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Large-scale patterns of stomatal traits in Tibetan and Mongolian grassland species

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Abstract

We aimed to disentangle the influence of environmental variables on the spatial patterns in stomatal occurrence and stomatal traits. We surveyed the stomatal occurrence and the stomatal length (SL), density (SD) and index (SI) of 99 species in 150 grassland sites on the Tibetan and Inner Mongolian Plateau to explore their spatial patterns and evaluate the influence of climate. Of all species studied, two thirds were amphistomatous. The species from the Tibetan Plateau had larger but fewer stomata than those from Inner Mongolia. Among the climate factors examined, temperature and insolation affected SD, SI and SL, whereas the CO_2 partial pressure and the relative humidity affected SD. The climatic variables showed similar effects on the spatial variation of the adaxial and abaxial stomatal traits. We conclude that the low temperature and high insolation at high altitudes may be responsible for the larger and fewer stomata in plants on the Tibetan Plateau. The stomatal parameters that are presented here can be used to model the gas exchanges at the ecosystem scale.

Zusammenfassung

Unser Ziel war es, den Einfluss von Umweltfaktoren auf die räumlichen Muster des Auftretens der Eigenschaften von Stomata zu entschlüsseln. Wir untersuchten das Auftreten von Stomata, ihre Länge (SL), ihre Dichte (SD) und den Verteilungsindex (SI) von 99 Arten aus 150 Grasländern auf dem Hochland von Tibet und in der Inneren Mongolei, um ihre räumlichen Muster zu erkunden und den Einfluss des Klimas zu bewerten. Von allen untersuchten Arten, waren zwei Drittel amphistomatisch. Die Arten vom tibetischen Hochland besaßen größere aber weniger Stomata als die aus der Inneren Mongolei. Von den untersuchten Klimafaktoren beeinflussten Temperatur und Sonneneinstrahlung SD, SI und SL, während der CO_2-Partialdruck und die relative Luftfeuchte SD beeinflussten. Die Klimafaktoren zeigten ähnliche Effekte auf die räumliche Variation von adaxialen und

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abaxialen Stomamerkmalen. Wir schließen, dass die geringe Temperatur und starke Sonneneinstrahlung in großen Höhen für die größeren und weniger zahlreichen Stomata auf dem Hochland von Tibet ursächlich sein könnte. Die Stomaparameter, die hier vorgestellt wurden, können benutzt werden, um den Gasaustausch auf Ökosystemebene zu modellieren.
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Keywords: Leaf epidermal cell; Stomatal index; CO_2 partial pressure; Chinese grasslands; Tibetan Plateau; Inner Mongolia

Introduction

Stomata are the essential connections between the internal air spaces of plants and the external atmosphere. Because they regulate plant water loss and carbon gain, they exert control over ecosystem water and carbon cycles (Hetherington & Woodward 2003). The evolution of stomata is considered a key event in the overall evolution of advanced terrestrial plants (Raven 2002). Stomata are present on both surfaces of many leaves (amphistomatous) or on only one surface, i.e., either the adaxial (hyperstomatous) or the abaxial (hypostomatous) surface. Even for amphistomatous species, some studies have found that stomata are frequently present in different numbers on both leaf surfaces (Taylor et al. 2012). Moreover, stomata vary in number and size within and among species (Hetherington & Woodward 2003). By addressing the relationship between the stomata occurrence (adaxial, abaxial or both leaf surfaces) and stomatal traits and the environmental variables, we can understand the adaptive mechanisms and strategies of plants at the scale of ecosystems.

Numerous studies have reported the patterns of stomatal structure and development (Bergmann & Sack 2007; Casson & Gray 2008; Casson & Hetherington 2010) and the responses of the stomatal traits such as stomatal size, aperture, density and index to atmospheric CO_2 concentrations (Woodward 1987; Franks & Beerling 2009; Mott 2009), light intensity (Hovenden & Vander Schoor 2006; Wang, Noguchi, & Terashima 2008; Mott 2009), water regimes (Lake & Woodward 2008; Xu & Zhou 2008) and temperature variation (Hovenden 2001; Luomala, Laitinen, Sutinen, & Vapaavuori 2005; Fraser, Greenall, Carlyle, Turkington, & Friedman 2009). A few studies have also focused on the spatial variation in the stomatal traits within specific species or groups of species along environmental gradients. For example, a study that investigated *Leymus chinensis* along a large-scale longitudinal gradient in Northeast China showed that both stomatal density and stomatal index were positively correlated with the mean annual precipitation (MAP) and the growing season precipitation (GSP; Wang et al. 2011). In a study of sedges in the Eurasian arctic, the stomatal density increased with temperature and precipitation, whereas the stomatal size showed the opposite response (Stenström, Jónsdóttir, & Augner 2002).

Among the studies of stomatal traits along the environmental gradients, the altitudinal variation is relatively well documented. The stomatal density of all 12 species of three life forms (trees, shrubs and herbaceous plants) declined with altitude in the Southern Alps in New Zealand (Körner, Bannister, & Mark 1986). Pteridophytes from the Bolivian Andes showed an increase in stomatal density with altitude for six species, and no correlation for another five species (Kessler, Siorak, Wunderlich, & Wegner 2007). Other studies suggest that stomatal density decreases (Gou et al. 2005) or increases (Kofidis, Bosabalidis, & Moustakas 2003; Kouwenberg, Kurschner, & McElwain 2007) with altitude or is independent of it (Li, Zhang, Liu, Luukkanen, & Berninger 2006). The variation in stomata occurrence and stomatal index has been rarely investigated.

Stomatal control of the exchange of CO_2 and water has been evaluated using stomatal conductance, which is directly influenced by the stomatal size and density (Willmer & Fricker 1996). In addition, the stomatal conductance of the adaxial and abaxial surfaces responds differently to environmental conditions such as light (Wang et al. 2008). Therefore, more comprehensive information of stomatal occurrences on leaves and their variation among species and functional groups may help improving our understanding of the stomatal regulation of gas exchange from the leaf scale to the ecosystem scale.

Here, we present a large-scale survey across the Chinese grassland biomes: from the temperate grasslands on the Inner Mongolian Plateau to the alpine grasslands on the Tibetan Plateau. Chinese grasslands provide an ideal opportunity for such studies because they have a large number of species and large gradients of atmospheric CO_2 concentration, insolation, temperature and precipitation (see Appendix A: Table 1). Our objectives were to: (1) document the patterns of stomatal occurrence and stomatal traits in different functional groups and biogeographic regions, and (2) determine the effects of climatic variables on the stomatal traits across Chinese grassland species.

Materials and methods

Study sites and sampling strategies

The study area covers the temperate grasslands on the Inner Mongolian Plateau and the alpine grasslands on the Tibetan Plateau (see Appendix A: Fig. 1). The climate of these regions is notably seasonal, with substantial annual variation in temperature, precipitation, relative humidity and insolation. Sample collection was conducted in late July and early August of 2003, 2004 and 2005. Sampling sites with flat topography were selected by visual inspection of the vegetation with a focus on sites that are subject to

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