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Community structure and dynamics

Community structure on unusual habitat islands: quartz-fields in the Succulent Karoo, South Africa

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Abstract

Quartz fields are edaphically arid, azonal habitats occurring under different macroclimatic conditions in several arid regions of southern Africa. They are the exclusive home of 142 plant species of which ca. 70% are local or regional endemics. This paper is an analysis of the quartz-field floras and growth form-soil relationships in two quartz field regions: the Knersvlakte in the Namaqualand-Namib Domain of the Succulent Karoo, and the western Little Karoo in the Southern Karoo Domain. The Knersvlakte supported 52 quartz-field specialists of which 39 were endemic to the region. Corresponding data for the Little Karoo were 11, and 10 species, respectively. In both regions, the average canopy cover on the quartz-field relevés was ca. 8%, and more than half of this comprised contracted, succulent nanochamaephytes. Cover and vegetation stature were markedly higher on adjacent zonal habitats. Quartz fields in both regions supported a similar array of compact, subglobose and subterranean nanochamaephytes, as evidenced by convergent patterns in two distantly related genera (*Argyroderma* N. E. Brown and *Gibbaeum* (Haworth) N. E. Brown, both Mesembryanthemaceae), endemic to the Knersvlakte and largely restricted to the Little Karoo, respectively. Analyses of vegetational and edaphic data of quartz fields and adjacent, zonal habitats were carried out using multivariate direct gradient analysis (Canonical Correspondence Analysis) in order to identify those factors that control the peculiar composition of growth forms on quartz fields. The results revealed highly similar patterns of growth form composition in relation to similar edaphic gradients in both regions. In general, the soils of quartz fields were shallower compared to those of adjacent zonal habitats. In both regions, two different groups of quartz-field edaphic habitats, representing extremes of a continuum, were identified. Group 1 was characterized by high salt content, neutral to slightly acid soil pH, and low stone content. Group 2 was characterized by low salt content, low soil pH, and high stone content. Group 1 quartz fields are the most edaphically arid habitats and support the highest relative cover and diversity of subglobose and subterranean chamaephytes. The combination of reduced competition from larger growth forms, shallow soils and high soil salinity, represents a regionally unusual selective regime. Some succulent lineages in the Mesembryanthemaceae have undergone diversification which has resulted in the fine-scale discrimination of subtle edaphic gradients within the saline quartz-patch habitats. Reliable seasonal rainfall and reduced thermal stress have also played a role in the evolution of quartz patch specialists.

Introduction

Quartz fields, as defined here, are geomorphological features of southern Africa‘s arid lands (Schmiedel 1994). They have a surface layer of white, angular quartz debris (0.2–6 cm in diameter) which originates from weathered quartz veins. The quartz sometimes covers up to 100% of the ground surface. The long axis of a single quartz field ranges between 1 m and more than 100 m. They are typically ‘island-like’, showing abrupt transitions in both floristic and growth form composition from the surrounding zonal habitats

Figure 1. Quartz fields in the Knersvlakte (southern Namaqualand).

(Jürgens 1986) (Figure 1). A striking feature within quartz fields is the occurrence of spatial micropatterns of various vegetation units with differing composition of growth forms.

Quartz fields are clustered into six regions in arid to semi-arid southern Africa (U. Schmiedel unpubl. data) (Figure 2). The Knersvlakte, Namaqualand Lowlands, Richtersveld, and Little Karoo quartz fields fall within the Succulent Karoo Region *sensu* Jürgens (1991) of the Greater Cape Flora, defined botanically by a high number of species of Mesembryanthemaceae (Mesembryanthema, Aizoaceae *sensu* Bittrich & Hartmann 1988) and a strong dominance of leaf-succulent growth forms. The Region is ecologically characterized by a relatively mild temperature regime, and highly predictable winter rainfall (Hoffmann & Cowling 1987; Cowling et al. 1999). The Warmbad and Pofadder regions are part of the Nama-Karoo Region of the Palaeotropis (Jürgens 1991), and are located in the subtropical transitional zone between winter and summer rainfall areas (rainfall peaks occur in spring and autumn).

A preliminary checklist (U. Schmiedel, unpubl. data) comprises 142 plant species entirely restricted to quartz fields of southern Africa, of which only 17 species (12%) occur outside the six regions mentioned above. Thus, 88% of the southern African quartz field flora are restricted to one or several of the six regions. The majority of these quartz-field species are leaf-succulent members of the Mesembryanthemaceae. Of the total quartz-field flora, 78 species (55%) are nanochamaephytes (dwarf shrubs < 5 cm); 31 species (22%) are microchamaephytes (shrubs 5–15 cm); and 19 species (13%) are geophytes (U. Schmiedel, unpubl. data). Phanerophytes (shrubs and trees $>$ 50 cm) are completely absent in the quartz field flora. The vast majority of these dwarf shrubs are succulents, including many subglobose (35 spp. or 45%), compact (27 spp. or 35%) and subterranean (12 spp. or 15%) forms. These areas, therefore, represent important sites for southern Africa's exceptionally rich and highly range-restricted flora of contracted succulents (Van Jaarsveld 1987; Hartmann 1991; Hammer 1993; Milton et al. 1997; Cowling & Hilton-Taylor in press). As such, they warrant further study.

Although the quartz fields of southern Africa represent an extraordinary azonal habitat of great ecological significance and conservation value, they have been the focus of surprisingly little research (Hilton-Taylor 1994, but see Jürgens 1986; von Willert et al. 1992; Schmiedel 1994). Jürgens (1986) analyzed the relationship between growth forms and edaphic features on the Knersvlakte quartz fields. His study showed that abrupt change in floristic and growth form composition across quartz field boundaries, is associated with a corresponding increase in soil conductivity and decline in soil pH. Jürgens (1986) also mentions identical sequences of similar growth form types along quartz-related soil catenas in the Knersvlakte and Little Karoo, which he interpreted as a result of multiple events of convergent evolution. Von Willert et al. (1992) showed that the reflectivity of quartz was considerably lower than in brown shale and red soil environments, and that this was correlated with differences of leaf temperatures of plants growing inside and outside the quartz fields. Eller (1982) investigated the solar radiation absorbed by *Argyroderma pearsonii* (N. E. Brown) Schwantes (Mesembryanthemaceae), a species restricted to the quartz fields of the Knersvlakte.

However, no comprehensive analysis has been undertaken of the relationships between growth forms and environmental variables on quartz fields of different regions. In this paper, we present a multivariate analysis of vegetation data in relation to edaphic variables for quartz fields in the Knersvlakte in southern Namaqualand, and those in the western Little Karoo (Figure 2). In particular, we were interested in determining whether there are similarities in growth form structure and environmental gradients in the two regions, in order to derive generalizations about these unique habitats.