South African Journal of Botany 103 (2016) 222–229

Contents lists available at ScienceDirect

South African Journal of Botany

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

Community structure and leaf trait heterogeneity in a deciduous thicket community of the Middle Zambezi River Valley, Zambia

Philip W. Rundel

Department of Ecology and Evolutionary Biology, University of California (UCLA), Los Angeles, CA 90095, USA

ARTICLE INFO

Article history:
Received 22 May 2015
Received in revised form 15 August 2015
Accepted 24 August 2015
Available online 7 December 2015

Edited by SJ Siebert

Keywords:
Leaf traits
$\delta^{13}C$
$\delta^{15}N$
Termites
Nitrogen fixation
Zambezi River

ABSTRACT

Deciduous Zambezi thicket forms a mixed-layered, dry woodland community on deep alluvial soils of the Middle Zambezi Valley. The dominant species are spiny, thicket-forming deciduous shrubs and small trees with no single dominant species and variable composition along the valley. A detailed community study of deciduous thicket along the Middle Zambezi River provided an indication of the wide variation of species-specific characteristics of growth form, phenology, and leaf traits that combine to produce a heterogeneous assemblage. Two families, the Capparaceae and Leguminosae, are particularly well represented. Leaf traits of nitrogen content, specific leaf area, $\delta^{13}C$, and $\delta^{15}N$ are highly variable between species, with indications of some consistency in family traits within the Capparaceae and Leguminosae. A number of species exhibit a strong pattern of association with termite mounds, and termitaria are known to have significant potential impacts on spatial patterns of soil nutrient availability and water relations in savanna communities. There remains a poor understanding of the significance of symbiotic nitrogen fixation in deciduous African thicket, and savanna, and woodland communities and its importance in ecosystem fluxes of nitrogen, and these issues cannot be resolved by simple measurements of $\delta^{15}N$ alone. Intraregional patterns of variation in leaf traits may impact the broad application of regional ecosystem models, as with those developed in the SAFARI 2000 program, when the variance between species is high, demonstrating that climatic controls on ecosystem $\delta^{15}N$ abundance are scale-dependent.

1. Introduction

Studies of subcontinental scales of carbon and nitrogen dynamics over broad precipitation gradients offer an important approach to the development of an understanding of vegetation structure and dynamics change across regional areas. The Southern African Regional Science Initiative (SAFARI) 2000 provided international attention to such efforts in southern Africa. This project focused on gradients of change in ecological processes across the Kalahari transect, from relatively arid areas of southern Botswana to moderate rainfall in miombo woodland in Zambia, across an otherwise climatically and geographically similar region with physically uniform soil and relatively little variation in elevation. Focused subjects for study included ecosystem structure and function, biogeochemistry, and modeling at the patch, landscape, and regional scale (Otter et al. 2002; Shugart et al. 2004; Swap et al., 2004).

While the Kalahari gradient studies did much to describe regional gradients of changes in foliar nitrogen levels, carbon/nitrogen (C/N) ratios, and stable isotope patterns of delta (δ) ^{15}N and delta (δ) ^{13}C), the research largely reported values for these traits based on small samples of relatively few species and thus did little to assess the intraregional patterns of variation in these measurements. The objectives of the current study have been to investigate the structure and functional attributes of a deciduous thicket community along the Middle Zambezi River in southern Zambia and to use these measurements to evaluate the level of interspecific heterogeneity in plant and leaf traits. In particular, the present study focuses on foliar patterns of nitrogen, stable isotope concentrations ($\delta^{15}N$ and $\delta^{13}C$), and carbon-to-nitrogen ratios (C/N), as a comparison to data collected in the SAFARI studies (Otter et al. 2002; Shugart et al. 2004; Swap et al., 2004), but additionally, leaf specific area and leaf specific nitrogen content. Variations in these traits are considered in relationship to termite activity, nitrogen fixation, and their potential significance of scale-dependency in predictive models of subcontinental gradients of biogeochemical cycling for carbon and nitrogen (Craine et al. 2009).

2. Materials and methods

2.1. Study site

The hot and dry valley of the Middle Zambezi River includes those portions of the river east of Victoria Falls and continuing for several hundred kilometers to the Cahora Bassa Gorge in Mozambique. Below the confluence of the Kafue River, the Zambezi meanders gently across a broad valley paralleling the escarpment of the Central African Plateau to its confluence with the Luangwa River (Davies, 1986; Coppinger

E-mail address: rundel@biology.ucla.edu.

http://dx.doi.org/10.1016/j.sajb.2015.08.019
0254-6299/

and Williams, 1994). Deciduous Zambezi thicket and dry forest, sharply distinct from the more widespread mopane and riparian woodlands and from miombo woodland communities on the slopes of the Central African Plateau, represents one of the community types that dominate the broad valley of the Middle Zambezi River between Kariba and the Cahora Bassa (Fanshawe, 1971; Guy, 1977, 1981; Dunham, 1989a; du Toit, 1993; Timberlake et al., 1993; Timberlake, 2000).

Field studies were carried out in April 2012 in stands of deciduous thicket located 1–4 km west of Lower Zambezi National Park in Zambia and at an elevation of about 380 m (15°43′ S, 29°19′ E). The study area was 1000–2000 m from the Zambezi River in an area of sandy colluvial and alluvial soils. The community, known locally as jesse vegetation (du Toit, 1993), forms a mixed-layered, dry shrubby woodland in the study area. It is dominated by a mix of spiny, thicket-forming deciduous shrubs and small multi-stemmed trees. It has no single dominant species in the study area and varies in composition along the valley. It is sometimes termed deciduous woodland or mixed shrubland and is largely restricted to the Zambezi and Luangwa River valleys where it covers as much as 10% of the area of the Middle Zambezi Valley (Poilecot and Gaidet, 2011). Under optimal growing conditions, this community may form a closed canopy woodland with a tree canopy up to 25 m above a layer of thicket-forming multi-stemmed species (Timberlake and Mapaure, 1992; du Toit, 1993; Timberlake et al., 1993). The thicket community in the study area merges gradually into riverine vegetation, having many species in common with gallery forest communities.

The primary vegetation on the extensive fine-textured sodic soils of the Middle Zambezi Valley is mopane woodlands, heavily dominated by *Colophospermum mopane* (Leguminosae, mopane), which form extensive pure stands on the valley floor and lower escarpment slopes (du Toit, 1993). Alluvial soils along the riverbank support riparian woodland characterized by large trees of species like *Kigelia africana*, (Leguminosae: Papilionoideae, sausage tree), *Garcinia livingstonei* (Clusiaceae, African mangosteen), *Ficus bussei* (Moraceae, Busse's fig), *Trichelia emetica* (Meliaceae, Natal mahogany), and *Philenoptera violacea* (Leguminosae: Papilionoideae, raintree). Monocultures of *Faidherbia albida* (Leguminosae: Mimosoideae, winterthorn) are widely present in areas of flood plains with secondary succession along the river (Dunham 1989a,b,c). Prior to the construction of the Kariba Dam in 1959, the floodplains of the river were subjected to strong seasonal floods at intervals of 2–3 years. Since the construction of the dam, major bank erosion and sand bank deposition are irregular but have continued to occur along the middle Zambezi River, promoting sandy floodplains along the river and transitory sand islands within the river channel with a dominance of *Phragmites mauritianus* (Attwell, 1970; Guy, 1977).

The deciduous Zambezi thicket in the study area is a semi-open stand of drought deciduous spiny shrubs and low trees typically 2–5 m in height, with occasional emergent trees. All of the dominant shrub and tree species in this community are relatively widespread in distribution. There are no weather records for the study area but mean annual precipitation is estimated to be about 500 mm. Kariba, about 220 km to the west in the Middle Zambezi Valley, has a good data record and receives a mean of 575 mm. Rainfall peaks in the summer months of December through February, while the dry season extends from April to October. The months of June through September are virtually without rain. Seasonal temperatures peak in October with mean daily high temperature of 36 °C and low temperatures of 24 °C, these fall to 27 °C and 12 °C, respectively, in July.

Extensive portions of the Middle Zambezi Valley are now protected. The south side of the Zambezi River in this area lying in Zimbabwe was declared as the Middle Zambezi Biosphere Reserve by UNESCO in 2010, with Mana Pools and Matusadona National Parks as core areas. The north side of the valley in Zambia includes Lower Zambezi National Park established in 1983 with extensive surrounding areas of game management. The landscape in this area slopes steeply from the escarpment of the Central African Plateau at elevations up to 1260 m down to the Zambezi almost 1000 m below. The park straddles southern miombo woodlands on the south-facing slopes and mopane woodlands on the gentle lower slopes of the valley.

2.2. Sample collections and analyses

Leaf samples were collected from 24 common species of deciduous thicket shrubs and trees at the field site (Table 1). The samples of current season mature leaves were collected from three individuals of each species in April 2012 at the end of the wet season and thus represent mature leaves not yet in senescent condition. Also noted were traits of plant height, spinescence, association with termitaria, and riverine distribution. Field observations were supplemented with information from the literature (White, 1962; African Plant Database, 2012; Bingham et al., 2012).

Air-dried samples of leaf tissue of all species with the exception of some of the microphyllous leaves were measured in the laboratory to determine leaf specific area in units of leaf area per unit dry weight as well as the inverse measure of leaf specific weight in units of mg cm^{-2}. Ground tissue samples for all species were analyzed for total nitrogen, total carbon, $\delta^{13}C$, and $\delta^{15}N$ by the Stable Isotope Analysis facility at the University of California, Davis. Samples were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Samples were combusted at 1000 °C in a reactor packed with chromium oxide and silvered copper oxide. Following combustion, oxides were removed in a reduction reactor (reduced copper at 650 °C). The helium carrier then flowed through a water trap (magnesium perchlorate) and an optional CO_2 trap (for N-only analyses). N_2 and CO_2 were separated on a Carbosieve GC column (65 °C, 65 mL/min) before entering the IRMS. The final delta values were expressed relative to international standards V-PDB (Vienna PeeDee Belemnite) and air for carbon and nitrogen, respectively. Values of total carbon and total nitrogen obtained from these analyses provided a means of calculating leaf N content (% dry weight), leaf nitrogen specific weight (mg N cm^{-2}), and carbon-to-nitrogen (C/N) ratio.

3. Results

Deciduous Zambezi thicket forms a distinctive community at the field site on deep alluvial soils of accumulated material deposited by erosion from the escarpment of the Central African Plateau to the immediate north. Unlike the southern bank of the Middle Zambezi River in Mana Pools National Park where there are extensive areas of flood plain soils covered by gallery forest and successional stands of *Faidherbia albida*, the north bank is dominated by a mosaic of mopane woodlands and deciduous Zambezi thicket. The thicket community at the study site can be readily distinguished in satellite images from miombo woodland on the escarpment slopes to the north, mopane woodlands to the west, and flood plain woodlands across the river in Mana Pools National Park (Fig. 1).

Many of the shrub and small tree species in the community are multi-stemmed from basal roots or root suckers. Although no single species dominates the community, five shrub species were particularly abundant, all typically 2–4 m in height. These were *Diospyros senensis* (Ebenaceae, spiny jackal berry), *Capparis sepiaria* (Capparaceae, wild caper bush), *Capparis tomentosa* (Capparaceae, wooly caper bush), *Acacia ataxacantha* (Leguminosae: Mimosoideae, flame acacia), and *Dichrostachys cinerea* (Leguminosae: Mimosoideae, sicklebush). *Friesodielsia obovata* (Annonaceae, northern dwaba-berry) is a semi-scandent or weak-stemmed low tree. *Combretum mossambicensis* (shaving brush combretum) and *Strophanthus kombe* (Apocynaceae, large-leaved poison rope) are climbers. Taller and emergent trees reaching up to 5–8 m or occasionally more included *Combretum erythrophyllum* (Combretaceae, river bushwillow), *Terminalia pruinoides*