Journal of Arid Environments 88 (2013) 70–77

Contents lists available at SciVerse ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

The altitudinal distribution center of a widespread cushion species is related to an optimum combination of temperature and precipitation in the central Tibetan Plateau

R. Li [a,e], T. Luo [a,*], Y. Tang [b], M. Du [c], X. Zhang [d]

[a] Key Laboratory of Tibetan Environment Changes and Land Surface Processes, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Datun Road 4A, Chaoyang District, Beijing 100101, China
[b] National Institute for Environmental Studies, Tsukuba 305-8506, Japan
[c] National Institute for Agro-Environmental Sciences, Tsukuba 305-8604, Japan
[d] Institute of Geographical Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China
[e] Graduate University of Chinese Academy of Sciences, Beijing 100049, China

ARTICLE INFO

Article history:
Received 16 December 2011
Received in revised form
29 July 2012
Accepted 31 July 2012
Available online 15 October 2012

Keywords:
Alpine meadow
Climate
Cushion plant
Distribution pattern
Limiting factor
Plant cover
Survival

ABSTRACT

Climate warming may threaten the survival of alpine cushion plants, which may have great implications for the stability of alpine ecosystems. However, little research has investigated the climatic causes of the altitudinal distribution of cushion plants. We hypothesize that for a widespread cushion species in semi-arid regions, there is a unimodal pattern of plant cover associated with an optimum combination of temperature and precipitation. We conducted a livestock exclosure experiment across the upper (5300 m) and lower (4430 m) limits of a widespread cushion species (*Androsace tapete*) along the south-facing slope of the Nyaiqentanglha Mountains during the period 2006–2010. The plant cover and survival across the fenced and unfenced quadrats were observed near weather stations at eight altitudes. There was a unimodal pattern in the coverage of *A. tapete* along the experimental gradient, which was confirmed by additional data from other species and mountains in this region. The coverage showed quadratic relationships with mean temperatures and the ratio of growing-season precipitation to the ≥5 °C accumulated temperature sum. Five-year monitoring data under fenced conditions demonstrated that the annual survival of *A. tapete* decreased away from the optimum distribution center. The results supported the hypothesis, suggesting a shift in the limiting factors of plant distribution between low and high altitudes.

1. Introduction

In the last 100 years, the air temperature has generally shown an increasing trend, but the trend of precipitation has varied with timescales and regions (IPCC, 2007), resulting in different combinations of temperature and precipitation at local to regional scales. Along a large altitudinal gradient in semi-arid grasslands, the plant growth and distribution can be mainly limited by drought at low altitudes (Webb et al., 1983; Epstein et al., 1997) and by low temperature at high altitudes (Klimeš and Doležal, 2010; Körner, 2003). This observation provides us with an ideal system to investigate the altitudinal distribution of a plant species and its response to the changes in the combination of temperature and precipitation. Cushion species, which are referred to as ecosystem engineers (Jones et al., 1994), are often very sensitive to variations in temperature and precipitation (Le Roux et al., 2005). Identifying climatic causes of the altitudinal distribution of cushion species is important to understanding and predicting the response of alpine grassland ecosystems to climatic change.

Cushion plants have a compact, flat growth form adapted to dry and cold habitats. Most previous studies indicate that the characteristic life form of alpine cushion species can create a unique microhabitat, where temperatures remain higher (Badano et al., 2006; Larcher, 2003) or more constant (Cavieres et al., 2007, 2006) than in the surrounding air and where the soil water and nutrient availability is improved (Badano et al., 2006; Cavieres et al., 2007, 2006; Neuner et al., 2000). The generated microhabitats then facilitate the survival and recruitment of other plant species (Badano and Marquet, 2008; Cavieres et al., 2006), resulting in an increase in species richness in alpine ecosystems (Arroyo

* Corresponding author. Tel.: +86 10 62849680; fax: +86 10 84097060.
E-mail address: luotx@itpcas.ac.cn (T. Luo).

0140-1963/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jaridenv.2012.07.018

et al., 2003). Current climate warming may threaten the survival of alpine cushion plants (Le Roux et al., 2005), which may have great implications for the survival of other coexisting species and the stability of alpine ecosystems. However, few studies have investigated environmental factors controlling the altitudinal distribution of cushion plants. In the high Andes of Central Chile (2600–3400 m), Armesto et al. (1980) indicated that the total cover of cushion plants is at a maximum at approximately 3000 m and then decreases markedly with increasing altitude. Because of the lack of climatic and soil data, explaining such a unimodal pattern of cushion plant cover along the altitudinal gradient is still difficult.

The cushion plant *Androsace tapete* (Primulaceae) is an endemic, perennial herb with living aboveground tissues over winter and is widely distributed in alpine steppes and meadows in the central Tibetan Plateau (Li et al., 1987, 1985). Most previous studies have focused on the phylogeny, biogeography and morphological evolution of *A. tapete* (Geng et al., 2009; Wang et al., 2004; Zeng et al., 2010), suggesting that *A. tapete* plays an important role in the formation and evolution of alpine steppes and meadows. To our knowledge, however, there are no field data documenting the climatic causes of the altitudinal distribution of *A. tapete*.

Many investigators have examined short-term changes in the heat and frost tolerances of cushion plants in response to extreme temperatures under laboratory conditions (Larcher et al., 2010; Neuner et al., 2000; Sierra-Almeida and Cavieres, 2010). However, such laboratory results still need to be tested by field observations across the upper and lower altitudinal limits of a cushion species because alpine cushion plants generally create a unique microhabitat decoupled from the atmosphere (Körner, 2003) and other interfering factors (such as snow cover and the soil condition) may be involved under field conditions (Bruelheide and Heinemeyer, 2002). Livestock grazing may disturb the climatically altitudinal pattern of alpine plants by altering soil conditions and species composition (Namgail et al., 2012; Retzer et al., 2006). Geographically, there are no experimental data examining the relative influences of environmental factors and grazing on the altitudinal distribution of cushion plants.

At high altitudes, extreme low temperatures may occur during the growing season, which is fatal to the survival of alpine plants because they have the weakest ability to resist the growing-season freezing temperatures (Körner, 2003; Mayr et al., 2012; Neuner and Hacker, 2012; Sierra-Almeida et al., 2009). In contrast, the heat-trapping characteristic of alpine cushion plants may increase the risk of occasional overheating during clear, calm and dry summer days at low altitudes (Larcher et al., 2010; Neuner et al., 2000; but see; Cavieres et al., 2006, 2007). The onset of functional disturbances in photosystem II of alpine cushion plants may occur at leaf temperatures >28(30)°C that are 12–25 °C higher than the air temperatures (Cabrera et al., 1998; Neuner et al., 2000). Geographically, our previous work indicated that stand biomass and productivity proportionally decrease away from the optimum distribution center of a vegetation type, which is associated with an optimum combination of climatic and soil factors in a common logistic function (Luo et al., 2004, 2005, 2009, 2002). In the central Tibetan grasslands, our recent data further indicated that the grazing did not alter the altitudinal pattern of the aboveground biomass and species richness and that the species composition did not differ between fenced and unfenced treatments (Wang et al., in press). Considering the unique microhabitats of the cushion form, we hypothesize that for a widespread cushion species in semi-arid regions, there is a unimodal pattern of the plant cover associated with an optimum combination of temperature and precipitation.

To test this hypothesis, we conducted a livestock exclosure experiment across the upper (5300 m) and lower (4430 m) limits of *A. tapete* along a south-facing slope of the Nyaiqentanglha Mountains during the period 2006–2010. Continuous measurements of the air and soil temperatures and precipitation were obtained from nearby weather stations at eight altitudes (4300–5300 m) along the slope. We investigated the generality of the altitudinal pattern of *A. tapete* using additional transect data for the same species in the northern T'ang-ku-la Mountains and for another cushion species (*Arenaria lancangensis*) in the northern Nyaiqentanglha Mountains. Our tasks included the following: 1) investigating whether there is a unimodal pattern in the coverage of *A. tapete* associated with climatic and soil factors along the experimental transect and whether a similar pattern also exists in other species and mountains; 2) examining whether the altitudinal limits of *A. tapete* are related to top-soil temperature extremes; and 3) examining to what extent interannual changes in temperature and precipitation during the period 2006–2010 can explain the interannual variations in the survival of *A. tapete* across fenced and unfenced quadrats.

2. Data and methods

2.1. Study sites

This study was conducted along the south-facing slope of the Nyaiqentanglha Mountains with altitudes from 4300 m to 5300 m a.s.l. (30° 30′–30° 32′ N, 91° 03′ E) in the central Tibetan Plateau. According to the meteorological observation from 1963 to 2008 at Damxung station (4288 m a.s.l., ca. 4 km away from our study site), the annual sunlight hours (directed sunlight hours of >120 W m^{-2}) were 2933 h, and the mean air temperatures for the year, January, and July were 1.7 °C, 9.4 °C, and 10.9 °C, respectively. The annual precipitation was 479 mm (290–700 mm, with >85% rainfall occurring in the growing season of May to September), which was much less than the annual pan evaporation of 1726 mm. During the above period, the annual mean air temperature increased by approximately 1.5 °C at a warming rate of 0.33 °C per 10 a, which is consistent with that of the whole plateau (0.36 °C per 10 a during the period 1960–2007, Wang et al., 2008). The annual precipitation showed a decreasing trend during the period 1963–1990 and an increasing trend during the period 1991–2006, but neither trend was statistically significant ($P > 0.10$). During the period of this study, the annual precipitation varied greatly between years, ranging from 333 mm in 2006 to 706 mm in 2008.

The Nyaiqentanglha Mountains lie in the zonal ecotone between the alpine *Stipa* steppe and alpine *Kobresia* meadow and are characterized by a semi-arid climate with decreasing aridity from low to high altitudes (Fig. 1). Along the south-facing slope, the vegetation changed from the alpine steppe-meadow with dominant species of *Kobresia humilis* and *Stipa capillacea* at 4300–4650 m to the alpine meadow with dominant species of *Kobresia pygmaea* and *A. tapete* at 4700–5210 m. At the community level, the total biomass and species richness generally increased with increasing altitude up to 4950–5100 m and then decreased above 5100 m (Wang et al., in press). Other coexisting species mainly included *A. lancangensis*, *Potentilla nivea*, and *Carex atrofusca*. The distribution of *A. tapete* ranged from 4430 m to 5300 m along the slope, with a break at altitudes of 4520–4690 m.

2.2. Altitudinal meteorological observations

In August 2005, we set eight HOBO weather stations (Onset Inc., Bourne, MA, USA) at different altitudes (4430 m, 4500 m, 4650 m, 4800 m, 4950 m, 5100 m, 5200 m, and 5300 m) along the south-facing slope of the Nyaiqentanglha Mountains. The air temperature (1.5 m aboveground), precipitation, and soil temperatures