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ScienceDirect
South African Journal of Botany 75 (2009) 268–275
SOUTH AFRICAN JOURNAL OF BOTANY
www.elsevier.com/locate/sajb

Gender-specific carbon discrimination and stomatal density in the dioecious tree of *Hippophate rhamnoides*

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Received 14 November 2007; received in revised form 3 December 2008; accepted 23 December 2008

Abstract

For a long time dioecious plants have played an important role in examination of the reproduction cost and determination of the sexual dimorphism evolution in life history. *Hippophae rhamnoides sinensis*, a dioecious, outcrossing plant, occurs mainly in the arid regions of northwest China, contributes to maintain the local ecosystems in these regions. In this study, $\delta^{13}C$ and the stomatal density of herbarium sheet were measured in *Hippophate rhamnoides sinensis*. It was found that the plants showed gender-difference in carbon isotope compositions: the males maintained higher $\delta^{13}C$ values and thus higher water use efficiency as well as slightly higher stomatal density than the females, moreover, the between-sex difference is stable in different contexts through carbon isotope discrimination. Although we found that the stomatal density had being reduced and is sensitive to atmospheric CO_2 level, $\delta^{13}C$ value and thus water-use efficiency did not significantly change from 1978 to 2001. Consequently, gender-specific $\delta^{13}C$ could play a decisive role in explaining gender differences in the developmental growth.

Keywords: Carbon isotope discrimination; Dioecious plant; *Hippophate rhamnoides sinensis*; Stomatal density

1. Introduction

In dioecious plants, substantial differences in the demand for resources are usually observed between females and males, which might be due to difference in reproduction cost (Lloyd and Webb, 1977). The male allocates resources to a flower for a short period (the flowering time only) whereas the female allocates resources not only to flowers but also to fruits, and the allocation in reproduction occurs for a longer period during fruit maturation. Thus, the female generally incurs greater reproduction cost than the male does (Gross and Soule, 1981; Lovett Doust and Lovett Doust, 1988; Allen and Antos, 1988, 1993; Dawson and Ehleringer, 1993; Kohorn, 1994; Obeso, 1997; Nicotra, 1999). It has been suggested that the different cost for reproduction should impose a very different resource demand on the plants and, consequently, gender specialization has been interpreted as an evolved response that may allow each gender to meet the specific resource demands associated with reproduction (Cox, 1981; Dawson and Bliss, 1989; Dawson and Ehleringer, 1993). Gender differences have been well documented in growth (Ramp and Stephenson, 1988; Jing and Coley, 1990), survival (Lovett Doust and Lovett Doust, 1988; Allen and Antos, 1993), reproductive patterns (Bullock and Bawa, 1981; Cipollini and Whigham, 1994), spatial distribution (Bierzychudek and Eckhart, 1988; Iglesias and Bell, 1989), resource allocation (Wallace and Rundel, 1979; Gross and Soule, 1981; Ramp and Stephenson, 1988; Vitale et al., 1987; Delph, 1990), shoot structure and function (Ueno and Seiwa, 2003), canopy and leaf display (Wallace and Rundel, 1979; Kohorn, 1994) and patterns of defense and herbivory (Jing and Coley, 1990; Krischik and Denno, 1990). However, because of the greater difficulties in gathering data on eco-physiological processes, much less has been known about gender specialization in physiology (Bourdeau, 1958; Crawford and Balfour, 1983; Dawson and Bliss, 1989, 1993; Dawson and Ehleringer, 1993; Hill et al., 1996; Obeso et al., 1998; McDowell et al., 2000). This is a crucial issue, as variation in ecophysiological

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doi:10.1016/j.sajb.2008.12.002

attributes may, by itself or in combination with factors such as allocation, determine the performance of each sex in different micro habitats and, ultimately, it may have consequences for growth, survival and population structure. Furthermore little is known about the physiological differentiation between sexes that may influence habitat partitioning between the sexes (Freeman and McArthur, 1982; Crawford and Balfour, 1983; Dawson and Bliss, 1989; Dawson and Ehleringer, 1993) and about how gender-specific physiology could account for the differences in growth and size distributions of both sexes (Dawson and Ehleringer, 1993; Obeso et al., 1998; McDowell et al., 2000; Retuerto et al., 2000).

Most of the characteristics used to investigate the physiological differentiation between sexes, such as photosynthetic activity, transpiration rate and other water-related parameters, are instantaneous measurements that do not allow integration of ecophysiological processes (Retuerto et al., 2000). The use of stable isotope techniques in plant ecological research has grown steadily during the past two decades and this trend will continue as researchers realize that stable isotopes can serve as valuable non-radioactive tracers and nondestructive integrators indicating how plants today and in the past have interacted with and responded to their abiotic and biotic environments. Plant $\delta^{13}C$ has been used in ecological research as a long-term integrator of ecophysiological processes such as leaf conductance, hydraulic capacity, potential water-use efficiency and photosynthetic capacity (Körner et al., 1988; Farquhar et al., 1989). One of its uses has been to compare the physiological performance between male and female individuals (Dawson and Bliss, 1989; Dawson and Ehleringer, 1993; Retuerto et al., 2000).

Hippophae rhamnoides sinensis is an important resource plant in China and exists as a pioneer plant with significant value for water and soil conservation. It grows mainly on sandy soils by riverbanks or along riverbeds, mountain slopes, and valleys. It is found on the eastern edges ranging from Qinghai Province in the west to Hebei Province in the east, from Sichuan Province in the south to Inner Mongolia and Hebei Province in the north, with an altitude from 400 to 3900 m (Lian, 2000). Here, we used herbarium sheet and explored the differences between sexes of the dioecious tree *Hippophae rhamnoides sinensis* in $^{13}C/^{12}C$ discrimination in different habitats and years. Our main interest was to know if gender made a difference in the long-term potential water-use efficiency, as estimated by carbon isotope discrimination and if physiological differences between sexes could be dependent on the environmental context. Such information would contribute to a better

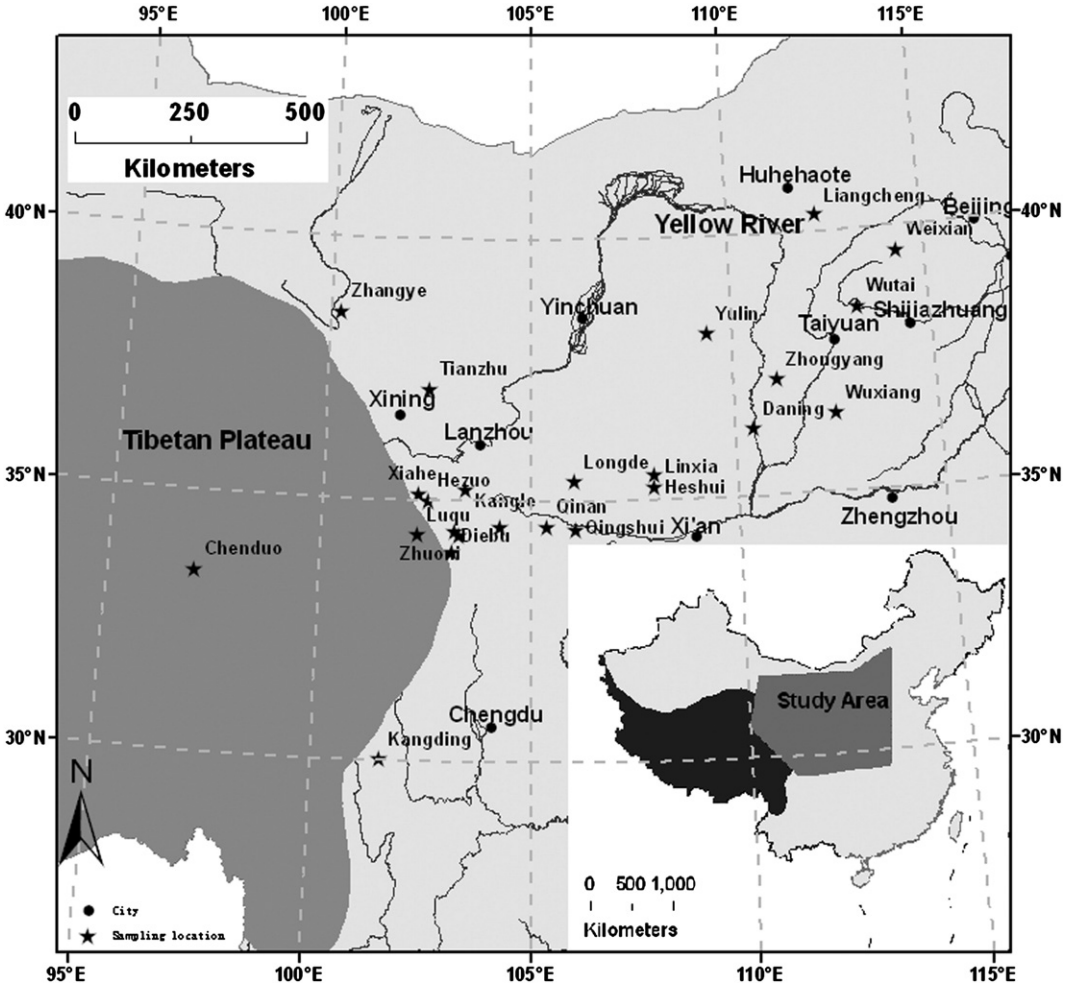

Fig. 1. Map of China showing locations of collecting areas for samples of *H. rhamnoides sinensi.*