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Community, structure and dynamics

Remarkable medium-term dynamics of leaf succulent Mesembryanthemaceae shrubs in the winter-rainfall desert of northwestern Namaqualand, South Africa

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Abstract

Populations of shrubs in a winter-rainfall (ca. 70 mm yr^{-1}) desert community (Succulent Karoo), dominated by leaf succulents, showed remarkable dynamics over a 17-yr period. After a severe drought in 1979, which caused high plant mortality, perennial species number in a permanent 10 m × 10 m plot doubled between 1980 and 1996, when the maximum of 41 species was recorded. Numbers of individuals of evergreen, leaf succulent shrubs also doubled over the same period, but showed fluctuations in response to dry years during the monitoring period. Detailed observations on the four dominant leaf succulent shrubs (all members of the Mesembryanthemaceae) between 1983 and 1996, showed species-specific patterns in population turnover. Mortality of all observed individuals ranged between 60% and 85%, and the proportion of the population that was recruited over this period ranged from 62% to 89%. In only one species did individuals persist throughout the monitoring period. Mean ages of individuals, excluding seedlings with lifespans of <1 yr, and individuals observed at the beginning of the monitoring period, ranged from 4.6 yr to 5.6 yr. Patterns of mortality and recruitment showed substantial differences among species and were not all attributable to rainfall patterns. Overall, the turnover of the shrub populations over the 15-yr monitoring period was remarkably high for a system of desert perennials. These unusual population patterns may explain the unique structure of leaf succulent-dominated communities in the Succulent Karoo.

Introduction

The woody plant component of most deserts is dominated by species that live for several decades or centuries, whereas the herbaceous component is dominated by opportunistic ephemerals (Beatley 1980; Vasek 1980; Goldberg & Turner 1986; Bowers et al. 1995). Owing to the low population turnover of desert shrubs, long-term changes in their density and composition have been determined directly by means of matching photographs taken at decades-long intervals (Shreve & Hinckley 1937; Martin & Turner 1977; Hoffman & Cowling 1990; Bowers et al. 1995), or predicted by models based on data collected over a limited timespan (McAuliffe 1988; Yeaton & Esler 1990; Wiegand et al. 1995). Goldberg & Turner (1986), however, analyzed data from permanent plots in the Sonoran Desert, sampled at irregular intervals over a 72-yr period. Despite large changes in absolute cover and density of many species, the relative cover of the dominant shrubs was generally similar within a given plot over the entire time sequence. Some 48% of the 39 perennial species in Goldberg & Turner's data set had maximum observed longevities of >40 yr; 31% lived for between 20 and 40 yr; whereas only 8 spp. (21%) had lifespans less than 12 yr.

Southern Africa's Succulent Karoo (Milton et al. 1997) is unusual amongst the world's deserts in that

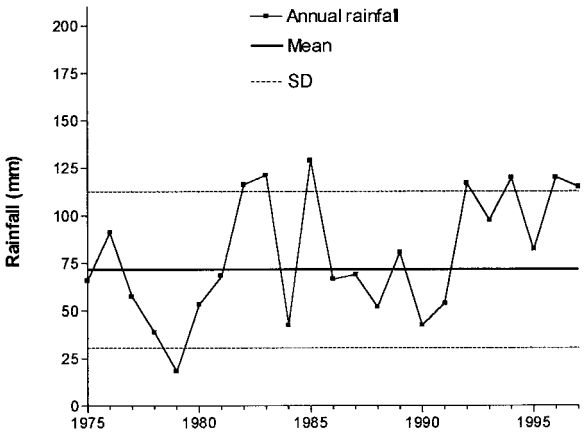

Figure 1. Annual rainfall patterns at Lekkersing (28°59 S, 17°06 E, 335 m) in the Richtersveld. Data supplied by the South African Weather Bureau. SD = standard deviation.

the vegetation is dominated by relatively short-lived leaf succulent shrubs, mainly members of the Mesembryanthemaceae (or Mesembryanthema, Aizoaceae, *sensu* Bittrich & Hartmann 1988) and Crassulaceae (Jürgens 1986; Cowling et al. 1994, 1998a). Assessments of shrub longevities and vegetation dynamics have come from anectdotal or inferential studies (Yeaton & Esler 1990; von Willert et al. 1992; Rundel et al. 1998; Stock et al. 1998). Given the importance of rapid shrub population turnover in explaining Succulent Karoo community structure and diversity (Cowling et al. 1994; Eccles et al. 1998), physiological and ecosystem processes (von Willert et al. 1992; Cowling et al. 1998a; Stock et al. 1998; Rundel et al. 1998), as well as the explosive diversification with short-lived shrub lineages (Cowling et al. 1998b; Desmet & Cowling 1998), a quantitative estimate of shrub population turnover is long overdue.

In this paper we report on the dynamics of Mesembryanthemaceae shrub populations, monitored in a 100 m^2 plot over a 15-yr period (1983–1997), in the arid (ca. 70 mm yr^{-1}) Richtersveld region of north-western Namaqualand. The aim of this contribution is to describe the extraordinarily rapid turnover of the populations of the dominant shrub species in this unsual desert ecosystem.

Methods

Study area

The study site is in the Numees Valley (28°17.92′ S and 16°57.85′ E) in the Richtersveld of north-western Namaqualand, South Africa. This area is part of Jürgens' (1991) Namaqualand-Namib Domain of the Succulent Karoo, a desert region characterized biologically by the overwhelming dominance of leaf succulent shrubs, and climatically by low but predictable winter rainfall (Desmet & Cowling in press). The Richtersveld falls within the Gariep Centre, a bioregion of exceptional succulent plant diversity and endemism (Hilton-Taylor 1996). The study area is extremely species-rich for an arid desert: 331 species have been recorded in 1.3 km^2 of the Numees Valley (von Willert et al. 1992).

The 10 m × 10 m monitoring plot was located at 360 m a.s.l. on a steep (29° inclination), SSW slope. The plot was dominated by dwarf, evergreen, leaf succulent shrubs and the dominant species were all leaf succulent members of the Mesembryanthemaceae, namely *Stoebaria beetzii* (Dinter) Dinter & Schwant., *Sphalmanthus decurvatus* (L.Bolus) L.Bolus, *Ruschia senaria* L. Bolus, and *Ruschia* subg. *Sarmentosa* sp. Other species (a maximum of 41 perennials was recorded at any one time during the monitoring period) comprised mainly succulent members of the Mesembryanthemaceae, Crassulaceae, Asteraceae and Euphorbiaceae (Jürgens 1986). Nomenclature follows the Bolus Herbarium (BOL).

The parent rock comprises quartzites of the Numees Formation, part of a massive group of sheared and folded sediments that were deposited between 900 and 500 million years ago in a rift basin that extended along much of the present west coast of Africa (Martin 1965). Soils are shallow and extremely rocky (Jürgens 1986). The mean annual rainfall, as determined from the nearest rainfall station in a physiographically similar position (Lekkersing, some 50 km south of the study area), is 71.5 mm, 75% of which falls in the winter (April–September) months (South African Weather Bureau pers. comm.) (Figure 1). The use of such a distant rainfall station is less problematic in Namaqualand than in other deserts since most rain is associated with widespread frontal showers rather than spatially restricted thunderstorms. Despite this low rainfall, the coefficient of variation of annual rainfall is only 57%. For this amount of rainfall, this measure of reliability is much higher than that recorded for other winter- and summer-rainfall deserts (Hoffman & Cowling 1987; Desmet & Cowling in press; Esler et al. in press). Occasional droughts, with one to two successive years with substantially below-average rainfall, do occur (Figure 1). The drought of 1979, which was preceded by two years of below-average rainfall, resulted in ex-