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Relationships between specific leaf area and leaf composition in succulent and non-succulent species of contrasting semi-desert communities in south-eastern Spain

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ABSTRACT

Much attention has been paid to differences in leaf form and composition among vegetation types, but less to the frequently substantial variation within vegetation types. We focused on the extent to which correlations between variables are the same in both succulent-poor and succulent-rich vegetation in semi-arid SE Spain. Mean foliar [N] of perennials varied among species over a 5-fold range. Across species, [N] was positively correlated with specific leaf area (i.e., leaf area divided by dry mass; SLA) and with water concentration at saturation (WCS) in the grasslands, excluding the one succulent species. In succulent-rich vegetation on marl, SLA was correlated with [N] but not WCS, and there was a wedge-shaped relationship between [N] and WCS. Foliar [N] and [P] were positively correlated in the grasslands, but not in succulent-rich vegetation on marl. The N/P quotient varied from 8 to 29, with mean 14 in grassland on limestone and mean 26 in grassland on deep soil over gypsum. Our chief finding is that most correlations among SLA, WCS, [N] and [P] found in the non-succulent vegetation are not found in the succulent-rich vegetation. The results are discussed in relation to global patterns and the problems of defining succulence.

1. Introduction

Much attention has been paid to differences in leaf form and composition among vegetation types, but less to the frequently substantial variation within vegetation types. This paper provides the first substantial information on leaf properties of perennial plants of semi-desert in the only part of Europe – except possibly south-eastern Crete (Grove and Rackham, 2001) – dry enough to carry such vegetation, i.e. southern Spain between Almería and Cartagena (Armas et al., 2011, Fig. 1). We use the term 'semi-desert' for areas with a diffuse incomplete cover of perennials, in contrast to true 'desert' in which perennials may occur extremely sparsely or only at run-on sites (Walter, 1964; Bornkamm and Kehl, 1990). Most of the semi-desert of SE Spain has a mean annual rainfall of 200–250 mm yr^{-1} with some sites receiving <190 mm yr^{-1} (Lázaro et al., 2001; see Appendix 1 for the long-term and recent history of the area, and the nature of its present vegetation cover). The area encompasses a variety of communities, depending on altitude, aspect, soil type and extent of human interference, each with several frequent species (Freitag, 1971a; Peinado et al., 1992).

We quantified the extent of variation in leaf properties, and any correlations among them, within four vegetation types with contrasting representation of succulent species: human-induced grasslands dominated by *Stipa tenacissima* on (a) limestone (6 species sampled, none described in the local Flora of Blanca et al. (2011) as having fleshy or succulent leaves), and (b) on deep soils over gypsum (11 species sampled; one leaf succulent), (c) vegetation of shallow soils on gypsum outcrops (5 species sampled; one leaf succulent), and (d) the semi-natural mixture of grass and shrubs on marl (16 species sampled; 4 leaf succulents, 2 shoot succulents).

We addressed nine questions on key aspects of leaf structure and composition in semi-deserts.

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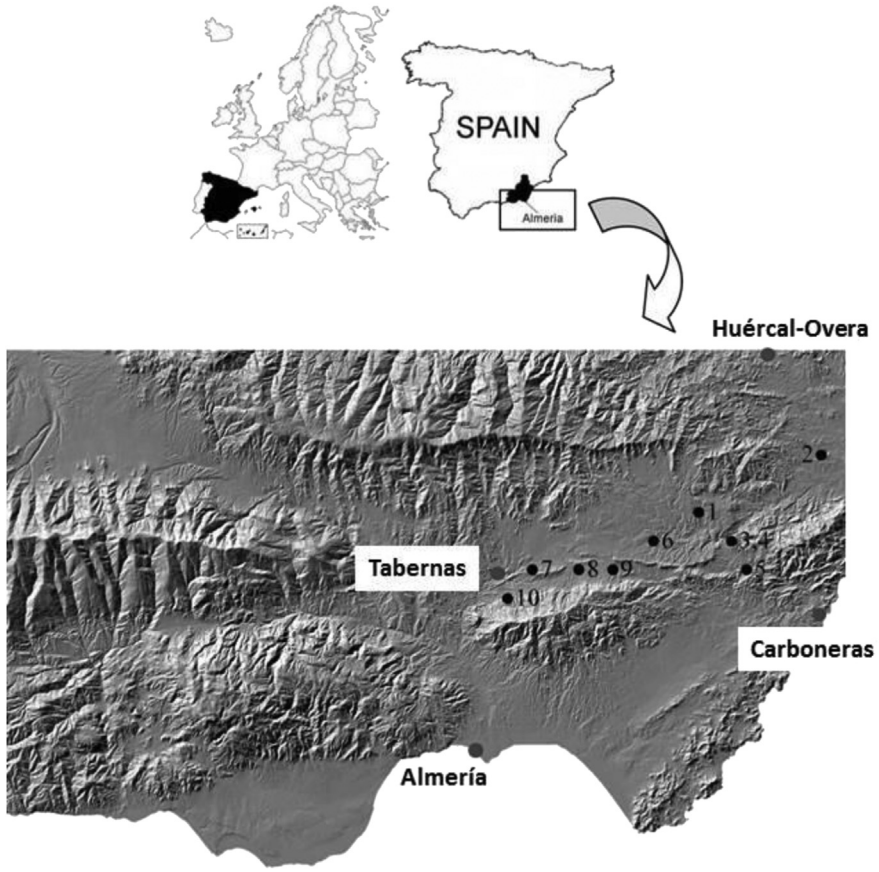

Fig. 1. The study area and the positions of the 10 sites sampled.

1. Is there substantial variation in foliar [N] among species within each of the types of vegetation studied? Foliar [N] is a critically important trait at the world scale (Wright et al., 2004a), and many studies have contrasted formation-types in their mean foliar [N]. For example, in the tropics lowland rain forests have mean foliar [N] 2–3 times greater than those of upper montane rain forests, corresponding to a greater availability of N, and lesser xeromorphy (Grubb, 1977; van de Veg et al., 2009), and in the subtropics low-rainfall woodlands can have mean foliar [N] about twice that of higher-rainfall forests, providing a higher water use efficiency of photosynthesis (Wright and Westoby, 2002). Much less attention has been given to the enormous range of foliar [N] among species of one functional group in a single vegetation type, e.g. up to five-fold variation among deeply shade-tolerant trees of tropical lowland rain forest, often greater than the differences between vegetation types (Grubb, 2002). In the Succulent Karoo semi-desert of South Africa, foliar [N] varied by more than four-fold among 13 shrub species at a single site (8.1–34.6 mg g^{-1}; Carrick, 2001).
2. How far are there similar relationships between specific leaf area and foliar [N] in the various types of vegetation studied? At the world scale specific leaf area (= leaf area/dry mass; SLA) is positively correlated with [N] (Wright et al., 2004a; Osnas et al., 2013). Despite this correlation, SLA and [N] can be independent correlates of light-saturated photosynthetic rate per unit leaf dry mass, A_{max}, and the correlation of A_{max} with SLA can be stronger than that with [N] (Reich et al., 1997; Wright et al., 2004b). In a wide-ranging study (rain forest to semi-desert) Reich et al. (1999) compared plants in six climatic regions in terms of the inter-relationships among [N], SLA and A_{max}; using logged data they found significant differences in the slopes but not the intercepts.
3. Is SLA correlated with water concentration at saturation (WCS) in the various types of vegetation, and are the concentrations of water and N correlated? In non-succulent plant communities, SLA can be tightly correlated with WCS (Wilson et al., 1999). However, among succulent species, a high WCS reflects degree of succulence (Ogburn and Edwards (2012)), and can coincide with a wide range of SLA (Von Willert et al., 1990; Vendramini et al., 2002). Just as foliar [N] is generally correlated with SLA, it can also be tightly correlated with WCS in vegetation lacking succulent species (Roderick et al., 2000) but this relationship has not been tested for communities including succulents.
4. *Do species with longer-lived leaves have lower SLA and/or lower [N] or WCS?* There is no doubt that at the world scale species with longer-lived leaves have lower SLA and [N] (Reich et al., 1997, 1999; Wright et al., 2004a; Osnas et al., 2013), but there is little evidence regarding WCS, especially in succulent-rich vegetation.
5. *Is SLA correlated with leaf area in any of the types of vegetation?* Among species of a given life-form in a particular habitat, leaves can show 'diminishing returns' in photosynthetic area per unit dry mass, i.e., a decline in SLA with increasing leaf size, within species or across species (Marañón and Grubb, 1993; Shipley, 1995; Grubb, 1998; Niklas et al., 2007; Milla and Reich, 2007). However, the opposite trend is often found in comparisons of different vegetation types (Turner, 1994); for example, in the wet tropics mean SLA is lower in the leaves of montane rain forest trees, which are relatively small, than in those of lowland rain forest trees, which are relatively large (Grubb, 1977). There