Journal of Arid Environments 114 (2015) 54–61

Contents lists available at ScienceDirect

Journal of Arid Environments

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

Seasonal variations in nutrients and secondary metabolites in semi-arid savannas depend on year and species

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ARTICLE INFO

Article history:
Received 17 December 2013
Received in revised form
5 November 2014
Accepted 13 November 2014
Available online

Keywords:
Functional trait
Growth
Defence
Herbivore
Phenology
Woody

ABSTRACT

Semi-arid savannas are characterised by alternating wet and dry seasons and large inter-annual rainfall fluctuations that affect plant growth. Carbon-based secondary metabolites (CBSMs) vary inversely with growth and nutrients because of the physiological trade-off between cellular growth and differentiation. We predicted that (1) nutrient concentrations decrease during the wet season, (2) CBSM concentrations increase during the wet season and (3) nutrient concentrations are lowest and CBSM concentrations are highest in the dry season. We measured nitrogen, phosphorus, total polyphenols and condensed tannins in six woody species (including one evergreen) seasonally at the Nkuhlu exclosure, Kruger National Park, South Africa, for three consecutive years, including one 'wet' year (above-average rainfall) and two 'dry' years (below-average rainfall). Neither N nor P consistently decreased during wet seasons, while CBSMs did not consistently increase. Neither N nor P in the evergreen species was consistently lowest in dry seasons, while CBSMs were not consistently highest in dry seasons. We discuss the inconsistent responses in the context of species-specificity and high inter-annual rainfall variation. We conclude that seasonal variations in N, P and CBSMs in semi-arid savannas cannot be easily generalised because they depend on species and year.

1. Introduction

Savannas are characterised by alternating wet and dry seasons that each last several months (Kutsch et al., 2008). Most subtropical savannas in Africa are semi-arid and water is the main limiting resource for plant growth for most of the year (Scholes et al., 2003; Jacobs et al., 2007). Nitrogen is most available early in the wet season when elevated soil water drives mineralization (Scholes et al., 2003). Plant growth is therefore intermittent and occurs for only brief periods, mainly early in the wet season (Williams et al., 2009). However, semi-arid savannas also experience large, inter-annual fluctuations in the timing and amount of rainfall that affect plant growth (Wiegand et al., 2006). When water and nutrients are abundant, e.g., early in the growing season, then woody species may be expected to have fast growth rates, high nutrient concentrations and low secondary metabolite concentrations (Herms and Mattson, 1992; Martz et al., 2010). Nutrients, such as N and P, contribute to a plant's overall value for mammal herbivores (Mårell et al., 2006) and their concentrations generally decrease during the growing season (Lesage et al., 2000; Nahm et al., 2007; Cernusak et al., 2011) and are generally lower in years with below-average rainfall (Nahm et al., 2007).

Carbon-based secondary metabolites (CBSMs), such as tannins and polyphenols, are ecologically important compounds in plants for various reasons, e.g., as protection against herbivores, pathogens or UV radiation (Skarpe and Hester, 2008; Tharayil et al., 2011). Their roles in plant–herbivore interactions include

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http://dx.doi.org/10.1016/j.jaridenv.2014.11.003

reducing plant palatability and intake or digestion by herbivores (Basha et al., 2013) and reducing internal parasite loads in herbivores (Copani et al., 2013). In leaf litter, CBSMs are a major source of carbon for soils and influence litter decomposition and nutrient cycling (Tharayil et al., 2011). Therefore, CBSMs are important components of ecosystems because of their roles in mediating vital ecological processes (Iason et al., 2012). Increased knowledge on how nutrient and CBSM concentrations vary seasonally and annually could contribute to understanding variations in herbivore populations and nutrient cycling (Covelo and Gallardo, 2001; Tharayil et al., 2011). High nutrient or low CBSM concentrations early in the wet season could compromise plant fitness, but may benefit herbivores.

Our aim was to determine the variations in nutrient and CBSM concentrations in foliage of abundant woody species in a semi-arid savanna, as affected by season and year. The abundance of mammal herbivores in Africa is high compared to other continents (Fritz and Loison, 2006), but the extent to which mammal herbivores directly influence nutrient and CBSM concentrations in woody plants in African savannas is unknown. Hence, our scale of interest was the foliage available for large, mammal herbivores, rather than individual leaves, and our framework was a basic mechanistic one as follows. Concentrations of CBSMs are assumed to be inversely related to growth and therefore are expected to increase when growth rate is relaxed late in the growing season. Surplus C accumulates and becomes available for production of CBSMs (Covelo and Gallardo, 2001; Gayler et al., 2007; Tharayil et al., 2011) because they are biochemical end-products (Riipi et al., 2002; Martz et al., 2010). However, the magnitude and timing of fluctuations in both nutrient and CBSM concentrations is species-specific and some species express minimal changes (Mårell et al., 2006; Cella-Pizarro and Bisigato, 2010; Narvaez et al., 2010; Basha et al., 2012).

We predicted that (1) nutrient (N and P) concentrations decrease during the course of the wet season, (2) CBSMs, measured as total polyphenol (TP) and condensed tannin (CT) concentrations, increase during the course of the wet season, and (3) nutrient concentrations are lower and CBSM concentrations are higher in the dry season, when nutrients are less available and the risk of herbivory by mammals is greater because of forage depletion, than in the wet season. We also expected that seasonal changes would be influenced by the year in which sampling occurred, because of inherently high inter-annual variability. We tested our hypothesis by sampling five deciduous and one evergreen species in Kruger National Park, South Africa, for three consecutive years. Including several species in the study allowed species-specific patterns to be explored. Sampling over three years allowed inter-annual variability to be considered. In particular, the study duration provided an opportunity to interpret our results in terms of annual variation in one of the strongest drivers of semi-arid vegetation, namely, rainfall. Our approach was at a scale that is useful for the management of extensive areas used for either biodiversity conservation or livestock production (Levick and Rogers, 2008).

2. Materials and methods

2.1. Study area and species

The study area comprised 30 ha at Nkuhlu (24° 58′ S, 31° 46′ E) directly east of the Sabie River in Kruger National Park, South Africa. The vegetation in the area was protected from fire and large herbivores by a firebreak and a fence since 2002, which allowed the study of intra- and inter-annual changes to be unaffected by either browsing or fire. The fence was designed to exclude mammal herbivores such as impala (*Aepyceros melampus*), African elephant (*Loxodonta africana*), hippo (*Hippopotamus amphibius*), black rhino (*Diceros bicornis*), white rhino (*Ceratotherium simum*), blue wildebeest (*Connochaetes taurinus*), Cape buffalo (*Syncerus caffer*), plains zebra (*Equus quagga*), greater kudu (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*), giraffe (*Giraffa camelopardalis*) and scrub hare (*Lepus saxatilis*). Elephant, impala, black rhino, kudu, steenbok, giraffe and hares include substantial woody plant material in their diets.

The climate of the study area is semi-arid subtropical with two broadly distinct seasons: a hot, occasionally wet, growth season (from October/November to April), and a warm, dry, non-growing season (Williams et al., 2009). Mean annual rainfall at Skukuza, 30 km west of Nkuhlu, is ~550 mm. Average daily temperatures at Skukuza are 15.7 °C in June and 26.6 °C in January. Average minimum temperature in June is 5.7 °C and average maximum temperature in January is 32.6 °C. Altitude ranges from 200 to 230 m above mean sea level.

The study area included the complete sequence of terrain morphology from footslope to crest in undulating landscape derived from granite. The crests and middle slopes were characterised by shallow, sandy, coarse soil overlying rock and the footslopes below the seepline were characterized by deep, sodic, duplex soil, which is a typical pattern on catenas in granite-derived, semi-arid landscapes (Khomo and Rogers, 2005). Vegetation on sodic soils is sparse and regarded as more nutritious than crest vegetation for large herbivores, especially grazers and mixed feeders (Levick and Rogers, 2008). Abundant woody species included *Acacia grandicornuta* and *Euclea divinorum* on the footslopes, and *Dichrostachys cinerea*, *Acacia exuvialis*, *Combretum apiculatum* and *Grewia flavescens* on the middle slopes and crests (Siebert and Eckhardt, 2008).

A. exuvialis Verdoorn and *A. grandicornuta* Gerstner (both Mimocaceae) are deciduous, leguminous trees with bi-pinnate microphyllous leaves and long straight spines in pairs at the nodes. *D. cinerea* (L.) Wright and Arn. subsp. *africana* Brennan and Brummitt (hereafter referred to as *D. cinerea*) (Mimocaceae) is a deciduous, leguminous, multi-stemmed large shrub with bipinnate microphyllous leaves and stem-spines (short shoots that have sharp tips). *C. apiculatum* Sond. (Combretaceae) and *G. flavescens* Juss. (Tiliaceae) are deciduous and simple-leaved, but *C. apiculatum* is a tree, while *G. flavescens* is a many-stemmed large shrub. *E. divinorum* Hiern (Ebenaceae) is an evergreen, simple-leaved, many-stemmed, large shrub.

2.2. Sampling

Unlike woody plant growth in temperate and boreal forests, growth in semi-arid subtropical savannas occurs in recurrent and unpredictable flushes. Therefore, the start, middle and end of the wet season can vary by several weeks between one year and another. Most leaf growth of woody species in the study area occurred at the start of the wet season, although additional, smaller flushes occurred at other times (Scogings et al., 2013a,b). We sampled *A. grandicornuta*, *D. cinerea*, *C. apiculatum* and *G. flavescens* during three stages of each wet season (start of the wet season in late November/early December, middle of the wet season in late January/early February and end of the wet season in late March/early April) for three successive wet seasons (2005/2006, 2006/2007 and 2007/2008). We also sampled *A. exuvialis* and *E. divinorum* at each stage of two wet seasons (2005/2006, 2006/2007), but not in the third wet season because of practical constraints. Furthermore, *E. divinorum* was sampled in two dry seasons (2005 and 2007). In the 2005/2006 wet season, rainfall was consistently above average, but rainfall was below average in the latter half of the 2006/2007 and 2007/2008 wet seasons (Fig. 1).