria huitzilopochtli* and *Pachycereus hollianus*. They further suggest that *Ferocactus flavovirens*, *Mammillaria pectinifera*, *Polaskia chende* and *Polaskia chichipe* would experience a 90% range reduction. The species they considered would have range contractions, and in only three cases by less than 50% (Tellez-Valdes and Davila-Aranda 2003). Differences in model parameters and assumptions (i.e. approaches to addressing the question) can provide differing conclusions. Combined with the different ecologies, limitations and tolerances of different species, more questions than answers remain. The complexities of climate change, the different variables (e.g. temperature, precipitation, changes in carbon dioxide concentrations) and their interplay have yet to be fully understood and disentangled.

Conclusions

Cacti are dominant features of the landscape in many arid environments. They may be rare or endangered, or may be keystone species in their ecosystems. Because most cacti are slow growing and many may live upwards of 200 years, we have limited data on their long-term demographics and populations cycles. New techniques are needed to more accurately approximate years of establishment, and those that are physiologic in nature (i.e. some inherent predictable biological features) would likely be the most accurate; remote sensing techniques (such as calculating height from shadows cast) at present would not likely provide the level of accuracy required, although there is potential for future use. Also needed is more extended sampling of populations range-wide, as most if not all species are poorly sampled and understood range-wide. The Tehuacan Valley in Mexico has a great diversity of columnar cacti, and should be a focus of continued research, along with other areas that have a great diversity of species,

as well as endemic or endangered species. Without demographic data, we cannot fully understand the complex interlinkages between cacti and climate (at all scales), between cacti and other species, the basic cycles of the desert biome, or the future of these species and the species that rely on them.

Population cycles of cacti have micro (e.g. nurses), local (e.g. site conditions, topographic setting), regional (e.g. periodic freezes) and global (e.g. El Niño, volcanism) components, and all of these need to be further understood. Demographic trends need to be considered in the context of environmental elements at all spatial and temporal scales, particularly in the face of climate change. Because many of the desert's keystone species are cacti, the potential ecosystem impacts are particularly important. Key questions remain unanswered, such as what will happen to rare and keystone species with climate change? How will increased carbon dioxide and the associated potential photosynthetic benefits offset other environmental changes? Will invasive cacti become even more problematic, and will they extend their range to new ecosystems? Will species ranges become reduced with increasing moisture and thus competition from more mesic species, or will increases in carbon dioxide cause a greening-up of the desert?

Short Biographies

Taly Dawn Drezner received her PhD in 2001 from Arizona State University. Her research interests include plant–climate and plant–plant interactions in deserts, including nurse–plant associations. She is particularly interested in the impact of El Niño, global volcanism and other environmental variations as they relate to cactus populations. Her article on the impact of volcanic eruptions all over the world on the population cycles of a keystone cactus will soon appear in the *Journal of Vegetation Science*.

Barbi Lynn Lazarus is a student in Geography and Environmental Studies at York University. She has had a long-standing interest in desert ecosystems, and has read extensively on desert environments. Her interests include cacti and succulents, desert geomorphology, and land use, human disturbance and conservation in the California desert.

Note

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