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Patterns and implications of plant-soil $\delta^{13}C$ and $\delta^{15}N$ values in African savanna ecosystems

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ABSTRACT

Southern African savannas are mixed plant communities where C_3 trees co-exist with C_4 grasses. Here foliar $\delta^{15}N$ and $\delta^{13}C$ were used as indicators of nitrogen uptake and of water use efficiency to investigate the effect of the rainfall regime on the use of nitrogen and water by herbaceous and woody plants in both dry and wet seasons. Foliar $\delta^{15}N$ increased as aridity rose for both C_3 and C_4 plants for both seasons, although the magnitude of the increase was different for C_3 and C_4 plants and for two seasons. Soil $\delta^{15}N$ also significantly increased with aridity. Foliar $\delta^{13}C$ increased with aridity for C_3 plants in the wet season but not in the dry season, whereas in C_4 plants the relationship was more complex and non-linear. The consistently higher foliar $\delta^{15}N$ for C_3 plants suggests that C_4 plants may be a superior competitor for nitrogen. The different foliar $\delta^{13}C$ relationships with rainfall may indicate that the C_3 plants have an advantage when competing for water resources. The differences in water and nitrogen use likely collectively contribute to the tree–grass coexistence in savannas. Such differences facilitate interpretations of palaeo-vegetation composition variations and help predictions of vegetation composition changes under future climatic scenarios.

Introduction

Savannas cover approximately 20% of the Earth's land area, including about 40% of Africa (Scholes and Walker, 1993). In Africa, savannas provide an ideal grazing/browsing habitat for both native herbivores such as the elephant, hippopotamus and buffalo as well as animals brought in by humans. Humans depend heavily on savanna ecosystems both as rangelands for livestock grazing, and for fuel wood harvesting (Aranibar et al., 2008).

The main savanna tree families evolved during the Cretaceous Period (150 million years ago) (Raven and Axelrod, 1974), the first grasses probably appeared in the Palaeocene Epoch (60 million years ago) (Clayton, 1981). The origin of the modern savanna biome in Africa is closely linked to the dramatic expansion of C_4 grasses in this continent during the Miocene (8 million years ago) (Beerling and Osborne, 2006). The C_3 and C_4 plant compositions in savanna ecosystems have undergone dramatic changes during the Holocene (Lamb et al., 2004; Vivo and Carmignotto, 2004) and modern savannas in Africa are still undergoing important changes, including those associated with bush encroachment (Roques et al., 2001).

Natural and anthropogenic disturbances associated with climate fluctuations, fire regime, grazing and browsing pressure contributed to determine conditions favorable to the existence of mixed tree–grass communities (Sinclair, 1979; Scholes and Archer, 1997). The non-successional persistence of trees and grasses (mainly the C_3 and C_4 plants) on the savannas has intrigued scientists for decades (e.g., Sarmiento, 1984; Scholes and Archer, 1997; Sankaran et al., 2005; Wang et al., 2007a); however, a few key aspects of savanna ecology remain poorly understood. For example, differences in the morphology and physiology of trees and grasses may explain their different access to nutrients and water, and their different efficiency in the use of these resources. It is still unclear how climate variables such as mean annual precipitation (MAP) may affect the relative efficiency of grasses and trees in the use of water and in the uptake of soil nutrients such as nitrogen (N), and how changes in rainfall regime may affect the coexistence of these two plant functional types.

The natural abundance of stable isotopes is routinely utilized as an indicator of ecosystem processes (Robinson, 2001). For example, foliar $\delta^{13}C$ is often used to determine plant water use efficiency (Farquhar et al., 1989), whereas ^{15}N is an integrator of N cycling and reflects numerous processes occurring in soil, plants, and atmosphere (e.g., nitrification and denitrification produced N_2O will have different $\delta^{15}N$ signatures) (Högberg, 1997; Robinson, 2001). In fact, the $\delta^{15}N$ signatures of plant leaves and roots, and of soil organic matter, result from a combination of a number of factors including access to different N sources and the effects of isotopic fractionation (Wang et al., 2007b, 2007c). A few studies have investigated the

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relation between foliar δ^{13}C and δ^{15}N along gradients of rainfall, substrate age and disturbance pressure at different temporal and spatial scales (Austin and Vitousek, 1998; Brenner et al., 2001; Aranibar et al., 2004, 2008; Swap et al., 2004; Sah et al., 2006; Wang et al., 2007c). However, the presence of co-varying factors (e.g., plant species composition and seasonality, or soil properties) along certain of these gradients has often prevented the interpretation of the ecosystem processes underlying the relation between foliar δ^{13}C and δ^{15}N, and the apparent influence of rainfall regime.

Situated in the central part of southern Africa, the Kalahari is the ideal location to study these water and N controls in savannas. In fact, this region hosts a variety of savanna ecosystems—ranging from fine-leaved open savanna in the south to broad-leaved savanna woodlands in the north—along a dramatic rainfall gradient on relatively homogenous soils, namely the deep Kalahari sands (Wang et al., 2007a). Identified by the IGBP (International Geosphere-Biosphere Programme) as one of the “mega-transects” for global change studies (Koch et al., 1995), the Kalahari Transect (KT) provides the ideal setting to study nutrient and vegetation dynamics without confounding soil effects.

The present study examines patterns of foliar δ^{13}C and δ^{15}N along the KT both in the wet and in the dry seasons, for two distinct plant functional types typical of African savannas, namely C_3 trees and C_4 grasses. Patterns of soil δ^{13}C and δ^{15}N from soil patches dominated by C_3 and C_4 plants are also investigated in both the dry and the wet seasons. The objectives of this study are 1) to provide new insights on tree–grass interactions in savanna ecosystems in the contemporary setting by examining the differences in foliar δ^{13}C and δ^{15}N (as indication of plant water and N use) between these two different plant functional types and seasons, and among different species within the same plant functional type; and 2) to improve the understanding of carbon (C) and N dynamics in savannas at the ecosystem level and their response to rainfall conditions. To this end, patterns both of foliar and of soil δ^{13}C and δ^{15}N are investigated along a relatively strong rainfall gradient.

Materials and methods

Study sites

The KT in southern Africa was used as a model ecosystem (due to its homogenous soils along a relatively strong rainfall gradient) to examine patterns of foliar and soil δ^{13}C and δ^{15}N under different climatic conditions. The northernmost site was situated in Mongu, Zambia (15°26′S, 23°15′E), with a MAP of 879 mm. The vegetation in Mongu is woodland savanna dominated by woody species such as *Brachystegia spiciformis* Benth. Three other sites from north to south were situated in Pandamatenga (18°40′S, 25°30′E), Ghanzi (21°39′S, 21°49′E) and Tshane (24°10′S, 21°53′E), Botswana (Fig. 1). The MAP in these three areas were 698 mm, 424 mm and 365 mm, respectively. The vegetation in Tshane and Ghanzi is typical of an open savanna dominated by *Acacia* species such as *A. luederizii* Engl. and *A. mellifera* Benth. The vegetation cover in Pandamatenga is a woodland savanna dominated by tree species such as *Kirkia africana* and grass species such as *Schmidtia pappophoroides* and *Pogonarihria squarrosa*. The soil type in this region is classified as “Shifting Sands” according to the USDA classification (Wang, 2008). The soil temperatures at the four sites were similar and the mean soil temperatures measured in January–February 2006 were 24.5°C, 23.7°C, 26.7°C and 25.4°C at Tshane, Ghanzi, Pandamatenga and Mongu, respectively. The detailed soil physical and chemical characteristics at each site can be found in Wang et al. (2007a). To summarize, the soil is sandy (>96%) and acidic. Soil colors vary between sites and also vary along soil depths, partly due to vegetation effects. Grain sizes are slightly finer at the drier sites (Tshane and Ghanzi) than at the wetter sites (Pandamatenga and Mongu).

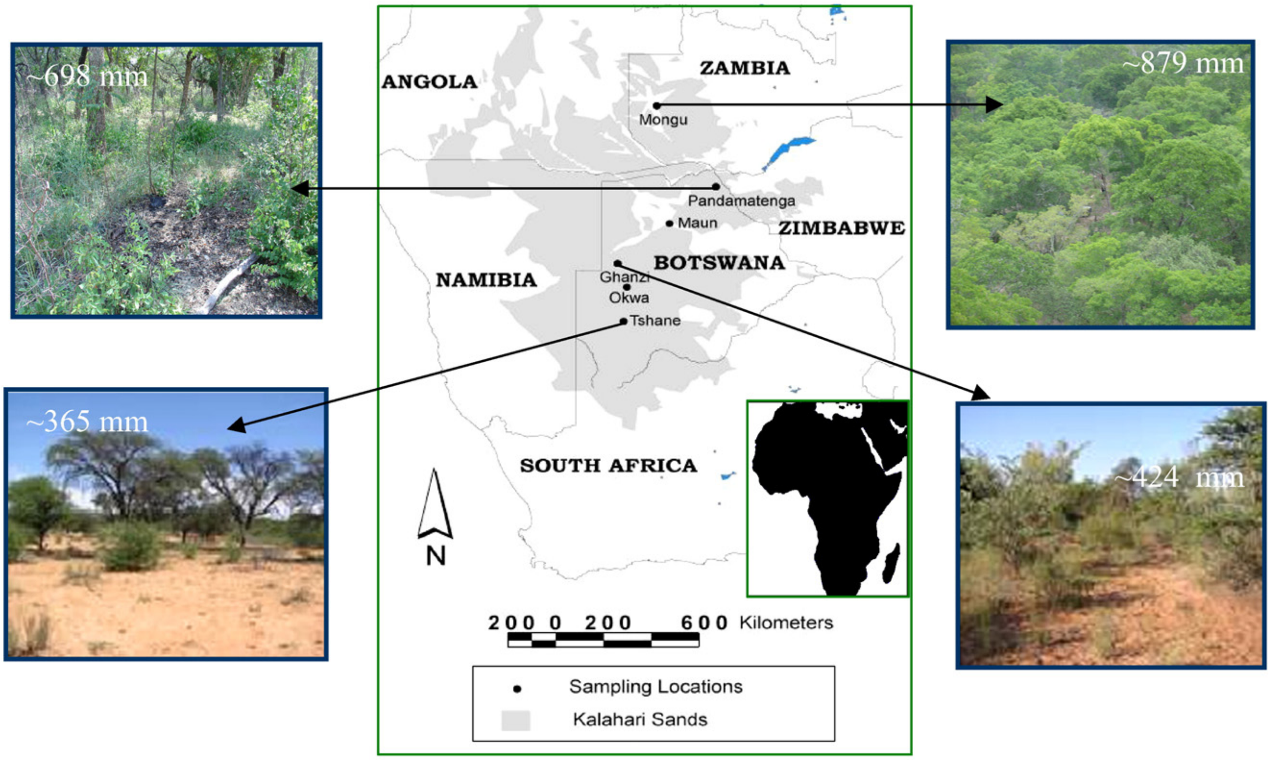

Figure 1. Sampling locations along the Kalahari precipitation gradient in southern Africa. Numbers in each photo are the mean annual precipitation.