The facilitative role of trees
in tree-grass interactions in savannas

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Thesis

submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
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Propositions

1. Understanding the role of soil organisms in mediating and sustaining nutrient transfer among plants, and between soil and plants is crucial for explaining tree-grass coexistence in savannas.

   (this thesis)

2. A comprehensive understanding of tree-grass interactions in savannas demands a broad, multitrophic approach rather than a narrow one based on Gaussian principles of competitive exclusion.

   (this thesis)

3. The fundamental tenet of natural resource economics and environmental economics is that all natural resources are substitutable or recyclable (Farley, J & R. Constanza, 2010, *Ecological Economics* **69**, 2060–2068) is flawed.

4. The notion of ecosystems being 'Natural Capital' and natural processes being 'Ecosystem Services'(Adams, W. M., 2014, *Science* **346**, 549–551) is fundamentally erroneous since such commodification of ecosystem and natural processes suggests that the natural world is otherwise worthless.

5. Arresting the unsustainable increase in human population is possible through reducing human fertility with modern contraception techniques and communication without religious and socio-political interference.

6. The distinction between freedom of action and freedom of will is that freedom of action is real and freedom of will is imaginary.

Propositions belonging to the Ph.D. thesis entitled:

'The facilitative role of trees in tree-grass interactions in savannas'

K. V. R. Priyadarshini

Wageningen, 24 May 2016

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GENERAL INTRODUCTION

Savannas represent one of the largest biomes of the world, comprising about 20% of the earth's land area (Shorrocks 2007, Huntley and Walker 2012). Most savannas occur in Africa occupying almost 50% of the land area of this continent that support not only a large fraction of its human population, rangelands and livestock, but also some of the highest densities and diversity of wild herbivores and carnivores in the world (Scholes and Archer 1997, Shorrocks 2007, Sankaran and Anderson 2009). Distinct dry seasons, highly variable inter- and intra-annual rainfall, fire and herbivory characterize savannas. A characteristic ecological feature of savannas is the co-existence of trees and grasses (Scholes and Walker 1993, Scholes and Archer 1997, Huntley and Walker 2012). The mechanisms that support tree-grass coexistence in savannas are not well understood. In this study, I examined tree-grass interactions in semi-arid and arid savannas to understand the ecological processes that may sustain tree-grass coexistence in dry savannas (< 800 mm of rainfall) of southern Africa.

TREE-GRASS INTERACTIONS IN SAVANNAS

Tree-grass interactions in savannas have long been viewed as that of intense competition for water and nutrients by these plants (Scholes and Archer 1997, Jeltsch et al. 2000, House et al. 2003, Sankaran et al. 2004) influencing the aboveground growth of both trees (Riginos 2009, February et al. 2013b) and grasses (Belsky 1994, Ludwig et al. 2004a). Therefore, the fundamental premise of all hypotheses is the concept of competition based on the Gaussian principle of niche or habitat differentiation (Schoener 1974). Furthermore, much of the research in savanna ecology seems to be focused on the subject of "Savanna-stability" (van de Koppel et al. 2002, Van Langevelde et al. 2003, Sankaran et al. 2005, Staver et al. 2011a, 2011b). Savanna stability refers to the conditions under which a *status quo* is maintained in the ratio of trees to grasses in savannas. However, minor changes occur from time to time but no large scale or irreversible changes are seen in the landscape (Scheffer et al. 2001). Savannas are said to become unstable when drastic biome shifts like desertification or conversion to a woodland or forest occur which are undesirable and can have high socio-economic and environmental costs (Rietkerk et al. 1996, Archer and Predick 2014,

Bestelmeyer et al. 2015). The causes cited for savanna instability range from the effects of climate change, human-interference (e.g. through suppression of fires, livestock grazing) resulting in increased or decreased tree densities that could either potentially competitively exclude grasses from savannas or lead to desertification (Dean et al. 1995, Van Langevelde et al. 2003, Sankaran et al. 2005, Buitenwerf et al. 2011). These biome shifts, also termed "regime shifts" are potentially economically undesirable changes to human kind (Scheffer et al. 2001, Folke et al. 2004, Kinzig et al. 2006). Consequently, much of the recent research is focused on landscape analysis, metadata analysis or modelling studies with much of the emphasis on the drivers that influence tree densities in savannas (Jeltsch et al. 2000, Van Langevelde et al. 2003, Sankaran et al. 2005, Bucini and Hanan 2007, Lehmann et al. 2009, Staver et al. 2011a, 2011b, Hirota et al. 2011, Dohn et al. 2013).

Several authors have proposed many hypotheses to explain tree-grass interactions in savannas. The most common and most debated concept invoked for tree-grass co-existence is the "Spatial-niche-separation" hypothesis based on the differences in rooting patterns of trees and grasses in savannas (Walter 1971, Belsky 1990, Scholes and Archer 1997, Sankaran et al. 2004, Scheiter and Higgins 2007). This hypothesis has both support (Knoop and Walker 1985, Aguiar and Sala 1994, Belsky 1994, Scholes and Archer 1997, Ludwig et al. 2004b) and arguments against it (Belsky 1994, Scholes and Archer 1997, Anderson et al. 2001, Ludwig et al. 2004a). Furthermore, studies seem to indicate a climatic influence in the way this hypothesis is manifest suggesting that niche separation might operate in drier areas but not in areas with a higher moisture content (Knoop and Walker 1985, Weltzin and Coughenour 1990, Belsky 1994, Weltzin and McPherson 1997, Ward et al. 2013). The "Pulse Reserve Hypothesis" proposes that the responses of different plant functional types to short but biologically relevant rainfall events (pulses) are different, for example, fast growth in grasses and slow growth in trees (Noy-Meir 1973, Ogle and Reynolds 2004, Reynolds et al. 2004).

Sankaran et al. (2004) reviewed the existing hypotheses that explain tree-grass interactions based on largely two aspects: the role of competition in tree-grass interactions and on demographic bottlenecks in the savanna tree ontogeny that potentially influence the densities of trees in savannas. The premise for the "demographic bottleneck" hypothesis is that a tree faces adverse conditions at different ontological stages of its life history, which may limit its growth and survival (e.g., competition with grass during the seedling stage, herbivory and fire). Sankaran et al. (2004) propose an integration of the "demographic

bottleneck" and "pulse reserve" hypotheses to explain tree-grass interactions in savannas. It is important to note that the significance of competitive exclusion in interspecific competition is increasingly being questioned since in many species rich communities, competitive exclusion has yet to be demonstrated (Hanski 1983, den Boer 1986, Walter 1988, Bengtsson et al. 1994). The role of resource storage in plants that play an important role in plant coexistence and competition (Chapin et al. 1990) is also poorly understood in savannas. Most hypotheses, except for the niche-separation hypothesis, focus on what controls tree and grass abundances at large spatial scales rather than the micro-level processes that occur at the level of an individual tree, which may potentially scale up to larger scales and control tree-grass coexistence in savannas (DeLucia et al. 2001, Gillson 2005, D'Odorico et al. 2010). However, there is a lack of understanding of the ecological processes that may be sustaining tree-grass coexistence at the single tree and the understory grass in savannas. Furthermore, the principal role of niche separation either spatially or through resource-use in tree-grass coexistence is yet to be demonstrated in savannas.

RESOURCE-USE AND TREE-GRASS INTERACTIONS

There are many examples where plants coexist using the same space and resources without outcompeting the other as a result of competition. Trees and grasses in savanna are such an example. However, this coexistence may be possible due to multiple mechanisms that operate in addition to competition, like resource partitioning, facilitation or differences in phenology (Schoener 1974, den Boer 1986, Walter 1991, Fargione and Tilman 2002, 2005, Callaway 2007). For example, how key resources like water and nutrients are used by plants, do they use the same resource or have complementary patterns in the way use these key resources? Therefore, resource-use patterns are an important aspect that will influence interactions among plants. Much of the tree-grass interactions have been evaluated largely with measurements of aboveground productivity and foliar nutrient contents (Casper et al. 2003, House et al. 2003, Ludwig et al. 2004a, 2004b). A few studies have used root trenching experiments and variation in stable isotopes to test root competition between trees and grasses; however, with ambiguous results suggesting both the absence (Knoop and Walker 1985, Weltzin and Coughenour 1990, Belsky 1994, Weltzin and McPherson 1997) and presence (Belsky 1994, Scholes and Archer 1997, Ludwig et al. 2004a, 2004b) of competitive effects of trees on grasses. Additionally, it has been shown that grasses also negatively influence tree growth (Riginos 2009, February et al. 2013b). Once again many questions have

been formulated on the basis of competition as the overriding interaction in trees and grasses in savannas and much less attention has been given to measuring tree-grass interactions or on the underlying operating mechanisms. For example, hydraulic-lift, a common phenomenon by which a tree supplies its canopy with water from the soil and could impact tree-grass interactions, has been shown to occur in almost all the biomes and identified to be in operation in almost 60 tree species worldwide (Prieto et al. 2012), but only a few studies have been carried out on savanna trees outside of North America (Burgess et al. 2000b, Scholz et al. 2002, Ludwig et al. 2003, Moreira et al. 2003, Bayala et al. 2008). Particularly in Africa, the studies are even fewer (Ludwig et al. 2003, Bayala et al. 2008). The way plants use resources substantially impacts their interactions (Schoener 1974, Chapin 1980, 1988, Connell 1983) and there is hardly any knowledge on resource-use patterns of trees and grasses in African savannas.

Trees form an important component of the savanna ecosystem and are reported to modify the under-tree-canopy environment (Vetaas 1992, Belsky et al. 1993a, Ludwig et al. 2004b). Under-tree-canopies are associated with higher soil N content, higher plant N content and lower evapotranspiration rates (Bernhard-Reversat 1982, Belsky et al. 1989, 1993a, Moyo et al. 2010). Trees influence ecosystem functioning through the capacity for nutrient and water redistribution which is the ecophysiological phenomena where trees access water and nutrients from deeper layers of the soil and move them to the upper soil profile making these resource available to shallow rooted plants (Bernhard-Reversat 1982, Burgess et al. 2000b, Jackson et al. 2002, Caylor et al. 2005, Lee et al. 2005, D'Odorico et al. 2007, 2010). This resource redistribution by trees potentially influences inter-plant interactions (Dawson 1993). The influence of plant physiology on inter-plant interactions and global biogeochemical cycles is only recently being recognized (DeLucia et al. 2001, D'Odorico et al. 2010). Also, the capacity of plants to use different forms of the same resource is overlooked in many of the savanna tree-grass coexistence models. An example is a study carried out in the arctic tundra which showed that the most productive plant species in this community, *Eriophorium vaginatum* (cotton grass), used the most abundant chemical forms of N which were glycine and ammonium, while the less productive species, *Carex bigelowii* (Bigelow sedge), used less abundant forms of N which was nitrate, indicating partitioning of differentially available forms of the same limiting resource indicating niche diversification in this arctic tundra community (McKane et al. 2002). The capacity of trees to utilize the tightly bound immobile water in the soil making this available to other plants is another example

(Brooks et al. 2010). These phenomenon are not yet known for savanna plants. Trees in savannas play a multifunctional role in the management of soil quality, and contribute to animal and human welfare. Presently, an alarming decrease in tree densities in human-use landscapes in savannas is being reported with negative repercussions on land quality (Muchena et al. 2005, Manning et al. 2006). By influencing water and nutrient cycles, trees can play a key role in better and sustainable natural resource management of land resources in savannas. The principal aim of this thesis is to understand tree-grass coexistence in African savannas, whether resource-use patterns of trees and grasses can explain tree-grass co-occurrence, and implications thereof to land-use management.

OUTLINE OF THE THESIS

In this thesis, I investigated the resource-use patterns in trees and grasses in a semi-arid savanna in South Africa. Additionally, I examined the effects of competition between trees and grasses on resource storage in perennial grasses in arid and semi-arid savannas of southern Africa. Further, I reviewed the knowledge status of resource use patterns of trees and grasses in savannas and discussed how these interactions can be exploited for better management of human-land-use systems in Africa.

Savanna systems are characterized by water limitation. Trees in savannas have been shown to hydraulically lift water to their canopy (Ludwig et al. 2003, Bayala et al. 2008). Hydraulic lift is the process of upward flow of water within a plant as a result of pressure differences caused by either transpiration during the day time or dry soil layers in the nighttime (Caldwell and Richards 1989). In Chapter 2, I report on my investigations of hydraulic-redistribution (the phenomena of upward, downward and lateral flows of water) by savanna trees to grasses and whether this phenomenon is advantageous to under-tree canopy perennial grasses. Additionally, I elaborate whether hydraulic-redistribution occurs throughout the year and if savanna trees with different functional characteristics show hydraulic-redistribution.

Nutrient resources are finite in most ecosystems, especially in savannas where the soils are very low in N content. The access to nutrients and the way plants use them would be key for survival, growth and reproduction. In Chapter 3, I report the outcome of investigation on the N sources for trees of different functional characteristics (described in the previous section) and grasses. Additionally, I report on the experiment that I carried out to assess

whether trees redistributed N from deep soil sources to the grasses and any seasonal influence on this redistribution.

Much of the research in tree-grass interactions in savannas has focused on responses of aboveground parts. However, belowground storage organs are vital for a plant's growth, survival and reproduction. This information is lacking for savanna grasses. Studies suggest that plants respond to competition and resource limitation by increasing allocation of resources to storage organs (Bloom et al. 1985, Busso et al. 1990, Chapin et al. 1990, Oosthuizen and Snyman 2003, Craine 2006, Snyman 2009). In Chapter 4, I report on the effects of competition between trees and grasses on root storage in perennial grasses occurring South African savannas with differences in rainfall. The underlying hypothesis for this work was that competition from trees and less rainfall will result in higher root storage in understory perennial grasses.

In Chapter 5, I explore the role of exploiting inter-plant interactions, in particular tree-grass interactions from the findings of the previous chapters applied to human-land-use systems. I illustrate the significant role of trees in dry savannas based on nutrient and water-redistribution capabilities of savanna trees, and provide an ecological perspective of the role of trees in two human land-use types in African drylands: agroforests and rangelands which include silvo-pastoral systems and mixed-game-livestock farming systems. I evaluate the causes for the loss of trees in these land-use types highlighting the role of trees for better land and sustainable natural resource management.

Finally, I synthesize the conclusions drawn from the preceding chapters in Chapter 6 and put the findings in the broader context of the role of trees, eco-physiology and inter-plant interactions for the coexistence of plants with resource limitations.

SEASONALITY OF HYDRAULIC-REDISTRIBUTION BY TREES TO GRASSES AND CHANGES IN THEIR WATER-SOURCE USE THAT CHANGE TREE-GRASS INTERACTIONS

K. V. R. Priyadarshini, Herbert. H. T Prins, Steven de Bie, Ignas. M. A. Heitkönig, Stephan Woodborne , Gerrit Gort, Kevin Kirkman, Fulco Ludwig, Todd E. Dawson, Hans de Kroon

ABSTRACT

Savanna vegetation is characterized by tree-grass co-existence that can experience intense water limitation, yet the water relations of these savanna plants are poorly understood. We examined the water-sources for trees and grasses in different seasons and investigated the importance of hydraulic-redistribution in three tree species inhabiting a semi-arid savanna in South Africa. We used natural variation in H and O stable isotope composition of source waters to identify the principal water-sources for these plants. We conducted an experiment by labelling deep-soil (2.5 m depth) with a deuterium tracer. Seasonal differences in the stable isotope composition of water in trees and grasses indicated that there was water-source use partitioning as well as overlap. Trees and grasses used water from the topsoil after rainfall indicating overlap of water-source use. All tree species shifted to groundwater or subsoil water-use when there was no water in the topsoil indicating partitioning of water-use. Grasses always used water from the topsoil. The seasonal changes in water-source use by trees and grasses indicated possible shifts in tree-grass interactions during different periods of the year. The tracer experiment confirmed hydraulic-redistribution in all the three tree species and water transfer to grasses via the topsoil. However, this occurred only in the dry-season. Our observations and experimental results indicate the potential for facilitation affects by trees to their understory grasses and show that dry season hydraulic-redistribution from trees to grasses could be an important facilitative mechanism maintaining tree-grass co-existence in savannas.

Keywords: Tree-grass interactions, water- source use, water stable isotopes, ^{2}H stable isotope tracer labelling, semi-arid savannas, hydraulic-redistribution, Andover Game Reserve, savanna trees

INTRODUCTION

Savanna vegetation experiences periods of intense water limitation that may lead to plant water stress. Savannas are also characterized by tree-grass co-existence (Scholes and Archer 1997, Shorrocks 2007, Huntley and Walker 2012) and the physiognomy of savannas may range from tree dominated savannas to grass dominated ones largely determined by the rainfall (Sankaran et al. 2005). The co-existence of trees and grasses has long been reported to lead to intense competition for water by these plants influencing the above-ground growth of both trees and grasses (Belsky 1994, Ludwig et al. 2004a, Riginos 2009, February et al. 2013b). Water relations of the trees and grasses that inhabit savanna ecosystems are still not fully understood. Water availability in savannas changes significantly with seasons (a 10 fold increase in topsoil moisture from dry to wet season) leading to seasonal water limitations. This in turn is predicted to influence the water-related interactions of trees and grasses in time and space. Walter's two layer model for savannas suggests that for trees and grasses to co-occur, trees are expected to use deep sources of water while grasses use shallow sources (Ward et al. 2013). Landscape level analyses suggest that trees may be facilitating understory grasses particularly in water limited environments (Dohn et al. 2013, Moustakas et al. 2013, Ward et al. 2013). The suggestion of tree-to-grass facilitation is based on assessing understory biomass and nutrient content, with higher plant biomass or nutrient content under the tree-canopy implying facilitation by trees. However, increased biomass or nutrient content may result from other processes as well, such as an increase in the rates of mineralization leading to higher soil nutrient content as a result of greater litter fall under trees compared with areas outside of tree crowns (Bernhard-Reversat 1982, Callaway et al. 1991, Belsky et al. 1993a, 1993b, Rhoades 1996, Ludwig et al. 2001). Additionally, the potential for the existence of hydraulic-lift in savanna trees has been suggested to be a viable mechanism by which facilitative processes may occur (Ludwig et al. 2004a, Dohn et al. 2013). Despite many studies, neither Walter's two-layer hypothesis, nor the demonstration of facilitation by one plant type towards the other has been clearly demonstrated. Hydraulic-redistribution has been shown in trees spanning temperate (Peñuelas and Filella 2003, Zou et al. 2005, Kurz-Besson et al. 2006), neo-tropical (Scholz et al. 2002, 2010) and Australian savannas (Burgess et al. 1998, 2000b, Armas et al. 2012) and recent reviews show a growing number of examples (cf. Prieto et al., 2012, Neumann and Cardon 2012, Sardans and Peñuelas 2014). However, in Africa, hydraulic-lift has been shown to occur only in a few tree

species (Ludwig et al. 2003, Bayala et al. 2008) and the consequent transfer of water due to hydraulic-redistribution to neighbouring plants, in particular, understory grasses has yet to be conclusively demonstrated.

The occurrence of extreme water limitation in savannas, caused by seasonality and recurring droughts may influence tree-grass interactions. Also, positive and negative interactions between plants may shift with changes in the environment and their growth related requirements (Callaway et al. 1991, Holmgren et al. 1997, Kikvidze et al. 2006). The possible shifts in resource use, particularly water-use, have largely been overlooked in tree-grass interactions. It is well documented that in water limited ecosystems, plants show spatial, seasonal and temporal variation in the water-sources they use (Dawson 1998, Scholz et al. 2002, Lee et al. 2005). Co-occurring tree species can also have different hydraulic-redistribution patterns and may use a range of water-sources which may in turn influence the tree's interactions with its understory grasses (Espeleta et al. 2004, Meinzer et al. 2007). The redistribution of water within and among plants is also known to mitigate the effects of water deficits and stress (Bauerle et al. 2008). Recent data suggest that hydraulic-redistribution can be a much more complex process than previously understood. For instance, the complex source-sink system for water-flow exists not only between plant-soil interface but also within the plant that in turn is influenced by a complex set of factors (Prieto et al., 2012, Sardans and Peñuelas 2014 and references therein).

Using the natural abundance stable isotope composition of water extracted from plant tissues, we determined the water-source use of different co-occurring semi-arid savanna tree species and their understory grasses. We also injected a deuterium (^{2}H) label into deep-soil to serve as tracer to investigate if all the tree species in our study showed hydraulic-redistribution and if there were seasonal changes in hydraulic-redistribution. Our central hypothesis is that competition between trees and grasses is expected to occur if they used the same water-source during a time of water limitation and partitioning was likely if they used different water-sources in the same seasons. A second and related hypothesis is that significant redistribution of deep water sources by the trees to the grasses has potential for facilitation effects on the grasses.

MATERIALS AND METHODS

Study site

The study was carried out in the 7100 ha Andover Game Reserve (Andover GR), South Africa, located between 24° 33' S and 24° 38' S, and 31° 10' E and 31° 17' E. The annual rainfall is 550– 650 mm (Cronje et al. 2008) and the precipitation occurs in summer, starting in the dry-wet transition season (Oct/Nov), and ending in the wet-dry transition season (Mar/April/ May; Fig. 2.1).

Andover GR is a broad-leaved savanna. The grass community is diverse but under-tree canopy plant cover is a near monoculture of *Panicum maximum* (Jacq.). We used the understory grass *P. maximum* and three commonly found co-occurring savanna tree species in southern Africa for our study. We used the broad-leaved deciduous tree species *Terminalia sericea* (Roxb.), broad-leaved semi-deciduous tree species *Philenoptera violacea* (Klotzsch) Schrire, and fine-leaved deciduous tree species, *Vachellia nilotica* (L.) Delile (formerly *Acacia tortilis*). No grazing by ungulates occurred under any of our study trees throughout the study.

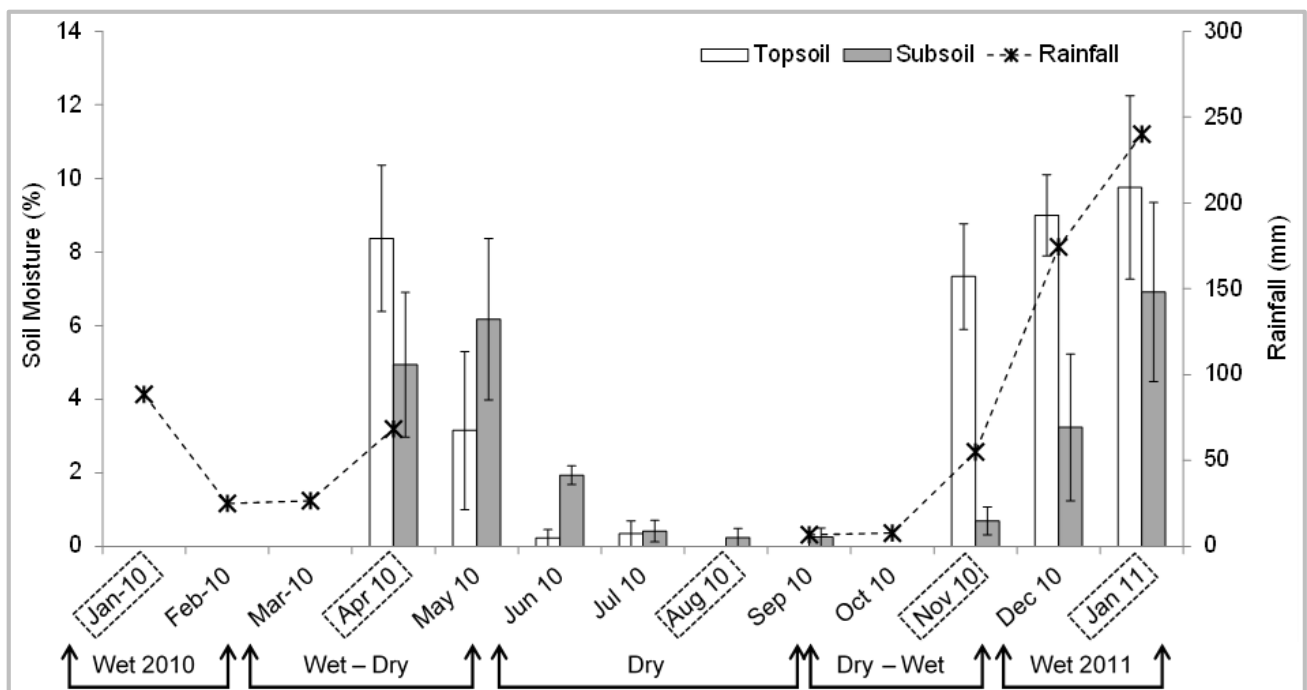Fig 2.1. Monthly volumetric soil moisture content (%) in the topsoil and subsoil on the primary Y-axis, and the distribution of rainfall on the secondary Y-axis, in Andover Game Reserve, South Africa. The months of sampling and labelling with the stable isotope tracer are indicated on the X-axis by dashed-line boxes. Soil moisture of Jan to Mar 2010 and Oct 2010 is not available. Error bars represent ± 1SEM for the soil moisture.

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Experimental set up

We conducted a fully factorial experiment on long, sandy crest tops. Five sets of paired experimental and control trees were identified for each of the tree species. Each pair was located within a small localized area within the larger study area. The control trees were located 30 m away from the experimental trees to prevent spreading of the ^{2}H isotope tracer between trees (Ludwig et al. 2003, Sternberg et al. 2004, Kulmatiski et al. 2010). The tree trunk diameter at 0.3 m height of the *V. nilotica* tree species ranged from 0.52 to 0.97 m, while that of *P. violacea* ranged from 0.55 to 1.05 m, and for *T. sericea* from 0.51 to 0.63 m. All trees in the study were fully grown adult specimens and were estimated to be more than 30 years of age. Grass samples were collected from under-tree canopy within circular plots of 1m radius with the tree trunk as the centre. We used a repeated-measures design where the same individual trees and the same grass plots were sampled repeatedly during different seasons.

Measurement of soil-moisture

One tree of each tree species was fitted with one automatic logger (H21-002, Hobo Micro station logger, Hobo-Onset Computer Corp., Bourne, Massachusetts, USA) attached to two soil-moisture sensors (S-SMC-M005, Hobo-Onset Computer Corp., Bourne, Massachusetts, USA) with the first in the topsoil (0.25 m) and second, in the subsoil (2.5 m) layers with a 15 min sampling frequency. The mean per-cent monthly volumetric soil-moisture content in the top and subsoil layers were calculated for the three species.

Use of stable isotopes

We used the natural variation in the H and O stable isotope composition of water on the site in combination with the addition of an enriched ^{2}H stable isotope tracer to first characterize the water-sources used by the different plants at the site and secondly to track water movement in plants without the complication of isotope fractionation (Moreira et al. 2000, 2003, Gebauer and Ehleringer 2000, Grieu et al. 2001, Brooks et al. 2002, Peñuelas and Filella 2003, Kulmatiski et al. 2010). Isotope values are expressed using the delta, "δ", notation which represents the difference between the isotope ratios of the measured sample relative to the international (IAEA) water standard Vienna Standard Mean Oceanic Water (VSMOW). The δ value is calculated as:

δ = [(R$_{SAMPLE}$/R$_{STANDARD}$) − 1] *1000

where $R_{SAMPLE}/R_{STANDARD}$ represents $[(^{18}O/^{16}O)$ SAMPLE $/ (^{18}O/^{16}O)$ STANDARD] for oxygen and $[(^{2}H/^{1}H)$ SAMPLE $/ (^{2}H/^{1}H)$ STANDARD] for hydrogen.

The Local-Meteoric-Water-Line: $\delta^{18}O$ and $\delta^{2}H$ in rain and ground water

The Local-Meteoric-Water-Line (LMWL) is the linear relationship between the H and O stable isotope composition of precipitation collected at our site (Craig 1961). We constructed the LMWL for our study site by collecting precipitation samples periodically during the study period during rain events. We then used the variation in plant water $\delta^{18}O$ and $\delta^{2}H$ values relative to the LMWL to explain the differences in water-source use (following Dawson and Simonin 2011). Groundwater was collected from five different boreholes within a 15 km radius of the study site and two were sampled during the dry and wet seasons to assess seasonal variability in stable isotope ratios of borehole water. The stable isotope ratios of O and H in our ground water samples did not differ between dry and wet seasons (paired sample t-tests; for $\delta^{18}O$: $t = 2.470$, $P = 0.132$, $df = 2$, mean difference ($\pm 1SE$) $= 0.708$ (± 0.44); for $\delta^{2}H$: $t = -0.112$, $P = 0.921$, $df = 2$, mean difference ($\pm 1SE$) $= 0.954$ (± 0.19)).

Application of $^{2}H_{2}O$ as a tracer

The deeper rooting zone around each of the experiment trees at a depth of 2.5 m was dosed with deuterium-labelled water ($^{2}H_{2}O$; Icon Services New Jersey, USA) at $\approx 100\%$ atom-% abundance of ^{2}H. Application of the isotope tracer was done via PVC tubes of 15 mm diameter that were installed vertically in the soil to a depth of 2.5 m in four cardinal directions at 1 m distance from the base of each experimental tree (following Lehmann et al., 2001). A 15 ml volume of the labelled water was added through each tube totalling 60 ml of the tracer for each tree. This was sufficient to spike the system with high abundance of ^{2}H without the effects of irrigating the plants since very little water was added (Lehmann et al. 2001).

We confirmed that a depth of 2.5 m was well below the grass rooting depth by coring grass tufts of *P. maximum*. We did not find grass roots below 100 cm. Injection tubes extended 10 cm above the soil and were sealed with nylon plugs before and after application of the tracer solution. The tubes were installed in the first week of October 2009 before the start of the wet season. Application of the ^{2}H tracer started in January 2010, after a substantial amount of rainfall. No tubes were installed around control trees and to test whether this affected the results we compared the stable isotope ratios between the experimental and control trees before

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commencing the tracer application. We did not find statistically significant differences in the stable isotope ratios (paired sample t-test; $^{18}O_{(tree)}$: $t = -1.048$, $P = -0.312$; $^{18}O_{(grass)}$: $t = 0.224$, $P = 0.826$; $^{2}H_{(tree)}$: $t = 0.725$, $P = 0.480$; $^{2}H_{(grass)}$: $t = -0.639$, $P = 0.533$) between experimental and control trees.

Applications of $^{2}H_2O$ were done during the wet season in Jan 2010, the wet-dry transitional season in April 2010, dry season in Aug 2010, dry-wet transitional season in Nov 2010 and wet season in Jan 2011 (Fig. 2.1).

Sampling of plant material

Six to eight suberized twigs, 2.5 cm in length, from the terminal ends of the tree branches were collected from all cardinal directions of the tree upper canopy ensuring all parts of the upper canopy were represented for each tree. These twigs were composited into a single sample for each tree. Non-green basal parts of the *P. maximum* grass tuft and roots of the grasses in the grass plots were collected from all cardinal directions around the tree trunk. These were composited into a single sample to represent the understory grass for that tree. The xylem water extracted from these plant parts represents the source water taken-up by plants from the soil where roots are functionally active because there is no fractionation of water by plant roots during the uptake process (Dawson and Ehleringer 1993). All samples were immediately placed in borosilicate air tight bottles (Glass Blowing Industries, South Africa) and sealed with Para-film to prevent evaporation. These were frozen (temperature range between $-12^{o}C$ to $-18^{o}C$) until laboratory analysis could be carried out (within 4-6 weeks of sampling). Sampling was carried out during Jan 2010 (wet season 2010), April 2010 (wet-dry transition), August 2010 (dry season), November 2010 (dry-wet transition), and Jan 2011 (wet season 2011, Fig. 2.1). Plant material was sampled each season before labelling with $^{2}H_2O$ to find if there was any residual tracer from the previous seasons stable isotope tracer application and these samples constituted the "pre-spike" samples. Tracer labelling was done immediately after pre-spike samples were collected. Samples from trees where labelling with $^{2}H_2O$ was not done constitute "control" samples and samples taken from trees labelled with $^{2}H_2O$ constitute "spike" samples. The control and spiked samples were collected concurrently one week after $^{2}H_2O$ labelling. Tree and grass samples were always collected concurrently.

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Determination of stable isotope ratios

All stable isotope analyses were carried out at the stable isotope laboratory of the CSIR, South Africa. Plant water was extracted from the plant tissues using a cryogenic vacuum distillation apparatus (Ehleringer and Dawson 1992). The extracted water was analysed for δ^2H and δ^{18}O using a TC/EA pyrolysis system coupled with a Delta V plus mass spectrometer using a Conflo IV interface (Thermo Electron Corporation, Bremen, Germany). Six aliquots were measured for each sample and the analyses that showed any evidence of drift (sample-to-sample memory effects) were rejected. Special attention was given to samples from the tracer experiment to ensure that the results were not affected by memory/carry-over effects between samples during the analysis. Any samples that showed signs of memory effects were reanalysed. On the TC/EA system a set of 6 known value standards were run at the start of each batch analyses and then after every 40 unknown samples. An internal laboratory standard was run after every 10 unknown samples. The samples were standardized to VSMOW. The precision was < 0.2‰ for both O and H.

Statistical analysis and data transformations

We used mixed linear models to separately analyse δ^2H and δ^{18}O values using the SAS software program version 9.2 (Littell et al. 2006). For the analysis of H, the fixed part of the model contained all the main effects and interactions of the four factors 1) group (pre-spike, spike, and control); 2) tree species (*V. nilotica*, *P. violacea*, and *T. sericea*); 3) plant functional type (grass and tree); and 4) season (wet 2010, wet-dry, dry, dry-wet, wet 2011). Although we used a single statistical model, the analysis itself was split into three parts: (1) natural abundance (controls) to distinguish between shallow and deep-soil water-source for plants, (2) effect of tracer application by comparing spike and control measurements to determine redistribution of the tracer by trees to grasses, (3) effect of residual tracer from the previous season by comparing pre-spike and spike measurements to ascertain if any of the isotope tracer still occurred in the tree from the previous season and whether any redistribution occurred like in (2). For the analysis of O, we excluded the measurements obtained after spiking with ^{2}H$_2$O tracer.

We transformed data of δ^2H and δ^{18}O before further analysis as their distributions were highly skewed (ranging from –73 to 30,500 ‰ for δ^2H and –13 to 40 ‰ for δ^{18}O). We applied Box-Cox transformations using the transformation function:

f(OR) = (OR^P–1)/p, with OR = (R$_{SAMPLE}$/R$_{STANDARD}$),

where the power *'p'* was optimized using PROC TRANSREG of SAS by fitting fixed effects models to the transformed odds ratio. The transformed responses are equal to "0" if the sample's isotopic value equals the standard's, and positive (or negative) if the sample had a higher (or lower) value than the standard's, similar to δ^2H or $\delta^{18}O$. The power $p = -10$ was chosen for hydrogen, and $p = -75$ for oxygen. More details of data transformations and the mixed linear model are presented in Appendix 2.1. We checked the studentized residuals from the fitted mixed linear models for approximate normality and constant variance.

RESULTS

Volumetric soil-moisture of top and subsoil layers under three savanna tree species

There was no moisture in the topsoil from June 2010 to Sep 2010 (Fig. 2.1) and no measureable subsoil (at 2.5 m depth) moisture under *P. violacea* and *T. sericea* during this same period and only small amounts (less than 2%) were recorded at depth under *V. nilotica* (Appendix 2.2). There was about 7-8% soil-moisture, corresponding to about 60 mm of rainfall, in Oct/ Nov 2010, the dry to wet transition season (Fig. 2.1). The % soil-moisture also seemed linked to the quantity of rainfall (Fig. 2.1). We identified the dry and dry-wet transitional seasons as the two periods of water limitation.

Natural abundance of $\delta^{18}O$ and δ^2H in trees and under-canopy grass

The $\delta^{18}O$ and δ^2H values of all under-tree canopy grasses and trees plotted below the LMWL during all seasons; this indicated evaporative enrichment and subsequent uptake of soil-water by the plants (Fig. 2.2). We found significant interactions between plant functional type and season for both $\delta^{18}O$ and δ^2H indicating strong seasonal differences in water-source use by the grasses and trees (Table 2.1, Fig. 2.2). There were no tree species differences. The isotope values that we obtained for both trees and grasses showed a concurrent seasonal decrease and increase respectively (e.g., the lower values for trees and higher values for grasses). The exception to this pattern was seen during the dry season when the grasses showed a decrease
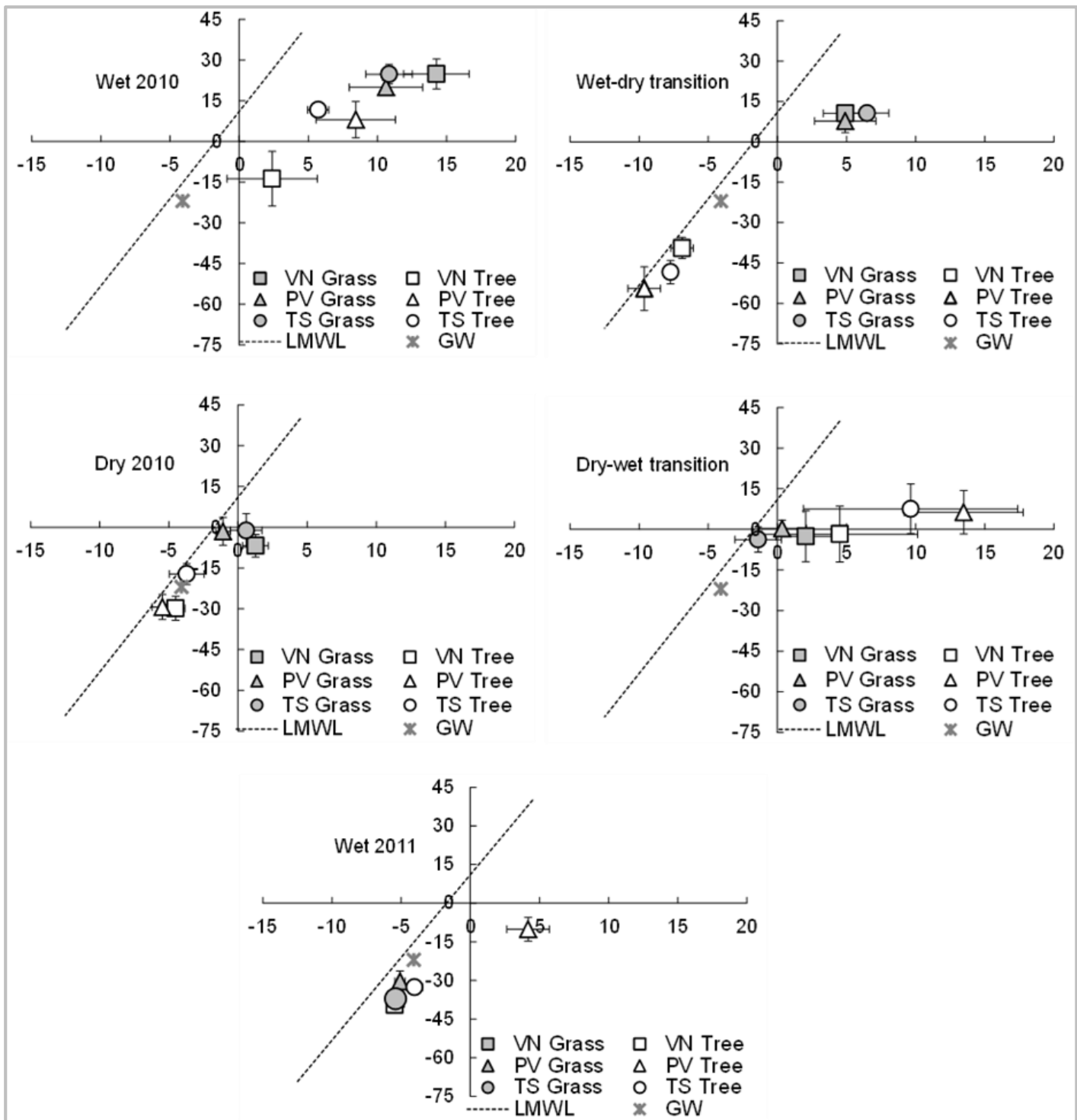
Fig. 2.2. Seasonal variation in the mean of $\delta^{18}O$ (‰) and δ^2H (‰) of different species of trees and the corresponding under-canopy grass *Panicum maximum* at Andover Game Reserve, South Africa. The X-axis represents $\delta^{18}O$ (VSMOW) of measured data and the Y-axis represents δ^2H (VSMOW) of measured data. Error bars represent ± 1SEM of the measured data and not calculated from mixed models. "VN Grass" represents *Panicum maximum* grass under *Vachellia nilotica* and "VN Tree" represents *Vachellia nilotica* tree; "PV Grass" represents *Panicum maximum* grass under *Philenoptera violacea* and "PV Tree" represents *Philenoptera violacea* tree; "TS Grass" represents *Panicum maximum* under *Terminalia sericea* and "TS Tree" represents *Terminalia sericea* tree; and "LMWL" represents the Local Meteoric Water line and GW represents the Ground Water for Andover Game Reserve, South Africa.

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Table 2.1. Summary of analysis of variance for natural abundance using repeated measures mixed linear models for stable isotope ratios of Oxygen and Hydrogen. The F-tests for hydrogen were extracted from a larger mixed model, focusing on the control trees only. The F-tests for natural abundance of oxygen were based on pre-spike and control data. The analysed responses are Box-Cox transformed Odds Ratios.

Effects	^{18}Oxygen			^{2}Hydrogen		
	F	*P*	*DF*	*F*	*P*	*DF*
Tree species	1.97	0.1814	2, 12	1.52	0.2606	2, 11
Plant functional type	61.29	<0.0001*	1, 27	100.40	<0.0001*	1, 22
Season	137.91	<0.0001*	4, 210	75.29	<0.0001*	4, 286
Species x Plant functional type	7.52	0.0025*	2, 27	1.85	0.1808	2, 22
Species x Season	8.40	<0.0001*	8, 210	3.19	0.0018*	8, 286
Plant functional type x Season	99.95	<0.0001*	4, 210	38.27	<0.0001*	4, 286
Species x Plant functional type x Season	6.31	<0.0001*	8, 210	1.75	0.0866	8, 286

$P<0.05$

(5.2‰ for δ^{18}O and 12.8‰ for δ^{2}H) and trees showed an increase (3.5‰ for δ^{18}O and 21.9‰ for δ^{2}H) from the preceding wet-dry transition. During the wet-dry transition, trees had the lowest δ^{18}O and δ^{2}H values (Fig. 2.2), suggesting that they were using a deep-soil water-source (Fig. 2.2). The δ^{18}O and δ^{2}H values of all three tree species were the highest during the dry-wet transition suggesting that trees shifted to using a shallow soil water-source during this period.

The dry season values were higher than those of the wet-dry transition but remained near groundwater values (Fig. 2.2).

Tracer experiment: hydraulic-redistribution in trees and transfer of water to understory grass

The addition of ^{2}H$_{2}$O increased the δ^{2}H values from plants in the spiked plots compared with control plants averaged over all groups ($P < 0.0001$; Table 2.2). These differences, however, were neither constant over time ($P < 0.0001$; Table 2.2) nor were they similar for grasses and trees over time ($P = 0.0018$; Fig. 2.3A). There were no tree species differences and the pattern of change in tree δ^{2}H over time remained similar for all groups (controls, spike and pre-spike, Fig. 2.3A and B). The differences between these groups were small except for the wet season of 2011 where spike tree showed the highest values (Fig. 2.3).

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Table 2.2. Summary of analysis of variance for the difference in stable isotope ratio of Hydrogen between spiked and pre-spike groups, spike and control groups, and pre-spike and control groups. The F-tests for the differences were extracted from a larger mixed linear model. The analysed responses are Box-Cox transformed Odds ratios.

Effects	Spike Vs Pre-spike			Spike Vs Control		
	F	P	DF	F	P	DF
Tree species	1.20	0.303	2, 286	2.33	0.099	2, 286
Plant functional type	4.66	0.0320*	1, 286	1.16	0.230	1, 286
Season	8.95	<0.0001*	4, 286	12.70	<0.0001*	3, 286
Species x Plant functional type	0.00	0.200	2, 286	0.01	0.200	2, 286
Species x Season	1.60	0.123	8, 286	1.56	0.135	8, 286
Plant functional type x Season	1.72	0.1460	4, 286	4.41	0.0018*	4, 286
Species x Plant functional type x Season	1.24	0.2747	8, 286	0.36	0.9423	8, 286

*$P<0.05$

Table. 2.3. Summary of comparisons of differences in least square means of $\delta^2 H$ as obtained from the repeated measures mixed linear model. The term "ftype" indicates the plant functional type.

Group comparisons		Differences between LS Means (± 1SEM)	P	T
Spike Versus Pre-spike				
Wet 10 (season)		0.002 (± 0.003)	0.650	− 0.46
Wet-dry transition (season)		0.009 (± 0.004)	0.030*	− 2.12
Dry (season)		0.018 (± 0.006)	0.005*	− 2.82
Dry-wet transition (season)		− 0.007 (± 0.003)	0.0391*	2.07
Wet 11 (season)		0.020 (± 0.003)	<0.0001*	− 5. 69
Spike Versus Control				
Wet 10 (ftype x season)	Grass	0.005 (± 0.004)	0.257	1.14
Wet-dry transition (ftype x season)	Grass	0.001 (± 0.003)	0.761	0.30
Dry (ftype x season)	Grass	0.059 (± 0.012)	<0.0001*	4.79
Dry-wet transition (ftype x season)	Grass	0.001 (± 0.005)	0.854	0.18
Wet 11 (ftype x season)	Grass	0.018 (± 0.004)	<0.0001*	4.38
Wet 10 (ftype x season)	Tree	0.002 (± 0.006)	0.730	0.34
Wet-dry transition (ftype x season)	Tree	0.011 (± 0.009)	0.191	1.31
Dry (ftype x season)	Tree	0.017 (± 0.005)	0.0003*	3.69
Dry-wet transition (ftype x season)	Tree	− 0.002 (± 0.006)	0.696	− 0.39
Wet 11 (ftype x season)	Tree	0.035 (± 0.006)	<0.0001*	6.04

*$P<0.05$
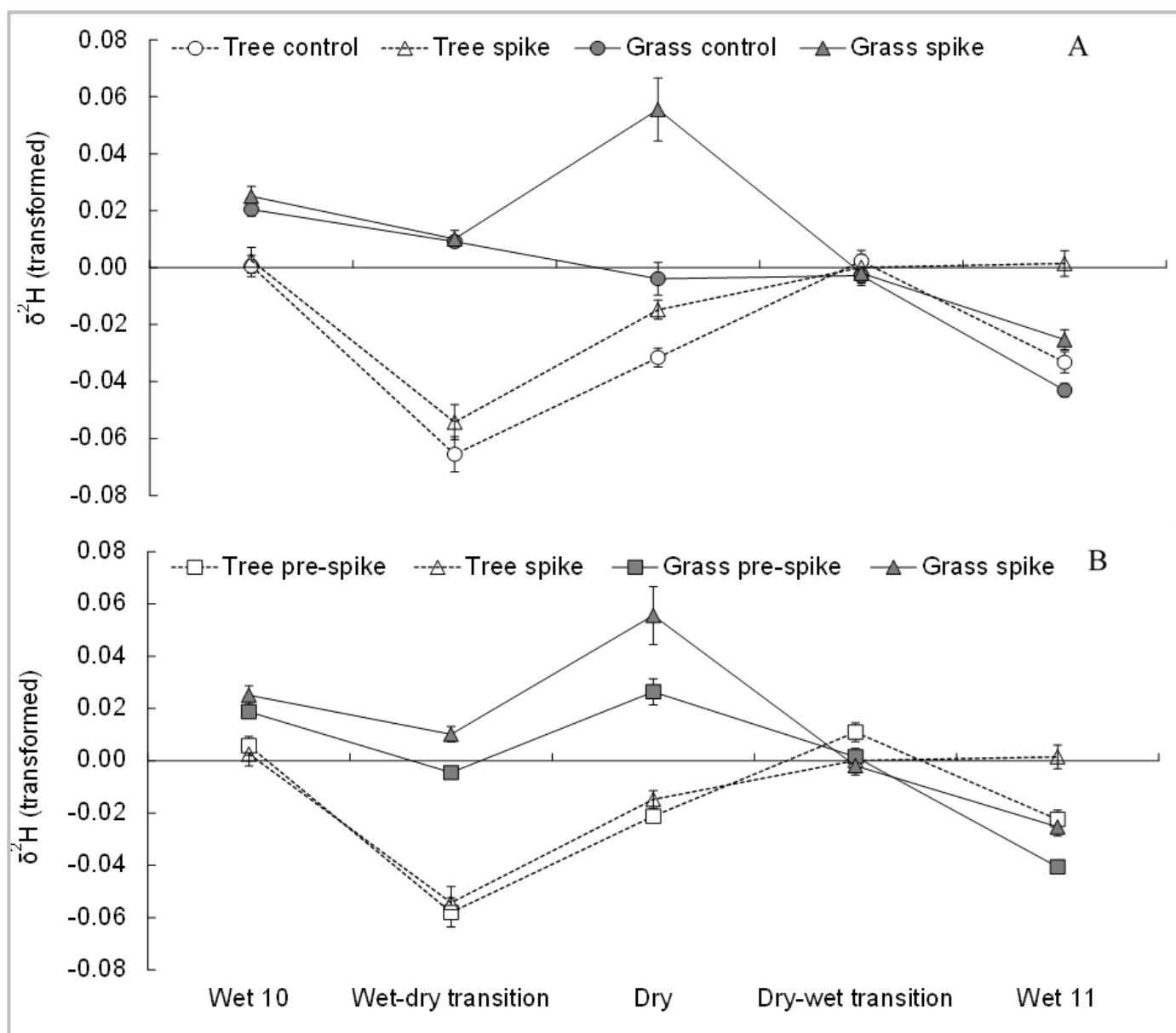
Fig. 2.3. Seasonal variation in the least square estimated means of δ^2H in A) Control and Spiked trees and their under-canopy grass, and B) Pre-spiked and spiked trees and their under-canopy grass at Andover Game Reserve, South Africa from a repeated measures mixed linear model. The least squares means are of transformed data. The open symbols are trees and filled symbols are grass, squares represent pre-spike, triangles represent spike and circles represent controls. The error bars are ±1SE of the least-square means.

Further, there seemed to be a gradual, albeit small, increase in $\delta^2 H$ in the spiked trees. This suggests that the tracer taken up over time was probably diluted with either stored tree-water or other sources of water taken up by the tree. Similar levels of dilution has been observed in other studies also (Peñuelas and Filella 2003, Kulmatiski et al. 2010). Therefore, despite the highly concentrated tracer that we used, the effect of tracer uptake on the tree was significant but small (Fig. 2.3B). This was in contrast to the grasses which showed extreme changes when the tracer was taken up (see below and Fig 2.3). We also found that there was no residual tracer in the pre-spike samples of grasses whose values lay within the natural range (dry season average for grasses was found to be the highest with a value of 18.79‰). Therefore, the previous season's tracer label did not interfere with the tracer experiment. The differences between pre-spike and control samples were largely due to the gap in sampling as pre-spike samples were collected 7-10 days prior to control sample (detailed results are presented in Appendix 2.3: Tables 2.3.1 and 2.3.2).

For grasses, the extremely high ^2H value of the spiked grass that we obtained during the dry season contrasted with not only the tree values but also with control and pre-spiked groups. This indicated the presence of the tracer in the grasses. The high $\delta^2 H$ tree value seen during the wet season of 2011 did not result in high $\delta^2 H$ values in the grasses. This shows that despite statistically significant differences, the $\delta^2 H$ grass values during this season were not high enough to indicate the presence of tracer in them. Additionally, the least-square mean differences were largest for grasses during the dry season indicating uptake of the tracer only in the dry season. Similar patterns over time were found in the spiked–pre-spiked comparison (Table 2.2; Fig 2.3B), with grasses showing on average larger differences than trees ($P = 0.0317$). This interaction was also mainly driven by what happened during the dry period, where the spiked–control difference was extremely large for grasses, but much less for trees (Table 2.3). These results suggest efflux of the tracer by tree roots to the surrounding soil where it was taken up by grasses. No main effects of, or interaction with, tree species were found for all sets of comparisons.

DISCUSSION

Our results show clear seasonal differences in water-source use by trees and grasses. Grasses used water from the topsoil during all seasons. All tree species were similar in their water-source use and were opportunistic by using shallow soil-water only after rains and used

ground or deep-soil water when the topsoil dried. Our results provide evidence of deep-soil water redistribution by all the tree species to grasses that was limited to the dry season.

Seasonal influence on water-sources of trees and grasses: Partitioning and overlap of water-sources

The results of our study support the findings for trees from other regions (Burgess et al. 2000a, Brooks et al. 2002, Bleby et al. 2010). In general, all three species of trees shifted their water-source use depending upon the season. Trees used topsoil water after rains and used a deep-soil or groundwater source when the topsoil was dry. Our study also shows a clear separation between the water-sources used by trees and those used by grasses in some seasons with overlap in others. Grasses primarily used water from upper soil layers. However, the large decrease in isotope values of the grasses we sampled in the dry season indicates the use of water redistributed by trees. Ludwig et al.*, (2004) came to a similar conclusion from the isotope values they obtained for understory grasses, tree roots of *Vachellia tortilis* (formerly *Acacia tortilis*) and the groundwater in Tanzania. Thus, water-resource partitioning as well as spatial overlap of water-source use for trees and grasses can and does occur and with a strong seasonal component. We do not know of any other report for African or other savannas that shows evidence for such a clearly dynamic water resource-use. In fact, seasonal influences on the water-sources used by the trees and grasses in our system explained more of the variation than any of the other factors we studied (plant functional type or tree species). Studies in other savannas have been seasonally limited in their scope (post-wet season, Bayala et al., 2008; Kulmatiski et al., 2010; Ludwig et al., 2003) and the tree species examined were shown to access only deeper water-sources. While studies from other regions have shown shifts in water-source use for trees only (Burgess et al. 2000b, Zou et al. 2005). In this study, during seasons when the upper layers of the soil contained water, the use of the same water-sources by trees and grasses clearly occurred. In contrast, during seasons when the upper soil layers were dry, water resource partitioning among trees and grasses occurred suggesting a likely shift in water related tree-grass interactions. However, during the first rains that occurred (during the dry-wet transitional season), both trees and grasses were using water from the top-layers of the soil. During this period there was still limited rainfall (about 60 mm) yet a usable amount of soil water was still available for plants to exploit (about 7% volumetric soil-moisture). This dry-wet transition season is associated with leaf expansion and green-up, and early growth of both the trees and grasses that would increase the plant demand for water (Scholes and Archer 1997, Shorrocks 2007,

Huntley and Walker 2012). As both trees and grasses use water in the topsoil during this season (when water is still quite limited), there is a high likelihood of competition for water between these plant functional types.

Hydraulic-redistribution in trees and transfer of water to understory grasses

The results of our tracer experiment confirmed that all the three tree species redistribute water from deeper layers (-2.5 m) of the soil to upper soil layers. However, this phenomenon is limited to the dry season (Table 2.2). The ^{2}H tracer (spike) taken up by the trees also increased over time compared with controls but did not show the extreme and high values we observed in the grasses. Further, we do not attribute the statistical differences observed in the 2011 wet season to the uptake of the tracer by grasses as a consequence of tree hydraulic-redistribution because the grass values were never high and remained within the lower range of natural abundance values (maximum value was 1.4‰). The wet season in southern Africa occurs during summer with high temperatures and variation in the daily amount of rainfall is high. Both of these factors can lead to fractionation in plant available water (evaporatively enriched relative to their original input values). It is highly likely that these factors contributed to the differences we observed between groups in the 2011 wet season (e.g. fractionation of the topsoil water before it was used by the plants). However, the differences we observed in 2011 were not observed during the wet season of 2010 as the variations in rainfall and daily temperature were very different. Therefore, it is evident that subsoil water-redistribution by trees was limited only to the dry season.

Two lines of evidence allow us to eliminate the possibility of direct tracer uptake by the grasses. Firstly, we obtained cores to assess rooting depth of *P. maximum* both under and outside tree canopies and found that there were no roots beyond 100 cm below the soils surface eliminating the possibility of any grass roots occurring at a depth of 2.5 m where the tracer was applied (*unpublished data*). Secondly, the ^{2}H$_{2}$O tracer, which was administered in all seasons, would have resulted in us seeing high values in grasses (above natural abundance) as observed in the dry season but were not observed in any other season. This finding was in contrast to the ^{15}NH$_{4}$ tracer study also performed on the same trees that showed up-take and subsequent redistribution of N by the trees to the grasses in all seasons (Priyadarshini et al. 2014). We conclude that hydraulic-redistribution of subsoil water from the trees to the grasses occurred only during the dry season. Seasonal hydraulic-redistribution has been demonstrated in trees of other regions (Burgess et al. 2000b, Peñuelas and Filella

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2003, Ryel et al. 2010, Brooksbank et al. 2011) but to our knowledge, has so far not been shown in African savannas.

Hydraulic-redistribution is widespread in plants with only a few reported instances where it has been shown not to occur (Lee et al. 2005, Prieto et al. 2012). Our results show that for African savanna trees hydraulic-redistribution may be more common than previously thought since the three tree species we studied, all of which exhibited hydraulic-redistribution, are abundant and widespread in southern African savannas, suggesting that the community and ecosystem impacts of hydraulic-redistribution in savannas could be potentially large. However, we acknowledge that our investigation could not quantify the magnitude of the hydraulic-redistribution affect nor its larger-scale ecological significance. Nevertheless, our data demonstrates, as reported in a few studies that shifts between competition and facilitation among co-occurring plants can occur (Callaway et al. 1991, Holmgren et al. 1997, Kikvidze et al. 2006). We show this in our study through water-resource sharing and facilitation by trees and grasses in savannas. Dry season water facilitation by trees to grasses may have significant ecological benefits as suggested by several hypotheses on inter-plant interactions (Ryel et al. 2003, Neumann and Cardon 2012, Prieto et al. 2012, Sardans and Peñuelas 2014). The benefits provided by hydraulic-redistribution for trees to withstand drought and its associated water stress, increase nutrient uptake, and the efficiency of nutrient capture by keeping the mycorrhizae alive are understood (Norton and Hart 1998, Brooks et al. 2002, Querejeta et al. 2007, Prieto et al. 2012). For savanna trees, dry season upward hydraulic-redistribution of subsoil water could be an important mechanism by which they keep the root system in upper layers of the soil active for water uptake and probable mass-flow nutrient capture during the first seasonal rains when they switch from deep-soil source to topsoil water (Matimati et al. 2014), and sustain growth related demands for early flush of leaves well before the onset of rains. The importance of seasonal redistribution of water to understory grasses in savannas, however, still needs to be determined. We did however note, that during the peak dry season when there was no moisture in the topsoil, there were abundant green basal meristems in the understory grasses compared with grasses outside of the tree canopy (also, the moisture content in understory *P. maximum* grasses was 100% higher than outside canopy, *unpublished data*). Therefore, a possible advantage of hydraulic-redistribution from trees to the understory grasses in savannas could be in that it prevents desiccation, helps maintain root resource-reserves and permits minimal photosynthetic activity by these perennial C_4

grasses in preparation for the coming growing season. In conclusion all the data presented here taken together show that dry season hydraulic-redistribution from trees to grasses could be an important facilitative mechanism maintaining tree-grass co-existence in savannas.

Acknowledgements

APPENDIX 2.1

Data transformations and the linear mixed model

We used Box-Cox transformation functions f (OR) = (OR ^{p}–1)/p for hydrogen and for oxygen, with OR the R$_{SAMPLE}$/R$_{STANDARD}$ ratios, where the power *'p'* was optimized using PROC TRANSREG of SAS by fitting fixed effects models to the transformed odds ratio. The power $p = -10$ was chosen for hydrogen, and $p = -75$ for oxygen. The transformation functions for oxygen and hydrogen were small for the majority of the observations (429 out of 440 δ^2H values were in the range –75 to 75, corresponding to the Odd Ratio (OR) values 0.925 to 1.075, yielding transformed values ranging from –0.12 to 0.051; the range for δ^{18}O was –13 to 25, corresponding to OR values 0.987 to 1.040, yielding transformed values within the range – 0.019 to 0.015).

In the mixed linear model, random effects were allowed for tree pairs, trees within pairs, and tree/grass observational units, on which repeated measurements were made. Of these, only random effects of tree pairs were found. The residual variances were different in some subgroups even after data transformation. Variances for tree and grass were found to be different for the dry-wet transition, wet-dry transition and dry seasons. Measurements after spiking were more variable than pre-spike measurements or measurements on control trees. Decisions about this heterogeneity were made by comparisons of models using Akaike's Information Criterion. No repeated measurements correlation structure (like auto-regression) was found. The test statistics for the different parts of the analysis were obtained using CONTRAST statements within the larger overall mixed model analysis.

For oxygen, a simpler model than that used for hydrogen could be used since an effect of group (pre-spike and control only) was neither expected, nor found. The fixed part of the model contained main effects and interactions of species, plant functional type, and season. In the random part of the model, random effects of tree pairs, trees within pairs, and tree/grass observational units were allowed to take care of the experimental design, but none of these appeared to be important. Residual variances were different for different grass/tree and season combinations. The largest variance was found in the dry-wet transition (Nov 2010), and smallest variance in the wet 2011 (Jan 2011) period. Trees had slightly larger variance than grass.

APPENDIX 2.2
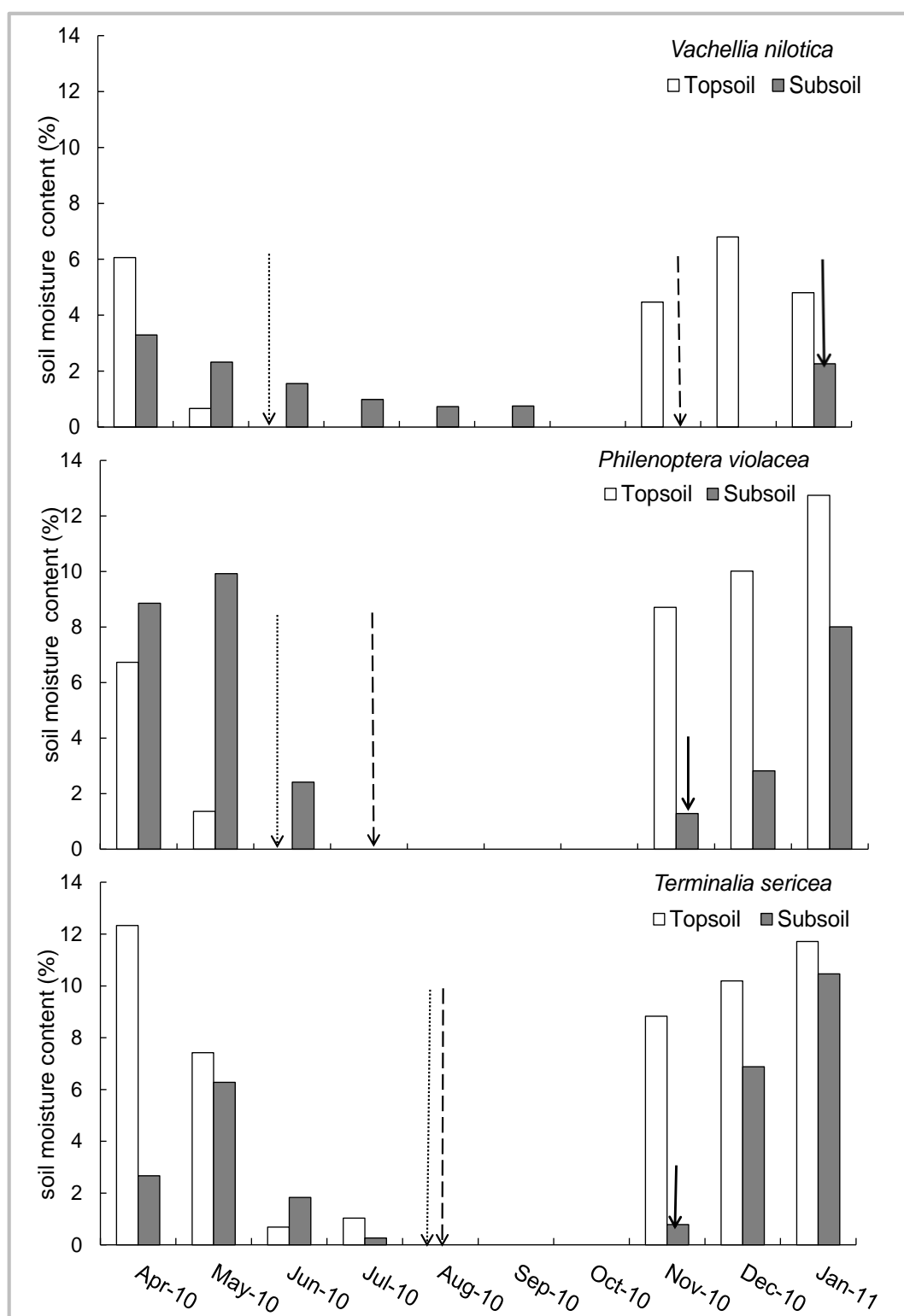
Monthly variation in average top and sub-soil volumetric moisture content (%) under three savanna tree species. The dotted arrow indicates start of dry top-soil and the long-dashed arrow depicts the start of dry sub-soil (2.5m) during the study period (Jan 2010 to Jan 2011). The black solid arrow represents sub-soil water recharge (Jan 2010 data is not shown since the loggers were not set up during that time and Oct data is not available due to the loss of loggers in September 2010)

APPENDIX 2.3

Table 2.3.1: Summary of ANOVA for the differences in δ^2H between pre-spiked and control groups. The F-tests for the differences were extracted from a larger mixed linear model. The analysed responses are Box-Cox transformed Odds ratios.

Effects	Pre-spike Vs. Control		
	F	*P*	*DF*
Tree species	0.64	0.530	2, 286
Plant functional type	1.96	0.162	1, 286
Season	6.17	0.0002*	3, 286
Species x Plant functional type	0.01	0.990	2, 286
Species x Season	1.83	0.071	8,286
Plant functional type x Season	3.08	0.016*	4, 286
Species x Plant functional type x Season	1.06	0.392	8, 286

P<0.05

Table 2.3.2: Summary of comparisons of differences in least square means of δ^2H as obtained from the repeated measures mixed linear model. The term "ftype" indicates the plant functional type.

Group comparisons of pre-spike Vs. control		Differences between LS Means (± 1SEM)	*P*	*T*
Wet 10 (season)		0.002 (± 0.003)	0.60	0.59
Wet-dry transition (season)		-0.003(±0.004)	0.45	-0.75
Dry (season)		0.020 (±0.004)	<0.0001*	4.84
Dry-wet transition (season)		0.006 (±0.003)	0.043*	2.03
Wet 11 (season)		0.006 (±0.002)	0.025*	2.26
Wet 10 (ftype x season)	Grass	-0.002 (±0.003)	0.555	-0.59
Wet-dry transition (ftype x season)	Grass	-0.014 (±0.001)	<0.0001*	-9.91
Dry (ftype x season)	Grass	0.030 (±0.008)	<0.0001*	4.00
Dry-wet transition (ftype x season)	Grass	0.004 (±0.004)	0.268	1.11
Wet 11 (ftype x season)	Grass	0.002 (±0.003)	0.410	0.83
Wet 10 (ftype x season)	Tree	0.005(±0.005)	0.305	1.03
Wet-dry transition (ftype x season)	Tree	0.007 (±0.008)	0.360	0.92
Dry (ftype x season)	Tree	0.010 (±0.004)	0.004*	2.87
Dry-wet transition (ftype x season)	Tree	0.009 (±0.005)	0.087	1.71
Wet 11 (ftype x season)	Tree	0.010 (±0.005)	0.034*	2.13

P<0.05

CHAPTER 3

OVERLAP IN NITROGEN SOURCES AND REDISTRIBUTION OF NITROGEN BETWEEN TREES AND GRASSES IN A SEMI-ARID SAVANNA

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ABSTRACT

A key question in savanna ecology is how trees and grasses coexist under nitrogen limitation. We used N stable isotopes and N content to study N source partitioning across seasons from trees and associated grasses in a semi-arid savanna. We also used ^{15}N tracer additions to investigate possible redistribution of nitrogen by trees to grasses. Foliar δ^{15}N values were consistent with trees and grasses using mycorrhiza-supplied nitrogen in all seasons except in the wet season when they switched to microbially-fixed nitrogen. The dependence of trees and grasses on mineralized soil nitrogen seemed highly unlikely based on seasonal variation in mineralization rates in the Kruger Park region. Remarkably, foliar δ^{15}N values were similar for all three tree species differing in the potential for N fixation through nodulation. The tracer experiment showed that nitrogen was redistributed by trees to understory grasses in all seasons. Our results suggest that the redistribution of nitrogen from trees to grasses and uptake of nitrogen was independent of water redistribution. Although there is overlap of nitrogen sources between trees and grasses, dependence on biological sources of nitrogen coupled with redistribution of sub-soil nitrogen by trees may contribute to the co-existence of trees and grasses in semi-arid savannas.

INTRODUCTION

Savanna soils are weathered, leached and deficient in nitrogen (Cole 1986, Scholes et al. 2003a). Nitrogen content of savanna soils across Africa is very low, typically <0.1% (Stroosnijder 1991, Sankaran et al. 2005). Despite this, savannas support a high plant diversity and are characterized by the co-existence of trees and grasses. A key question in savanna ecology is how trees and grasses co-exist in the face of N limitation. Resource partitioning has been suggested as an important mechanism (Schoener 1974, Fargione and Tilman 2005, Dybzinski and Tilman 2007), but resource partitioning between trees and grasses as well as their sources of nitrogen in savannas are poorly understood. Resource partitioning of several types has been invoked to explain the plant diversity, e.g., use of topsoil vs. subsurface soils, use of different N compounds (ammonium, nitrate, or nitrogen in its organic forms) and seasonal differences in N uptake (Lehmann et al. 2001, McKane et al. 2002, Wang and Macko 2011). Vertical partitioning of nutrients in savannas where grasses use resources from the topsoil and trees use resources from the sub-soil, commonly referred to as Walter's two-layer hypothesis, is a long-standing explanation for tree-grass co-existence (Walter 1971). There is evidence supporting this hypothesis (Hesla et al. 1985, Knoop and Walker 1985, Sala et al. 1989), but other results are contradictory (Ludwig et al. 2004a, February and Higgins 2010). Nitrogen sources of co-occurring plants may influence inter-plant interactions but are poorly understood in savannas. The influence of seasonal limitations of plant-available nitrogen in savannas on inter-plant interactions is also unclear.

In this study we examined nitrogen use by co-occurring trees and their under-canopy grasses. By using natural variation in foliar δ^{15}N, foliar nitrogen content and an experiment with ^{15}N enriched NH_4 tracer, we specifically investigated:

1. What are the sources of nitrogen for co-occurring trees and grasses in a dry savanna?
2. Do these sources change seasonally and are they different for different tree species?
3. Do trees redistribute nitrogen from the subsoil to the under-canopy grasses?
4. Do redistribution patterns change seasonally and is this different for different tree species?

Our hypotheses were that competition between trees and grasses occurs if they used the same nitrogen-source and that nitrogen resource partitioning was likely if they used different sources within the same season. Significant redistribution of nitrogen by trees to grass would be indicative of facilitation.

METHODS

Study site

We carried out this study in Andover Game Reserve (Andover GR) with an area of 7100 ha located between 24˚ 33' S and 24˚ 38' S, and 31˚ 10' E and 31˚ 17' E. The precipitation in this region occurs during summer, starting in the dry-wet transition (Oct/Nov), and ending in the wet-dry transition (April) varying between 550–650 mm. The bedrock in Andover GR is granitic and the soils of this region are alkaline with ammonium being the dominant form of soil nitrogen (Scholes et al. 2003a). Although the grass community is diverse, the under-canopy grasses occur in *Panicum maximum* monoculture. Andover GR has a low herbivore density (below 1 large grazer per 10 ha, Eksteen and Nkosi 2009). Herbivory is close to absent on the crests (personal observation KVR Priyadarshini) with no grazing occurring under any of the study trees.

Andover GR follows a block burn fire management strategy with each block being burnt once in five years. An accidental fire burnt 97% of the reserve on 17th of September, 2010 during the study period. There was low mortality of trees in general and only one tree of the species *Acacia nilotica*[#] was lost for further experimentation. There was epicormic post-fire leaf flush for trees.

Study grass and tree types

We studied *Panicum maximum*, the dominant understory grass that grows beneath three commonly found co-occurring tree species. The trees were broad leaved brevi-deciduous *Philenoptera violacea* (Klotzsch) Schrire, broad-leaved deciduous *Terminalia sericea* (Roxb.) and fine-leaved deciduous *Acacia nilotica*[#] (L.) Delile. Of the three species, *Acacia nilotica*[#] is reported to be a nitrogen-fixing species; *Philenoptera violacea* is reported to be a "facultative" fixer having a multiple nitrogen use strategy being a nitrogen-fixer under competition or nutrient limitation (Jacobs et al. 2007); and *Terminalia sericea* is not a nitrogen-fixer but is reported to have VA mycorrhizal association (Högberg 1990).

[#] Name is changed to *Vachellia nilotica*

Experimental set up

We conducted a full factorial experiment on a sandy crest top, where five pairs of experiment and control trees of each species were identified. Control trees were located 30m away from any of the experiment trees to avoid the spread of stable isotope tracers (Sternberg et al. 2004, Kulmatiski et al. 2010). All trees used in this study were adult trees with heights in a range of 15-20m, their estimated ages were above 30 years and they had well-established root systems.

We carried out a repeated measures design with the same individual trees and the same grass plots sampled repeatedly during different seasons. Application of isotope tracer was done via PVC tubes of 15mm diameter that were installed vertically in the soil to a depth of 2.5m in each of four cardinal directions at 1m distance from the base of each experiment tree (Lehmann et al. 2001). We confirmed that this depth was well below grass rooting depth by coring grass roots of *P. maximum* (core diameter = 10cm, $N = 26$, depth = 120cm). We found no grass roots beyond 100cm. Tubes extended 10cm above the soil and were sealed before and after application of the stable isotope labelling solution. The tubes were put in place in the first week of October 2009 at the start of the wet season to enable the under-canopy soil and grasses to overcome disturbance due to digging and regenerate. The stable isotope labelling was started in January 2010, after a considerable amount of rainfall. We did not install tubes around control trees. However, we compared the stable isotope ratios before the start of the first labelling between the experiment and control trees to confirm whether the tubes affected the results. We found no influence of the tubes (paired sample *t*-test between experiment and control trees; P for $^{15}N_{(tree)} = 0.988$ & $t = 0.015$, P for $^{15}N_{(grass)} = 0.356$ & $t = -0.956$ with $Df = 14$ for both the groups).

Natural variation in ^{15}N stable isotope ratios

The variation in natural abundance of foliar $\delta^{15}N$ reflects the different nitrogen sources and allows inferences on the nitrogen sources of plants because there is little fractionation during uptake of nitrogen by mature plants (Handley and Raven 1992, Nadelhoffer and Fry 1994, Robinson 2001). We used this property of $\delta^{15}N$ to investigate the sources of nitrogen for plants in our study: low $\delta^{15}N$ values close to zero indicate the use of microbial fixed nitrogen (Nadelhoffer and Fry 1994, Högberg 1997, Robinson 2001), high values >4-6‰ and close to or above soil nitrogen isotopic values indicate use of mineralized nitrogen (Nadelhoffer and

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Fry 1994, Robinson 2001), while intermediate values ranging from +2 to +5‰ indicate mycorrhizal mediated nitrogen (Högberg and Alexander 1995, Craine et al. 2009b) or a mixed use of N from fixation and soil sources.

The foliar δ^{15}N values were calculated with atmospheric N isotope ratio as the standard with the formula: δ^{15}N = {[(^{15}N/^{14}N) SAMPLE) / (^{15}N/^{14}N) STANDARD] – 1} *1000. The (^{15}N/^{14}N) STANDARD represents the stable isotope ratio of the international standard for nitrogen which is atmospheric nitrogen and (^{15}N/^{14}N) SAMPLE represents the stable isotope ratio of the sample.

Labelling with ^{15}N as a tracer

A tracer solution was prepared comprising 5g of ^{15}NH$_4$Cl with a +99‰ (100% ^{15}N) isotope ratio of ^{15}N and diluted with one litre of ^{2}H$_2$O (both tracers sourced from Icon Services, New Jersey, USA). Results of ^{2}H$_2$O labelling are described elsewhere (Priyadarshini et al. in review). The deeper rooting zone around each of the experiment trees at 2.5m depth was dosed with15ml of the tracer solution via each PVC tube totalling 60 ml of the tracer per experiment tree. This was sufficient to spike the system with high abundance of ^{15}N without effects of fertilization or irrigation (Lehmann et al. 2001). The tracer was applied during the wet season in Jan 2010, the wet-dry transition season in April 2010, dry-wet transition season in Nov 2010 and wet season in Jan 2011. We repeated tracer application seasonally because it has been reported that tracer was lost after 36 days for fruit trees (Lehmann et al. 2001). Our sampling interval was longer than this period. To measure the residual label in the leaves, we also collected samples 2-3 days before application of the label every season (pre-spike sample: described below in detail). We did not apply the tracer during the dry season as this is the dormant season for plants in savannas but we sampled the plants before complete leaf fall to determine the residual label from the previous season's application.

Sampling of plant material

The youngest and fully expanded leaves of terminal ends of the upper canopy branches were sampled following Lehmann et al (2001). Samples were collected from all cardinal directions of the upper tree canopy and composited into a single sample. Concurrently, fresh and new grass blades from 1m radius around the base of the tree were collected from all cardinal directions. These were also composited into a single sample to represent the under canopy

grass for that tree. Plant material was sampled before applying the stable isotope (Pre-spike) and then one week after the application of the isotope (Spike) during all seasons. Therefore, pre-spike and spike samples are of the same tree before and after the labelling. Material from control trees (Control) was sampled similarly and concurrently as the experimental trees. Sampling was done during wet season of 2010, wet-dry transition season, dry season, dry-wet transition season, and wet season of Jan 2011. Plant samples were oven dried to constant weight at less than $60^{\circ}C$ to prevent heat loss of nitrogen, finely ground, and stored until laboratory analysis.

Sampling of soil

Soil samples were collected at the beginning of the experiment from 0.25m depth and 2.5m depth in the four cardinal directions from the base of experiment and control trees. Soil was composited and a subsample was pulverized (Mintek Laboratories, South Africa). The pulverized soil was first treated with dilute hydrochloric acid to remove the soil carbonates and thoroughly rinsed with de-ionized water and oven-dried for further analysis in the mass spectrometer.

Determination of stable isotope ratios and %N

Sample aliquots of approximately1mg of plant material or 40mg of soil were weighed into clean tin capsules (Elemental Microanalysis Ltd, Okehamptom, UK) at the CSIR laboratory in Pretoria, South Africa using a micro-balance (Mettler-Toledo Inc. Ohio, USA). Samples were analyzed using a Flash EA 1112 system coupled with a Delta V plus mass spectrometer using a Conflo IV interface (Thermo Electron Corporation, Bremen, Germany). Precision is <0.2‰ for $\delta^{15}N$.

Statistical analysis and data transformations

We used linear regression to test for relationships between foliar %N and foliar $\delta^{15}N$, and between soil %N and soil $\delta^{15}N$. Foliar $\delta^{15}N$ and Nitrogen (% dry weight) were analyzed using mixed linear models that are the most appropriate tool for studies with repeated measures (Littell et al. 2006). We used the SAS software program version 9.2 for the analysis. More details on the linear mixed model are presented in Appendix 3.1. We split the analysis into three parts:

1. ANOVA for control trees only (changes in natural abundance of δ^{15}N and %N) testing for differences in nitrogen source between tree species and between trees and understory grasses.
2. ANOVA for differences between spiked (experiment trees after labelling) and control trees testing for uptake and redistribution of the ^{15}N label.
3. ANOVA for differences between pre-spiked (experiment trees before labelling) and control values testing for the residual label applied in the previous season.

We used Log (%N) for Nitrogen concentrations to obtain near normal distributions. Due to the extremely skewed distribution of δ^{15}N in the tracer experiments with values ranging from -3.8 to 5644.5‰, the mixed model was formulated for transformed δ^{15}N as "y = – exp (–0.16* δ^{15}N)". This transformation was chosen empirically so that mixed linear models applied to the transformed δ^{15}N yielded studentized residuals which were approximately normally distributed. More details on the δ^{15}N transformation and linear mixed model is presented in Appendix 3.1.

RESULTS

Soil

The two soil layers showed differences in nitrogen concentration (% dry weight) but not in δ^{15}N (Fig. 3.1). The three tree species showed small but significant differences in soil nitrogen concentration (see Table 3.2.1 in Appendix 3.2 for detailed results).

Variation in foliar %N and natural abundance of δ^{15}N

The foliar %N showed large differences between seasons and small differences between trees and grass (no significant plant functional type differences; Fig. 3.2A and B, and Table 3.1). All three tree species and their corresponding understory *P. maximum* grass showed the highest increase in foliar %N from the dry to dry-wet transition season. The increase was almost two-fold in all cases showing extreme seasonality in nitrogen increase (Fig. 3.2A and B, and Table 3.2.2 in Appendix 3.2). There was an increase in foliar %N from the wet to the wet-dry transition season for grasses (Fig. 3.2B) but not trees (Fig. 3.2A) which resulted in a significant seasonal difference between trees and grasses (interaction between plant functional type and season, Fig. 3.2A and B, and Table 3.3.2 in Appendix 3.2).
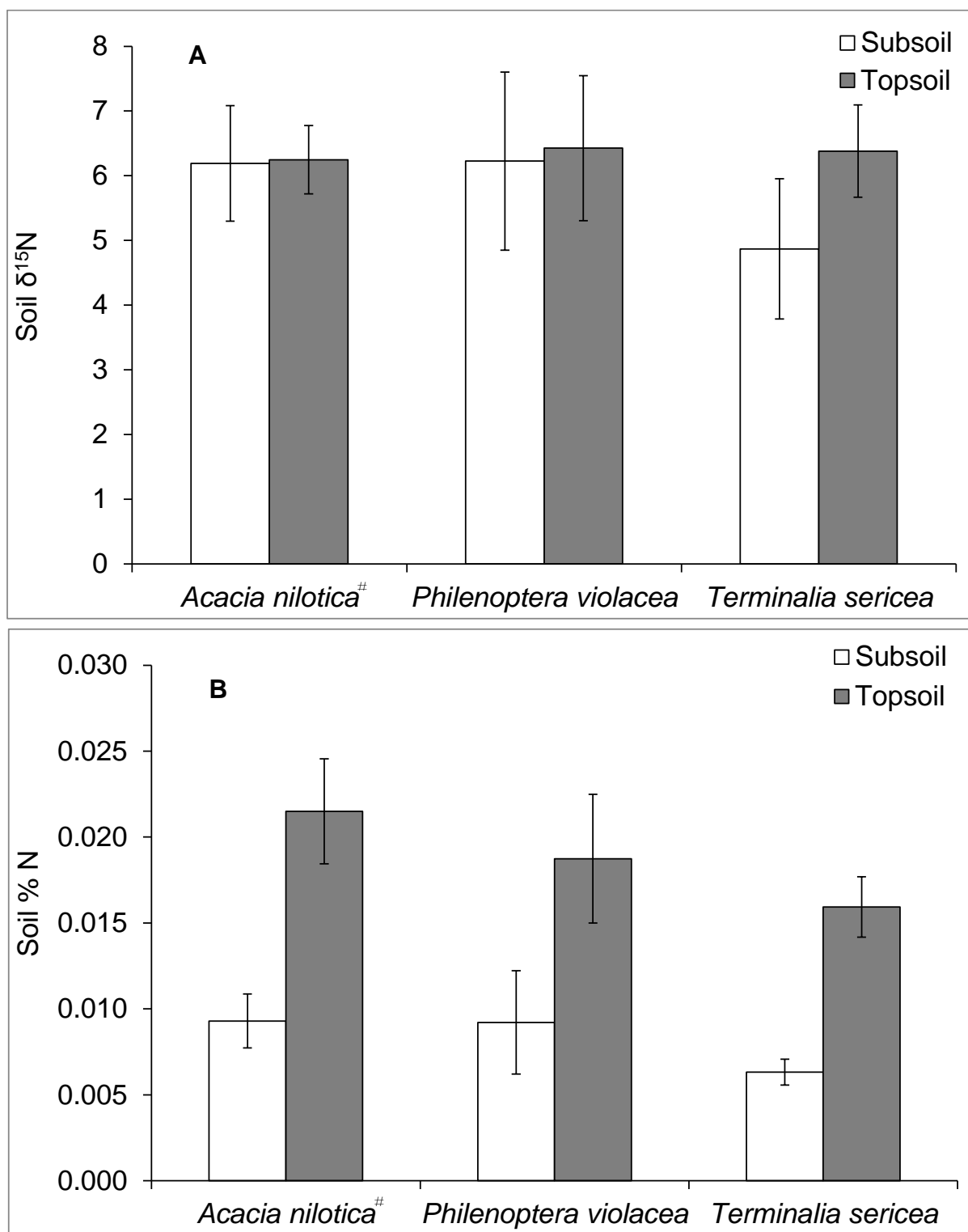
Figure 3.1. Soil $\delta^{15}N$ (‰) in A) and total soil Nitrogen (%N) in B) in Andover Game Reserve, South Africa sampled during Wet-dry transition (Oct 2009) season. The open un-shaded bar represents subsoil and the grey shaded bar represents the topsoil in both figures. Error bars are ± 1 Standard deviation. [#] The name of *Acacia nilotica* has been changed to *Vachellia nilotica*.

Table 3.1. Summary of analysis of variance of natural abundance of foliar δ^{15}N and nitrogen (% dry weight, log transformed) using repeated measures mixed linear models.

Effects	% Nitrogen			^{15}N		
	DF	F	P	DF	F	P
Tree species	2, 12	70.26	< 0.0001*	2,11	0.37	0.70
Plant functional type	1, 12	0.02	0.90	1, 22	1.12	0.30
Species*Plant functional type	2, 12	7.47	0.0078*	2, 22	2.32	0.12
Season	4, 94	27.07	< 0.0001*	4, 277	6.93	<0.0001*
Species*Season	8, 84	1.50	0.12	8, 277	1.34	0.22
Plant functional type*Season	4, 94	10.49	< 0.0001*	4, 277	1.39	0.24
Species*Plant functional type*Season	8, 94	4.56	0.0001*	8, 277	0.66	0.73

*Significant at P < 0.05.

There were also seasonal differences in foliar %N for the three tree species. Foliar %N of the understory *P. maximum* were influenced by the tree species they grew under, with *P. maximum* having the lowest nitrogen content under *T. sericea* compared to the other two tree species (interaction between tree species and plant functional type, Table 3.1). These differences in grass foliar %N were similar to those of the top-soil-nitrogen pattern (Fig. 3.1).

There were no plant functional type differences, differences between tree species or any interactions between trees and grasses for foliar δ^{15}N. But some small seasonal differences were significant (Fig. 3.2C and D, and Table 3.1) suggesting the absence of resource partitioning but use of multiple sources in a year. The largest change was from the dry-wet transition season to the wet season (2011) where there foliar δ^{15}N decreased significantly by 0.19‰ (Fig. 3.2C and D, and Table 3.2). This was followed by an increase from wet (2010) to wet-dry transition, and then by a decrease from wet-dry transition to dry season. We did not find differences in the foliar δ^{15}N values between dry and dry-wet transition seasons. Overall, the changes in the foliar δ^{15}N isotope values remained small (< 1.15 ‰, Table 3.3) and the mean values were generally less than 3‰ (Fig. 3.2C and D) suggesting that the plants were not relying solely on soil mineralized nitrogen because soil δ^{15}N values were >4‰ (Fig. 3.1). Foliar δ^{15}N and %Nitrogen were unrelated over all seasons and species (Fig 3.2). The seasonal changes in foliar δ^{15}N were not concordant with the
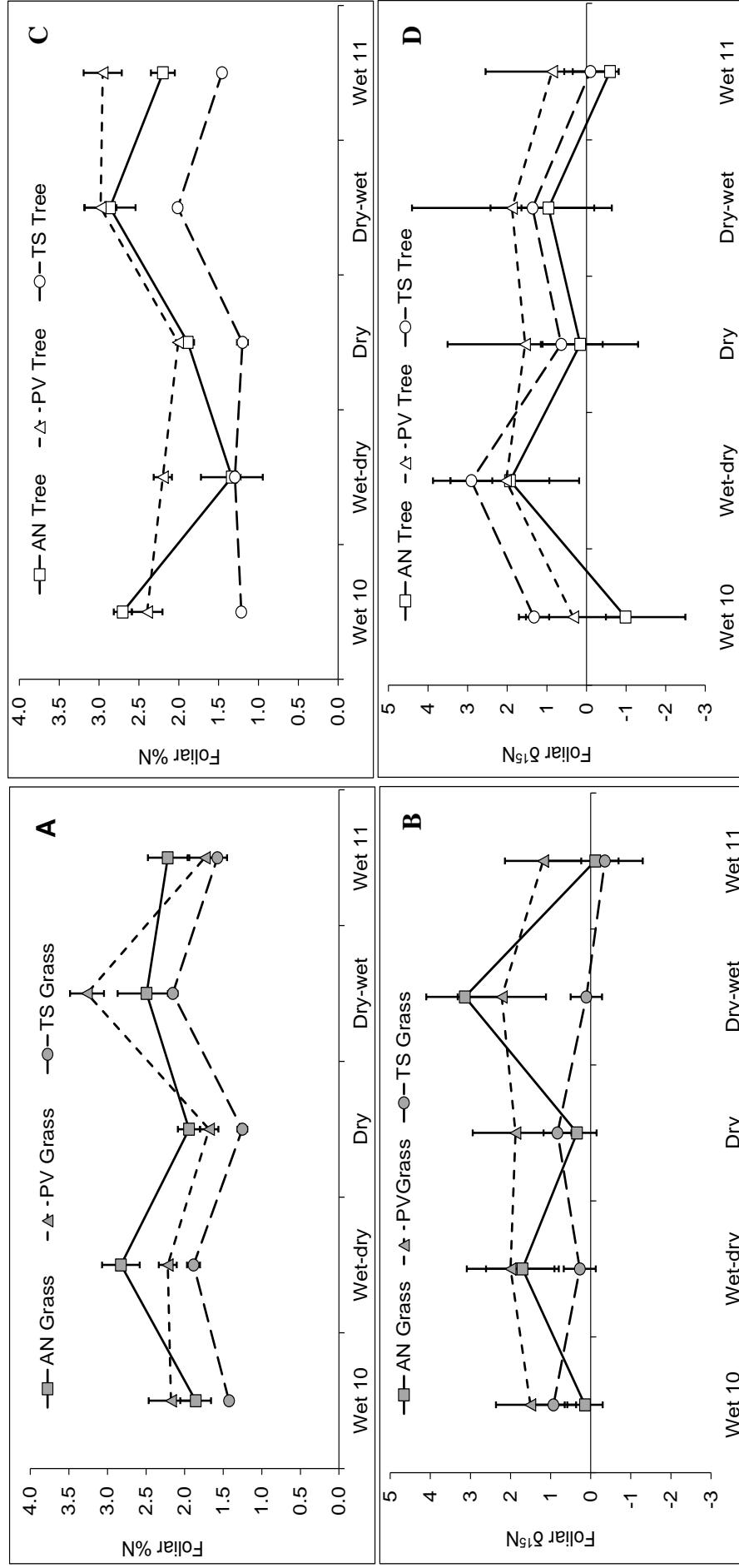
Figure 3.2. Foliar % N in A) grasses and C) trees; and foliar δ^{15}N (‰) in B) grasses and D) trees in Andover Game Reserve during different seasons on the X-axis. Error bars are ± 1 SEM. All shaded symbols represent grass and open symbols represent trees. The shaded squares and a solid line represent *P. maximum* grass under *Acacia nilotica*[#] trees, the shaded triangles and a short-dashed line represent *P. maximum* grass under *Philenoptera violacea* tree, and the shaded circles and a long-dashed line represent *P. maximum* grass under *Terminalia sericea* trees. The open squares and a solid line represent *Acacia nilotica* trees[#], the open triangles and a short-dashed line represent *Philenoptera violacea* trees, and the open circles and a long-dashed line represent *Terminalia sericea* trees.

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[#] Name is changed to *Vachellia nilotica*

seasonal changes in foliar nitrogen content (results of linear regression for trees: $R^2 = 1 \times 10^{-5}$, $Adj\ R^2 = -0.01$, $F = 0.001$, $P = 0.98$; for grasses: $R^2 = 0.03$, $Adj\ R^2 = 0.02$, $F = 2.26$, $P = 0.14$). The changes in %N were different for different groups compared but, overall, the largest change for both trees and grasses was from dry season to the dry-wet transition season (Fig. 3.2A and B, and Table 3.3.2 in Appendix 3.2). However, the largest changes for $\delta^{15}N$ were from dry-wet transition to the wet season or 2011 (Fig. 3.2C and D, and Table 3.3) suggesting that it is unlikely that a shift in the nitrogen source was the cause of nitrogen increase in trees and grasses.

The tracer experiment: ^{15}N redistribution by trees to under-canopy grass

Tracer enrichment occurred in all seasons as reflected in the large difference between spike and control groups (Fig 3.3A and B, Table 3.3 and Table 3.3.3 in Appendix 3.2), and an increase from pre-spike to spike after every label application for the grasses (Fig. 3.3F). However, ^{15}N values after spiking increased only moderately in trees compared with the pre-spike (Fig 3.3E).

A very small enrichment was seen in the dry-wet transition season suggesting that the label became diluted due to increases in the foliar nitrogen concentrations (Fig. 3.2A) as a result of tree growth. We did not label during the dry season and so there is no comparative data with spike values for this season. We could not discern the season of maximum nitrogen re-distribution from trees to grasses although the results (Fig 3.3A and B) suggest that the transfer may be happening throughout the year.

Over the experimental period the difference in $\delta^{15}N$ between the labelled and control plants gradually increased. This was especially true for the trees, and apparent in both the spike – control (Fig. 3.3A) as well as the pre-spike – control comparisons (Fig. 3.3C). Higher pre-spike values than control values indicate that label is still contained in the plants from the previous labelling, suggesting that a significant proportion of the label is stored and redistributed in the trees but perhaps also in the grasses (Fig 3.3D).

DISCUSSION

Remarkably, plants were similar in their $\delta^{15}N$ values and their seasonal %N changes. Onset of rains were associated with the largest N changes and these changes were parallel for all species. The plant community thus seemed much unified in N dynamics, a unity perhaps

dictated by the overall dry conditions in the savanna. Little evidence was found for resource partitioning among species or across seasons, with tracer experiments showing that N transfer could occur from trees to grasses. We discuss these major results in the following paragraphs.

Table 3.2. Summary of seasonal differences in means of foliar δ^{15}N of grasses and trees in Andover Game Reserve. The ‰ equivalent differences between medians is also given for clarity. *Significant at P<0.05.

Time	Differences between Means (± 1SEM)	t	P	‰ equivalent differences [a]
Wet 2010 – Wet-dry transition	0.15 (± 0.05)	3.01	0.0029*	– 1.06
Wet-dry transition – Dry	– 0.11 (± 0.05)	– 2.23	0.0268*	0.72
Dry – Dry-wet transition	0.06 (± 0.05)	1.25	0.2112	– 0.47
Dry-wet transition – Wet 2011	– 0.19 (± 0.05)	3.79	0.0002*	1.13

[a] the ‰ equivalent are the median differences calculated from the measured data without transformation.

Table 3.3. Summary of analysis of variance of foliar δ^{15}N (transformed) comparing spiked (experiment) values of trees and grasses with pre-spike values (prior to application of tracer label) and control values using repeated measures mixed linear models.

| Effects	Spike Vs Control			Pre-spike Vs Control		
	DF	F	P	DF	F	P
Tree species	2, 277	1.85	0.160	2, 277	1.58	0.207
Plant functional type	1, 277	13.82	0.0002*	1, 277	7.63	0.006*
Species*Plant functional type	2, 277	0.34	0.709	2, 277	1.92	0.148
Season	2, 277	19.81	<0.0001*	2, 277	30.32	<0.0001*
Species*Season	6, 277	5.46	<0.0001*	8, 277	2.90	0.004*
Plant functional type*Season	3, 277	3.05	0.030*	4, 277	3.41	0.009*
Species*Plant functional type*Season	6, 277	1.54	0.166	8, 277	1.96	0.051

*Significant at P<0.05
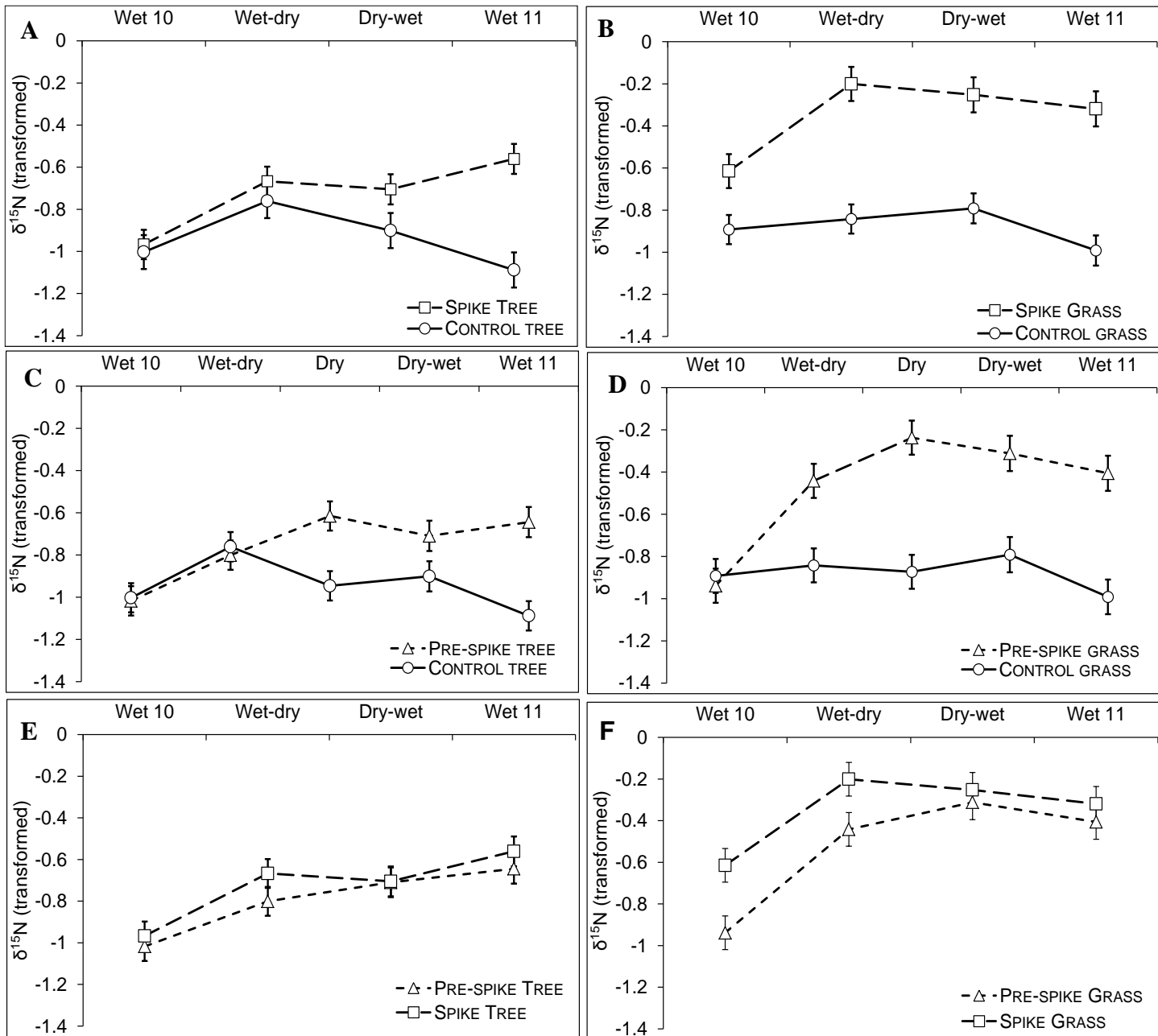
Figure 3.3. $\delta^{15}N$ (transformed) as obtained from the ^{15}N enriched stable isotope tracer experiment in different seasons on the X-axis showing comparisons between A) values of trees after tracer application (spiked trees represented by squares and a dashed line) with control trees (represented by circles and a solid line); B) values of grass under labelled trees after tracer application (spiked grass represented by squares and a dashed line) with grass under control trees (control grass represented by circles and a solid line); C) values of trees before tracer application (pre-spike trees represented by triangles and a dashed line) with control trees (represented by circles and a solid line; D) values of grasses under labelled trees before application of tracer (pre-spike grasses represented by triangles and a dashed line) with grass under control trees (control grass represented by circles and a solid line); E) values of trees before tracer application (pre-spike trees) with trees after tracer application (spike trees represented by squares and a long-dashed line); F) values of grass under labelled trees before tracer application (pre-spike grass represented by triangles and a dashed line) with grass under labelled trees after tracer application (spike grass represented by squares and a long-dashed line). Error bars are ±1 SEM as obtained from the mixed model. Panels C and D have an extra data point since pre-spike sampling occurred in the dry season together with control trees, but trees were not labelled.

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Sources of nitrogen for plants as indicated by natural abundance of foliar $\delta^{15}N$

The soil $\delta^{15}N$ was not useful in determining the depth differences in the soil source of nitrogen for trees and grasses because all soil $\delta^{15}N$ were similar (Fig. 3.1A). Furthermore, foliar $\delta^{15}N$ values were much lower than the soil $\delta^{15}N$ throughout the year for all our plant samples which suggested other sources of nitrogen for plants in our study site. However, our soil $\delta^{15}N$ values were not anomalous and similar values of soil $\delta^{15}N$ in top and subsoil were also reported for dry site in northern Kruger National Park (unpublished data Stephan Woodborne). Top soil values were similar to those reported previously (Craine et al. 2009a).

In addition to being lower than soil $\delta^{15}N$, foliar $\delta^{15}N$ showed seasonal variation although the magnitude of variation was small. Seasonal variation in foliar $\delta^{15}N$ in southern Africa has not been reported previously. Most work on natural abundance of foliar $\delta^{15}N$ have been landscape level studies relating rainfall or soil $\delta^{15}N$ to foliar $\delta^{15}N$ (Swap and Aranibar 2004, Aranibar et al. 2008, Craine et al. 2009b, 2009a). In our study, seasonal variation in N sources might best explain the plant ^{15}N variation throughout the year. We eliminated the possibility of plants using nitrified nitrogen based on the seasonal variation in nitrification in southern Africa (Coetsee et al. 2008) and the associated foliar $\delta^{15}N$ values. The denitrification process increases the $\delta^{15}N$ values and nitrification decreases the $\delta^{15}N$ values tremendously (to the extent of – 60‰, Handley and Raven 1992). The single study that measured the actual *in situ* mineralization in Kruger National Park using resin bags showed that maximum net mineralization (with nitrification greater than immobilization) occurs during March/April which is the wet to wet-dry transitional season (Coetsee et al. 2008) when actually the foliar $\delta^{15}N$ increased in our study. Our results question whether nitrification is an important soil process for nitrogen supply to plants in savannas at all.

Foliar $\delta^{15}N$ values showed little average seasonal variation (Table 3.2) but ranged from 0 to 3‰ in our study suggesting that trees and grasses most likely used mycorrhizal supplied nitrogen through a large part of the year with a shift to microbially fixed nitrogen (around 0‰ (Shearer and Kohl 1986, Vitousek et al. 1989, Abbadie et al. 1992)) during the wet season. The typical foliar $\delta^{15}N$ associated with mycorrhizal mediated nitrogen ranges from +2 to +5‰ (Högberg and Alexander 1995, Craine et al. 2009b). This seemed to best explain the variation in foliar $\delta^{15}N$ values in our study. On a global scale also foliar $\delta^{15}N$ has

been reported to be less than the soil $\delta^{15}N$ as a general rule and this has been attributed to fractionation by mycorrhizae (Craine et al. 2009b). Furthermore, we did not find any relationship between foliar $\delta^{15}N$ with either the soil $\delta^{15}N$ or the foliar %N which is typically the case with plants that use mycorrhizal mediated N supply (Craine et al. 2009b). The occurrence of mycorrhizae in southern African plants is not well documented but there are a few studies that show mycorrhizal infections in several grasses and trees in the Kruger Park and other areas in Africa (Högberg and Piearce 1986, Hartnett et al. 2004). However, little is known yet of the quantitative importance of this nitrogen source and may play an important role in explaining tree-grass co-existence in nitrogen poor dry savannas.

Nitrogen transfer by trees to grasses: ^{15}N tracer experiment

The high $\delta^{15}N$ values of labelled trees relative to controls and corresponding high values of $\delta^{15}N$ in understory grass confirmed redistribution of subsoil label from trees to grasses. This was found to occur in all three tree species and redistribution was detected throughout the year. To our knowledge, this study is the first of its kind in savannas to show significant subsoil nitrogen redistribution by savanna trees to the understory. Alternative explanations for redistribution of nitrogen from the subsoil to the topsoil can be discarded as unlikely. First, we did not detect grass roots beyond 100cm from root cores. Second, capillary rise of the label is unlikely to happen since the study site is semi-arid, soils are sandy, highly aerated with large pores, the water table is deep (26m in the valley bottoms and the experiment trees were on crests). In Senegal and Australia the presence of a capillary fringe close to the tree roots or the water table has been documented but capillary rise to the topsoil was suggested to be unlikely (Gaye and Edmunds 1996, Zencich et al. 2002). An experimental study in South Africa found no capillary rise of water even in a soil column of 32cm (Hawkins et al. 2009) and in our study the tracer was supplied at a depth of 2.5m. Together these results corroborate our conclusion that the increase in ^{15}N label in the grasses can only be explained by redistribution of the subsoil label through the trees.

The redistributive capacity of trees is recognized in agro-forestry systems and mixed cropping is recommended for better use of soil resources (Lehmann et al. 2001, Gathumbi et al. 2003). In our study we could not calculate the proportion of redistributed nitrogen relative to nitrogen uptake by grasses themselves from the topsoil. However, the nitrogen redistribution by trees to understory grasses in all seasons in a highly nitrogen deficient semi-

arid savanna is suggestive of facilitative interactions between trees and grasses, independent of the N-fixing potential of the tree species.

There was a large degree of dilution of the tracer in the trees, particularly in the dry-wet transition season during leaf-flush (Archibald and Scholes 2007) suggesting that dilution was related to growth. Two other reasons may have accounted for the ^{15}N dilution in trees. Firstly, the large biomass of trees may have caused dilution with un-enriched ^{15}N. We found similar levels of dilution with a ^{2}H tracer (Priyadarshini et al. 2015). A second reason may be related to complex characteristics of storage and mobilization of reserves in trees (Tagliavini and Millard 2005, Frak et al. 2005). The gradual increasing difference between the tree pre-spike and control values over the experimental period (Fig. 3.3B) suggest that a significant part of the label is stored and later used for growth. The nitrogen accretion is most likely a result of internal cycling of nitrogen (Hobbie et al. 1999, Robinson 2001). In temperate trees nitrogen redistribution of internal nitrogen pools has been shown (Tagliavini and Millard 2005, Millard and Grelet 2010). Also in grasses, the pre-spiked ^{15}N values increased rapidly and remained high (Fig. 3.3B). Therefore, similar storage and remobilization may have occurred in the grasses. Internal cycling is an adaptation to increase the supply of nitrogen to the apical buds for growth during early flush in trees (Tagliavini and Millard 2005, Cooke and Weih 2005), which may be similar for grasses where initial growth is from internally stored reserves (Danckwerts and Gordon 1990).

Comparing the seasonal pattern of ^{15}N redistribution with ^{2}H redistribution (Priyadarshini et al. 2015) of the same trees suggests that N and water were taken up and distributed independently. We injected a ^{2}H label along with a ^{15}N label and sampled such that the leaves and roots of the same grass tufts were analyzed for isotopes in water and nitrogen. In contrast to significant ^{15}N tracer enrichment in the grasses in all seasons, ^{2}H tracer redistribution by trees was limited to the dry season (Priyadarshini et al. 2015). Nitrogen distribution by mass flow thus likely occurred only during the dry season. During the other seasons when hydraulic lift was absent, we must conclude that nitrogen derived from deep-soil was exuded in topsoil and taken up by grasses. Nitrogen can be taken up actively by plants independent of water (Gebauer and Ehleringer 2000, Glass 2005, Masclaux-Daubresse et al. 2010), but to our knowledge our results are the first to indicate that grasses can derive nitrogen exuded from co-occurring tree roots.

Conclusion

Our results suggest that partitioning of nitrogen sources between trees and grasses is insignificant in dry savanna and that mycorrhizal symbiosis may be of greater significance for the co-existence of trees and grasses than previously acknowledged. The natural abundance values in foliar $\delta^{15}N$ seemed to suggest that both growth forms use multiple resources (mycorrhizal, microbial). Redistribution of deep soil N from trees to grasses occurred throughout the year suggesting that the trees in part could be facilitating understory grasses. Further work might examine N use and possible resource partitioning by grasses outside the immediate influence of trees. The present study is consistent with the notion that although N levels are very low and perhaps limiting at times in savanna systems, other factors such as water availability or other limiting nutrients like phosphorus may be the more persistent limiting factor, allowing plants to coexist while using use the same N resources.

APPENDIX 3.1

The Mixed Linear Model and Data transformations

A mixed linear model was used to analyze the fixed effects of treatment (application of the stable isotope tracer), tree species, plant functional type (tree or grass) and season. The repeated measures design included random block effects of tree pairs (pairs of control and experiment trees), individual trees within pairs, and repeated measurements for paired grass and tree observational units. Of these, random effects of individual trees had the smallest and insignificant variance component. Additional to these random effects, mixed models allow the residual variances to be different for different subgroups. The variance component for tree pairs was found to be different among species with the largest variability for the tree species *Philenoptera violacea* and the smallest for *Terminalia sericea*. Different residual variances were found for species and tree-grass combinations with more residual variability of measurements on grasses compared to trees, and relatively small variance for *Philenoptera violacea*. The AIC criterion was used to make decisions about heteroscedasticity. No repeated measurement correlation structure (like autoregressive) of repeated measurements on individual grass or tree observational units could be found. The test statistics for the ANOVA's were obtained using CONTRAST statements (in SAS) within the larger overall mixed model analysis as we split the analysis for presentation simplicity. Post-hoc comparisons are a result of t-tests done within the Linear Mixed models using ESTIMATE statements (in SAS).

In the case of $\delta^{15}N$, the mixed linear model was not formulated for $\delta^{15}N$ itself but for transformed $\delta^{15}N$ due to its extremely skewed distribution. The mixed model was formulated for the transformed response $-\exp(-0.16*\delta^{15}N)$. This transformation was empirically chosen so that mixed linear models applied to the transformed response yielded studentized residuals, which were approximately normally distributed and showed desired patterns of residual analysis as required for valid statistical inference. To illustrate the effect of the transformation: within the range (-4‰, +4‰), containing 66% of the $\delta^{15}N$ values, the transformation function is mild, yielding transformed values (-1.90, -0.53); however for large $\delta^{15}N$ values (say > 50) the effect of the transformation is very strong, making these values essentially equal to zero on the transformed scale.

APPENDIX 3.2

Table 3.2.1. Summary of analysis of variance of soil δ^{15}N and nitrogen concentrations (% N) using repeated measures mixed linear models. The soil sampling was done only before the start of experiment in Dry-wet seasonal transition (Oct/Nov 2009). *Significant at P<0.05.

	Effects	DF	F	P	Comparisons	Differences in Mean (±1SEM)	DF	t	P
δ^{15}N	Tree species	2,24	1.94	0.17	--	--	--	--	--
	Soil layer	1,24	3.54	0.07	--	--	--	--	--
	Tree species*Soil layer	2,24	2.18	0.13	--	--	--	--	--
%N	Tree species	2,12	4.2	0.04*	AN – PV	0.0014 (±0.0015)	12	0.95	0.36
					AN – TS	0.0042 (±0.0015)	12	2.84	0.015*
					PV – TS	0.0028 (±0.0015)	12	1.90	0.082
	Soil layer	1,12	299.8	<.0001*	--	0.0104 (±0.0006)	12	17.32	< 0.0001*
	Tree species*Soil layer	2,12	2.1	0.16	--	--	--	--	--

Table 3.2.2. Summary of seasonal differences in means of % N (Log transformed) of control trees between under canopy grasses of different tree species and of differences between their foliar nitrogen content in Andover Game Reserve, South Africa. *Significant at P<0.05.

Comparisons	Grass			Tree		
	Differences between means (± 1SEM)	T	P	Differences between means (± 1SEM)	T	P
Acacia nilotica# (AN)						
Wet 10 – Wet-dry transition	0.185 (±0.047)	3.94	0.0002*	– 0.268 (± 0.047)	– 5.73	<.0001*
Wet-dry transition – Dry	– 0.160 (± 0.047)	– 3.43	0.0009*	0.112 (± 0.047)	2.39	0.0187*
Dry – Dry-wet transition	0.099 (± 0.050)	0.98	0.0507*	0.174 (± 0.050)	3.49	0.0007*
Dry-wet transition – Wet 11	– 0.044 (± 0.050)	– 0.89	0.3741	– 0.100 (± 0.050)	– 2.00	0.0482*
Philenoptera violacea (PV)						
Wet 10 – Wet-dry transition	0.019 (± 0.047)	0.40	0.6867	– 0.035 (± 0.047)	– 0.74	0.4609
Wet-dry transition – Dry	– 0.122 (± 0.047)	– 2.61	0.0106*	– 0.037 (± 0.047)	– 0.80	0.428
Dry – Dry-wet transition	0.288 (± 0.047)	6.15	<0.0001*	0.168 (± 0.047)	3.58	0.0005*
Dry-wet transition – Wet 11	– 0.282 (± 0.047)	– 6.03	<0.0001*	– 0.005 (± 0.047)	– 0.11	0.909
Terminalia sericea (TS)						
Wet 10 – Wet-dry transition	0.121 (± 0.047)	2.58	0.011*	0.026 (± 0.047)	0.54	0.5874
Wet-dry transition – Dry	– 0.178 (± 0.047)	– 3.80	0.0003*	– 0.034 (± 0.047)	– 0.72	0.4729
Dry – Dry-wet transition	0.237 (± 0.047)	5.06	<0.0001*	0.227 (± 0.047)	4.86	<.0001*
Dry-wet transition – Wet 11	– 0.140 (± 0.047)	– 2.99	0.0036*	– 0.140 (± 0.047)	– 3.00	0.0035*
AN – PV	0.015 (± 0.024)	0.65	0.529	--	--	--
AN – TS	0.131 (± 0.024)	5.56	0.0001*	--	--	--
PV – TS	0.116 (± 0.023)	4.96	0.0003*	--	--	--

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Name is changed to *Vachellia nilotica*

Table 3.2.3. Summary of seasonal differences in least-square means of foliar δ^{15}Nitrogen (power transformed) of grasses and trees in Andover Game Reserve comparing Spike values with control values and pre-spike values as obtained from the mixed linear model. [a] Control and pre-spike samples were same for this season as this was the start of the experiment. *Significant at P<0.05.

Comparisons	Grass			Tree		
	Differences between Means LS (± 1SEM)	T	P	Differences between Means LS (± 1SEM)	T	P
Spike – Control						
Wet 10	0.278 (± 0.09)	2.95	0.0034	0.035 (± 0.07)	0.49	0.627
Wet-dry transition	0.641 (± 0.09)	6.83	<0.0001*	0.094 (± 0.07)	1.28	0.203
Dry-wet transition	0.540 (± 0.09)	5.48	<0.0001*	0.192 (± 0.07)	2.53	0.012*
Wet 11	0.672 (± 0.09)	6.88	<0.0001*	0.528 (± 0.07)	6.96	<0.0001*
Pre-spike – Control						
Wet 10[a]	--	--	--	--	--	--
Wet-dry transition	0.400 (±0.09)	4.26	<0.0001*	− 0.398 (± 0.07)	− 0.54	0.590
Dry	0.635 (± 0.09)	6.76	<0.0001*	0.331 (± 0.07)	4.49	<0.0001*
Dry-wet transition	0.480 (± 0.09)	4.87	<0.0001*	0.192 (± 0.07)	2.47	0.014*
Wet 11	0.586 (± 0.09)	6.00	<0.0001*	0.444 (± 0.07)	5.86	<0.0001*

COMPETITION WITH TREES DOES NOT INFLUENCE ROOT CHARACTERISTICS OF PERENNIAL GRASSES IN SEMI-ARID AND ARID SAVANNAS IN SOUTH AFRICA.

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ABSTRACT

Savannas support mixed tree-grass communities and interactions between these are typically viewed as being competitive based on studies that focused on grass aboveground production. However, an important plant response to competition and resource limitation is an increase in root reserves. We investigated root characteristics of perennial grasses in the presence and absence of trees as a proxy of competition in South African savannas in three sites that differed in rainfall. We based our study on the hypothesis that competition from trees and water limitation will result in increased storage in roots of grasses under trees. Results indicate no significant effect of variation in rainfall of the different study locations on root characteristics of grasses. Furthermore, trees did not significantly influence most grass root characteristics that we measured. The only exception was nitrogen-content that showed an increase with rainfall and tree presence through potentially higher mineralization rates and nitrogen availability in the under-tree canopy environment. As the study sites are in the drier rainfall range in South Africa, it is likely that trees and grasses in these dry savannas may have a positive relationship conforming to the stress-gradient hypothesis. Alternatively, grasses and trees may be using complementary water and nutritional resources.

Keywords: Tree-grass competition, savannas, South Africa, dry-season root characteristics, perennial grasses, root biomass, %N, Starch, Sugars, C: N Ratio, δ^{15}N

INTRODUCTION

Mixed tree-grass communities characterize savannas and tree-grass interactions in savannas are typically viewed as being competitive (Scholes and Archer 1997, Ludwig et al. 2004b, Sankaran et al. 2004). Trees in savannas (beyond the seedling, sapling and juvenile stages) are regarded to have a higher nutrient capture capability due to their extensive spread of roots than grasses, consequently reducing grass aboveground production (Belsky 1994, Scholes and Archer 1997, Ludwig et al. 2004b, Sternberg et al. 2004). However, this is not a general rule and the absence of competition also has been shown under varying climatic conditions (Belsky 1994, Simmons et al. 2008). Data on grass and tree root distributions show that there is no spatial segregation of tree and grass roots as proposed by the Walter's two layer hypothesis (Hipondoka et al. 2003, February and Higgins 2010) indicating the dependence on the same pool of soil resources by both the plant functional types. Furthermore, meta-analysis and landscape level studies based on grass aboveground production suggest that the relationship between trees and grasses varies from competitive to facilitative with increasing aridity conforming to the stress-gradient-hypothesis (Dohn et al. 2013, Moustakas et al. 2013). Most studies addressing tree-grass interactions have focused on the effects of trees on aboveground grass production (Belsky 1994, Ludwig et al. 2001, 2004a, 2004b, Simmons et al. 2008, Dohn et al. 2013, Moustakas et al. 2013). However, aboveground responses of plants to competition cannot be extrapolated belowground since plant allocation of resources to roots is neither predictable from the aboveground parts nor proportionate to it (Casper and Jackson 1997, Zobel and Zobel 2002). The roots of grasses are the principal belowground organs that not only capture nutrients but are also the primary storage organs. In this study, we examined the influence of trees and increasing aridity on the roots of perennial grasses in South Africa.

Resource limitation is reported to influence interplant interactions (Chapin et al. 1990). Studies suggest that plants respond to resource limitation by increasing allocation of resources to storage organs (Bloom et al. 1985, Busso et al. 1990, Chapin et al. 1990, Oosthuizen and Snyman 2003, Craine 2006, Snyman 2009). For example, a water stress experiment done with the perennial grass *Themeda triandra* (Forssk.), a dominant grass species in arid and semi-arid regions of southern Africa, found that both biomass and starch content of roots in non-defoliated plants increased by about 20% with 25% increase in water stress (Oosthuizen and Snyman 2003). Most arid and semi-arid savannas in southern Africa

are dominated by perennial grasses (O'Connor 1991) and the consequences of resource limitation or competition on the roots of these grass types remain poorly understood. Adequate reserve storage in roots, particularly for perennial grasses, is not only critical for growth and reproduction but also as a buffer against effects of aboveground herbivory and fire (Danckwerts 1993, Thornton et al. 2000, Fargione and Tilman 2002).

In this exploratory study, we examined whether competition with trees influences root characteristics (as proxies of storage) of under-tree canopy perennial grasses compared with root characteristics of perennial grasses in gaps between trees (outside-tree canopy) and are outside the influence of tree roots. We did this in different sites in South Africa that varied in rainfall reflecting differences in water availability since water limitation intensifies competition among plants (Chapin et al. 1987, Gersani et al. 2001, Craine 2006). The underlying hypothesis is that competition with woody species and water limitation results in higher allocation of resources to roots of grasses. Specifically we investigated the following:

1. Does variation in rainfall at the different study sites affect root characteristics of perennial under-tree canopy grasses?
2. Are the root characteristics of under-tree canopy perennial grasses affected by the presence of trees in these different study sites?
3. Does the presence of trees and the variation in rainfall at the different study sites influence the root characteristics of these perennial under-tree canopy grasses?

METHODS

Study sites

The study was carried out in three study sites – Tswalu Nature Reserve (200 mm – Dry site), Venetia-Limpopo Nature Reserve (400 mm – Intermediate site) and Andover Game Reserve (600 mm – Wet site) in South Africa that vary in the mean annual rainfall (Fig 4. 1). In all sites most of the rain occurs between October and March. All three sites were chosen such that the soils were sandy and nutritionally poor with prominently a granitic bedrock. However, there were differences in vegetation composition largely due to the differences in the annual precipitation. The location, type of bedrock, mean annual precipitation and the common trees and grasses found in the three study sites are given in Table 4. 1. Fire is not common in Tswalu and Venetia-Limpopo Nature Reserves. However, in the latter fire management is practiced on a multi-year rotational basis that is decided by the reserve managers. In Andover GR, the Park management practices fire management with rotational
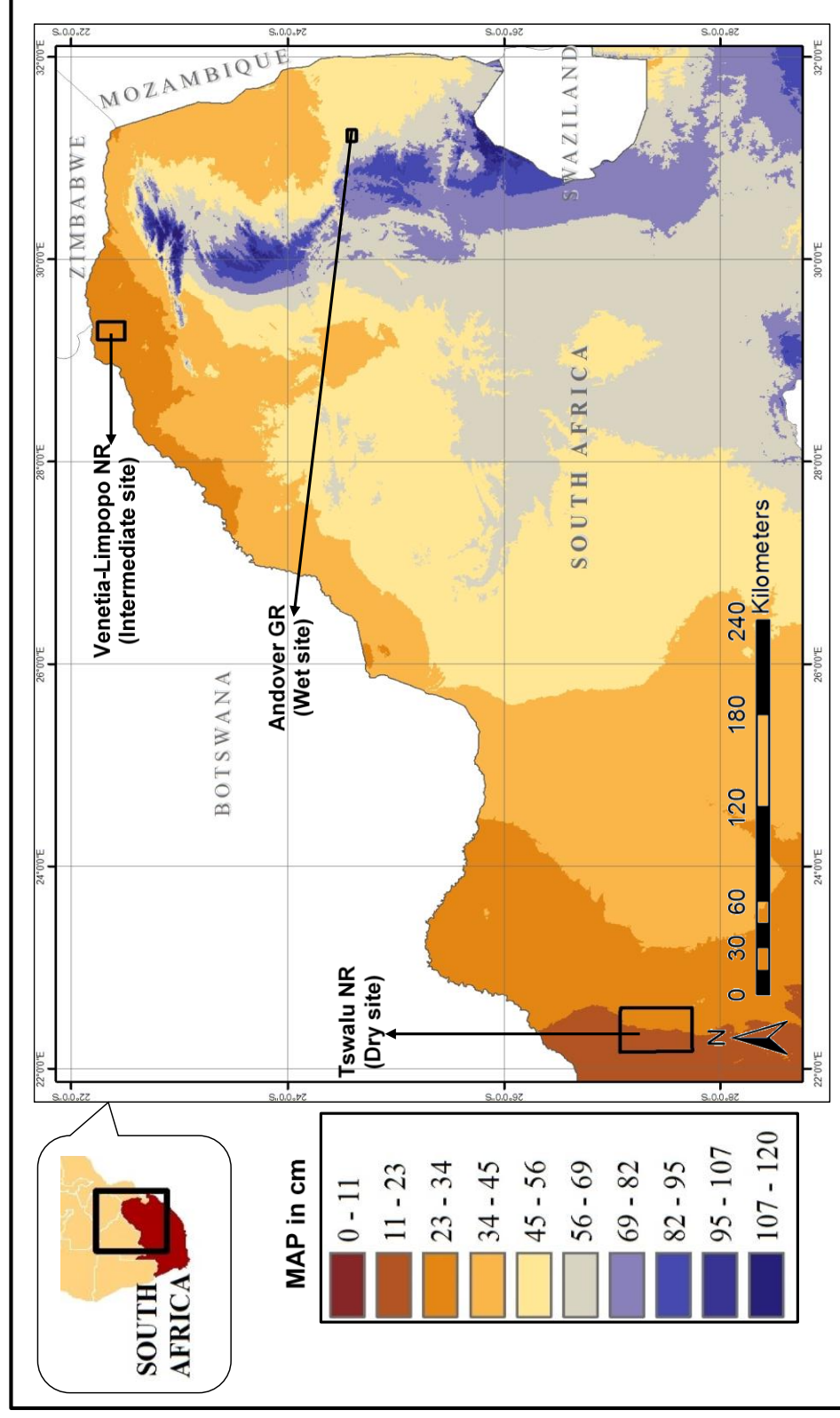
Figure. 4. 1. Location of the three study sites: Tswalu NR (dry site), Venetia-Limpopo NR (intermediate site) and Andover GR (wet site) in South Africa showing the Mean Annual Precipitation (MAP) in cm (source: World Clim).

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Table 4. 1. Description of the three sites in South Africa where the study was carried out.

Study site	Location	MAP (in cm)	Type of bedrock	Common trees/woody shrubs	Common grasses
Tswalu NR (dry site)	S 27° 04' – 27° 44', E 22° 10' – 22° 36'	20 – 25	Granitic	*Vachellia erioloba* (E.Mey.), *Senegalia mellifera* (M. Vahl), *Boscia albitrunca* (Burch.)	*Aristida stipitata* Hack *var stipitata*, *Eragrostis lehmanniana* Nees, *Stipagrostis uniplumis* (Licht. ex Roem. & Schult.)
Venetia-Limpopo NR (intermediate site)	E 29° 12' – 29° 23', E 29° 12' – 29° 23'	30 – 40	Archaean granitic	*Vachellia tortilis* (Forssk.), *Colophospermum mopane* (Kirk ex Benth.; Kirk ex J.Léonard), *Terminalia sericea* (Roxb.)	*Aristida stipitata* Hack *var stipitata*, *Chloris virgata* Sw.., *Urochloa mosambicensis* (Hack.)
Andover GR (wet site)	S 24° 33' – 24° 38', E 31° 10' – 31° 17'	55 – 65	Granitic	*Vachellia nilotica* (Linn.), *Terminalia sericea* (Roxb.), *Philenoptera violacea* (Klotzsch)	*Panicum maximum* (Jacq.), *Digitaria eriantha* Steud., *Eragrostis curvula* (Schrad.) Nees

block burning every 5 years. The study sites hereater will be referred to as Dry, Intermediate and Wet sites.

Study design and vegetation sampling

We used a split-plot sampling design. Within each study site we sampled 12 main plots. From each main plot two ungrazed subplots, one under the tree canopy and the other outside the tree canopy were sampled. The ungrazed subplots were not situated inside exclosures in any of the three study sites. Grazing was not prevalent in these sites as the animal densities were very low. We were careful that there was no grazing on these subplots as there could be grazing related compensatory growth by the grasses due to defoliation. We wanted to avoid this and solely focus on the effects of trees. A tuft of grass was selected for sampling from each subplot. We took care that all the grass tufts were similar in size in all the study sites in terms of grass height (range 55-60 cm) and grass tuft diameter (range 8-10 cm).

We selected commonly occurring acacia tree species in all three sites for sampling under-tree canopy areas. The tree species were *Vachellia nilotica* (Linn.) in the wet site, *Vachellia tortilis* (Forssk.) in the intermediate site and *Vachellia erioloba* (E. Meyer.) in the dry site. The grass species sampled under- and outside-tree canopy were all perennial tuft grasses: *Panicum maximum* (Jacq.) in the wet site, and *Aristida stipitata* Hack *var stipitata* in the intermediate and dry sites. These were the dominant under-tree canopy grasses in the three sites but were also found in a high abundance outside the tree canopy. Grass tufts were sampled around the base of the tree (under-tree canopy site) within a radius of 1m around the tree trunk and in the paired adjacent area at a 30 m distance away from the tree canopy in the open grassland (outside-tree canopy site). We maintained a distance of approximately 30 m which is considered well outside the rooting zone of any of the trees (Ludwig et al. 2003, Sternberg et al. 2004).

Sampling and analysis of roots

All sites were sampled for grass roots during the peak dry season (August 2010) when grass root reserves are expected to be at their maximum and the root turnover dynamics would be minimal (Coyne and Cook 1970, White 1973, Danckwerts and Gordon 1990, McNaughton et al. 1998). The aboveground grass leaf and stem material was removed. We collected the base of the grass tuft with the stolon, rhizomes, and the roots with root crowns of the grass tuft where the maximum storage in tropical grasses is reported (Coyne and Cook 1970,

Danckwerts and Gordon 1990). Using an auger with a diameter of 10 cm, the grass tuft was cored at the centre of the tuft until a depth of 120 cm in 20 cm increments. For analysis, the biomass of only the first 20 cm was used as both the number of roots and associated biomass became almost negligible below this depth.

Root samples along with the soil were collected and sieved with 2 mm sieves using fine water jets for separating root material. Dead root material was determined visually (whenever needed, a handheld lens was used for confirmation) and was removed. Root biomass is essentially the dry weight of the roots per unit volume of soil. The roots were air dried in an oven at 50°C (to avoid loss of organic compounds such as sugars and starch as well as to prevent volatilization of N from the plant tissues) to constant weight. The samples were finely ground in a grinding mill (2 mm mesh size) for further analysis. Root biomass was measured for all 12 main plots (24 grass tufts per site) whereas root characteristics (described below) were measured in the laboratory for only 5 main plots (10 grass tufts) per site due to laboratory time and analysis cost constraints. We carried out a post-hoc sample size estimation to ensure that a type II statistical error is unlikely (details in Appendix 4. 1).

The plant samples were lyophilized (freeze dried) before further grinding to analyse the soluble sugars and starch concentrations using an HPAEC-PAD (Dionex Corporation, Sunnyvale, CA, USA) with a DionexCarboPac PA 1 column (4 mm diameter). This was done by first extracting the soluble carbohydrates, and then enzymatically hydrolysing the starch (carried out at the laboratories of the Plant Sciences group of Wageningen University, the Netherlands). The %N, δ^{15}N, and C:N ratios were measured by weighing 40 mg sample aliquots of the plant root material into tin capsules (Elemental Microanalysis Ltd, Okehamptom, UK) at the CSIR laboratory in Pretoria, South Africa using a micro-balance (Mettler-Toledo Inc. Ohio, USA). Samples were analysed using a Flash EA 1112 system coupled with a Delta V plus mass spectrometer using a Conflo IV interface (Thermo Electron Corporation, Bremen, Germany). Atmospheric N isotope ratio was used as the standard (Mariotti 1983) and the precision was <0.2‰ for δ^{15}N. δ^{15}N was calculated with the with the formula (Shearer and Kohl 1986):

δ^{15}N = {[(^{15}N/^{14}N) SAMPLE / (^{15}N/^{14}N) STANDARD] – 1} *1000.

We do not completely exclude the possible competitive effects between grasses of the same species in the tree-gaps (outside-tree canopy areas) as we sampled plots of monoculture grass stands, which would experience typical intraspecific competition. However, interspecific competition largely outweighs intraspecific competition (Connell 1983) and

plants adapt root growth and function when surrounded by individuals of a different species (de Kroon 2007). Furthermore, Ludwig et al. (2004a) in an experimental study in East-Africa showed that competition from trees on grasses suppressed aboveground biomass which is consistent with the notion that interspecific competition may be more severe than intraspecific competition. We only selected plots for outside-tree canopy without any other woody species or tree cover with the closest tree more than 30 m away to avoid any effects of tree presence.

Measurement of root characteristics in perennial grasses

We measured the following root characteristics parameters as responses to tree presence as a proxy of competition from trees:

1. Root biomass (g/cm^3), starch and sugar content (% W/W), representing the root storage. Most storage in grasses occurs in the form of starch and sugars (Weinmann 1948, White 1973).

2. N-content (%) and C: N ratios, representing stored N in the roots.

3. Presently the use of $\delta^{15}N$ is not common in plant eco-physiology since it is still at the pattern generating and hypothesis development stage. However, it can function as a reliable parameter for the response of plants to competition (Robinson et al. 2000). Furthermore, plant $\delta^{15}N$ is found to be an indicator of both water limitation and disturbance (Handley et al. 1994, 1999). For a global dataset of plant $\delta^{15}N$, rainfall explained the maximum variation (35%) out of all the variables that were considered (Handley et al. 1999). $\delta^{15}N$ is a ratio of $^{15}N/^{14}N$. So when nitrogen content in plants increases, the concentration of ^{14}N in them increases, reducing the overall value of $\delta^{15}N$, as this lighter form is taken up more easily and is more abundant in the environment than ^{15}N. Therefore, lower $\delta^{15}N$ means higher retention capacity of N and lower losses of stored N in the roots.

Soil moisture

We measured the gravimetric soil moisture content (% W/V) by auguring soil with an incremental auger of 10 cm diameter and up to the depth of 120 cm in 20 cm increments. Soil moisture was determined by weighing fresh soil and dry soil after air drying in an oven at $100^o C$ to constant weight.

Statistical analysis

We fitted mixed linear models for split-plot designs to the different response variables, using the MIXED procedure of the SAS software program version 9. The fixed factors were: 1) rainfall (we treat rainfall as a main-plot factor, but in essence it represents study site); 2) tree canopy (under-tree canopy and outside-tree canopy subplot factor). Main plots within sites were entered into the model with random effects. For all response variables, we studied the distributions of the residuals after fitting the mixed models and found the distributions of soil moisture, root biomass, starch, sugar, and C: N ratio to be right skewed. Arcsine-square root transformations of soil moisture (g/ cm^3) and sugar, square root transformation of biomass, logit-transformation of % starch, and log transformation of C: N ratio gave approximately symmetrical distributions of the residuals. For soil moisture, four observations were removed because of unreliably large values (rendering n=67), which were due to storage problems in the field. We addressed the three questions concerning interaction between study site and canopy, and main effects of the study site and canopy, as earlier mentioned, for all the response variables. For post-hoc comparisons, t-tests and Tukey's HSD test were performed in the MIXED procedure of SAS.

RESULTS

Interaction of trees and study site (rainfall)

The linear mixed model analysis revealed that there was no significant interaction between rainfall and tree presence (under or outside-tree canopy) for soil moisture ($P = 0.08$, $F = 2.80$, $Df = 2, 29$). We also did not find any significant interactive effects of study site (rainfall) and the presence of trees on any of the root parameters that we measured (Table 4. 2).

Effect of study site (rainfall)

Soil moisture levels were well below 2 g/cm^3 during the season sampled (dry season) and differed significantly between the study sites ($P <0.0001$, $F = 35.54$, $Df = 2, 32$; Fig. 4. 2). As expected the wet site had the highest soil moisture content (1.25 g/cm^3), followed by the intermediate site (0.85 g/cm^3) while the dry site had the lowest soil moisture content (0.29 g/cm^3, Fig. 4. 2). The differences among all three sites were significant (Tukey's HSD; Wet site – Intermediate site: $P = 0.009$; Wet site – Dry site: $P < 0.0001$; Intermediate site – Dry site: $P < 0.0001$).

The root characteristics of perennial grasses showed variable responses in the different study sites most likely due to changes in rainfall (Figs.4. 3A to 4. 3F, Table 4. 2). The starch content of grass roots in the dry site was the lowest and significantly different from both the wet and intermediate sites, while starch content in grass roots in the wet and intermediate sites were similar (Table 4. 3). The %N content in the roots of grasses was highest in the wet site (0.7%), which was significantly higher than in the intermediate and dry sites (both 0.5%; Fig. 4. 3D, Table 4. 3). We did not find any significant differences in the root biomass, sugar content, and C: N ratio among the sites (Table 4. 2). The δ^{15}N of roots seemed to be influenced by rainfall (Table 4. 2). We found statistically significant differences between the dry and wet sites, and dry and intermediate sites (Table 4. 3). However, the δ^{15}N of roots were found to be similar between wet and intermediate sites.

Effect of trees

We did not find a statistically significant difference in soil moisture between under- and outside-tree canopy soils ($P = 0.23$, $F = 1.48$, $Df = 2, 29$; Fig. 4. 2). Furthermore, there were mixed responses to the tree presence on the roots of grasses with some of the root characteristics showing differences and others not, similar to our finding for the variation across the different sites. The % N was about 0.2 % higher under-tree canopy than outside (Tukey's HSD $df = 12$, $P = 0.003$; Fig 4. 3D, Table 4. 3) and the C: N was significantly higher outside-tree canopy than under-tree canopy (Tukey's HSD $df = 12$, $P = 0.03$; Fig 3E, Table 4. 3).

DISCUSSION

The starch, %N content, and δ^{15}N in roots were found to be different among study sites indicating influences related to rainfall but not to trees. The presence of trees (as a proxy for competition) positively influenced the %N content and C: N ratio. However, the other root characteristics that we measured (root biomass, starch and sugar content, and δ^{15}N) were not influenced by the presence of trees in the different study sites.

Effect of study site (rainfall)

The variation in rainfall in the three sites influenced % starch, %N, and δ^{15}N of the roots of grasses. The starch content was the lowest in the dry site, while it was similar for the other two sites. This eliminates the possibility that there could be a grass species effect, as the grass
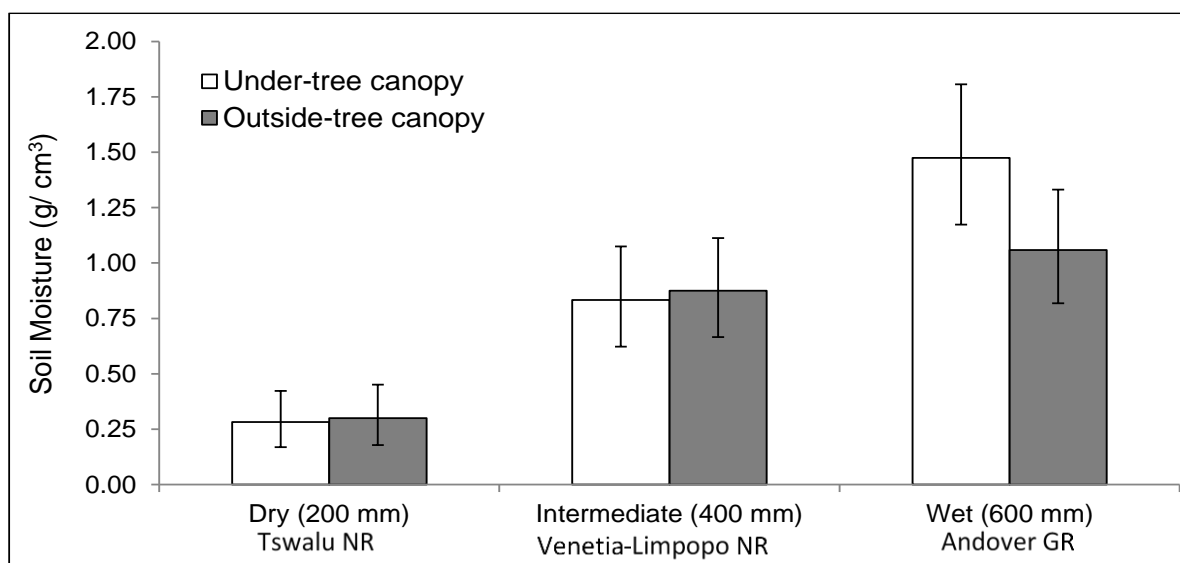
Figure 4. 2. The soil moisture content under and outside-tree canopy in three study sites in South Africa. The error bars represent the 95% confidence intervals of the mean.

Table 4. 2. Summaries of mixed linear model analyses results for differences in perennial grass root characteristics in three savannas of South Africa with different annual rainfall.

Root characteristics	Study site (Rainfall)			Under/Outside-tree Canopy			Study site* Under/Outside-tree Canopy		
	Df	*F*	*P*	*Df*	*F*	*P*	*Df*	*F*	*P*
Biomass (square-root transformed)	2, 33	0.08	0.93	1, 33	0.68	0.42	2, 33	1.24	0.30
Starch (logit-transformed)	2, 12	6.74	0.01*	1, 12	1.53	0.24	2, 12	0.94	0.42
Sugars (arc-sine square-root transformed)	2, 12	1.28	0.31	1, 12	0.03	0.86	2, 12	0.37	0.70
%N	2, 12	4.82	0.03*	1, 12	13.06	0.003*	2, 12	1.40	0.29
C:N ratio (Log_{10} transformed)	2, 12	1.57	0.25	1, 12	6.11	0.03*	2, 12	0.41	0.67
$\delta^{15}N$	2, 12	7.92	0.006*	1, 12	0.00	0.99	2, 12	2.25	0.14

* $P<0.05$

Table 4. 3. Summary of Tukey's HSD *post-hoc* comparisons of differences in the root characteristics obtained from the mixed model-split plot analysis. Results for Biomass and sugars are not included here as they were not significantly different. "Dry" is Tswalu NR, "Intermediate" is Venetia-Limpopo NR and "Wet" is Andover GR.

| Variable	Effect	Comparison of means	Mean difference (± 1SE)	Df	T	P	Adj. P	Confidence Interval Low	High
Starch (logit-transformed)	Site	Wet–Intermediate	−0.30 (±0.33)	12	−0.91	0.38	0.643	−1.176	0.576
		Dry–Intermediate	−1.16 (±0.33)	12	−3.54	0.004*	0.011	−2.038	−0.285
		Wet–Dry	0.86 (±0.33)	12	2.62	0.02*	0.054	−0.015	1.738
%N	Under/Outside tree canopy	Outside–Under	−0.18 (±0.05)	12	−3.61	0.003*	0.004	−0.290	−0.072
	Site	Wet–Intermediate	0.18 (±0.06)	12	2.94	0.012*	0.031	0.017	0.343
		Dry–Intermediate	0.04 (±0.06)	12	0.60	0.557	0.821	−0.126	0.200
		Wet–Dry	0.14 (±0.06)	12	2.34	0.037*	0.089	−0.020	0.306
C:N ratio (Log$_{10}$ transformed)	Under/Outside tree canopy	Outside–Under	0.13 (±0.05)	12	2.47	0.03*	0.029	0.016	0.252
δ^{15}N	Site	Wet–Intermediate	− 1.87 (1.03)	12	− 1.82	0.206	0.206	−4.622	0.878
		Dry–Intermediate	2.22 (1.03)	12	2.16	0.050*	0.119	−0.524	4.976
		Wet–Dry	−4.09 (1.03)	12	−3.98	0.001*	0.005	−6.848	−1.348

* P≤0.05
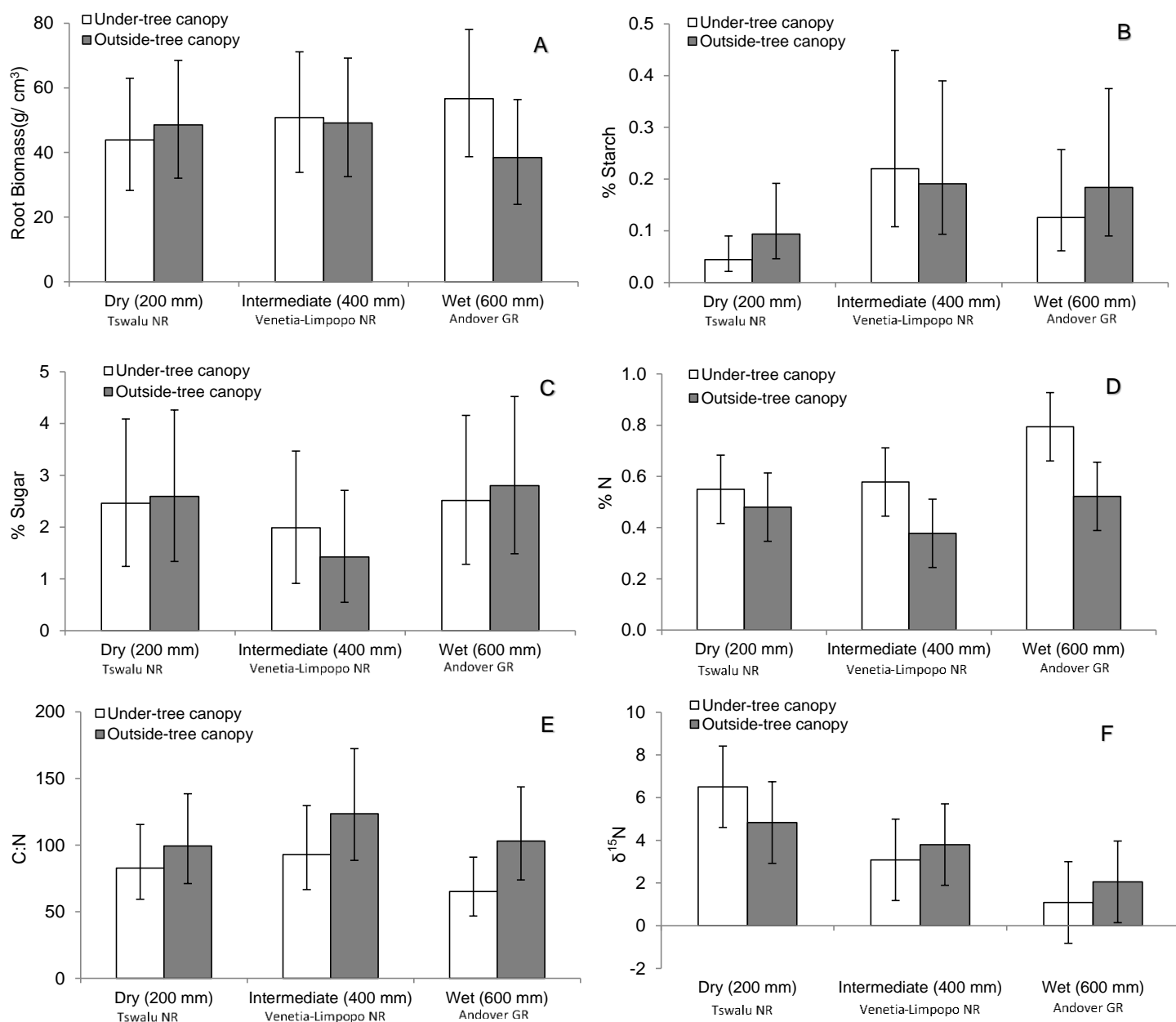
Figure 4. 3. Variation in A) the root biomass (g/ cm^3) from root cores of 10 cm diameter, B) the total starch content (%), C) The total sugar content (%; sucrose and fructose), D) The N content (% N), E) the C:N ratio, and F) the δ^{15}N – in roots of under- and outside-tree canopy perennial grasses in three study sites in South Africa. The error bars represent the 95% confidence intervals of the mean.

species in the dry and intermediate sites were the same. Of the total nonstructural carbohydrates which are the main form of root storage in perennial C_4 grasses, starch formed a comparatively smaller fraction for both the grass species that we investigated in the three study sites.

The soluble sugars (fructose and sucrose) formed a larger proportion of nonstructural carbohydrate in roots of grasses for all the three sites and the two grass species, Our underlying hypothesis on which we based this study was that with decreasing water availability the root reserves in plants will increase as they are the primary storage and nutrient acquiring organs (Chapin 1980, Bloom et al. 1985, Chapin et al. 1990, Oosthuizen and Snyman 2003, Craine 2006, Snyman 2009). Contrary to our expectations we did not find any differences in the soluble sugar content in the grasses of the three sites. Sucrose is the predominant nonstructural carbohydrate in most tropical C_4 grasses (White 1973, Busso et al. 1990, Souza et al. 2010) and reportedly aids fast aboveground growth during early wet season in dry savannas or after moderate defoliation (Danckwerts and Gordon 1990, Souza et al. 2010). Soluble sugars are more labile than starch and can be easily broken down to simpler sugars compared to starch which can be used by plants. However, sugars when in surplus are converted to starch for long-term storage (Zeeman et al. 2010, Börnke and Sonnewald 2011). It is likely that outside the dry season, soluble sugars may show different patterns from our study. However, it is unclear how useful these may be for longer term storage and likely used up for the vegetative and reproductive growth related carbon demands (Zeeman et al. 2010).

In the case of starch, our data indicate a likely relationship between rainfall and starch content of roots where starch content increased with rainfall. However, this difference was small but statistically significant (study site) even with our small data set (Fig. 3B, Tables 2 and 3). This is contrary to what several studies have reported which is an increase in the total nonstructural carbohydrates in the presence of competition or resource limitation. However, these studies do not mention starch and sugars separately (Busso et al. 1990, Oosthuizen and Snyman 2003). One thing to note is that starch and sugars are interchangeable. Therefore, surplus sugar synthesis by some plants may result in these sugars being converted to starch and breakdown of starch to simple sugars when needed (Börnke and Sonnewald 2011). It is likely that under higher rainfall conditions, grasses in savannas synthesized surplus sugars converting them to starch as is indicated by higher starch content in the wet site in this study. Furthermore, it is also likely that grasses in the dry site were locally adapted to the low rainfall conditions that made it possible for the grasses to survive even with such small starch

reserves. Although starch is a smaller fraction of the total nonstructural carbohydrates in the perennial grasses in all our study sites, it has an important role to play for long-term storage. It is one of the essential reserves for plants to use in times of stress during droughts, excessive defoliation, nutrient limitations or competition from other plants (Chung and Trlica 1980, Busso et al. 1990, Danckwerts and Gordon 1990, Danckwerts 1993).

The %N content of grass roots was higher in the wet site, while those of the other two sites with lower rainfall were similar. We could rule out the differences in $\delta^{15}N$ due to sampling of different grass species since the grass species in the intermediate and dry sties were *Aristida stipitata* which showed larger differences in the $\delta^{15}N$ values compared to *Panicum maximum*, indicating that the grass root $\delta^{15}N$ reflected the overall influence of rainfall on the cycling of N in those sites rather than the grass species differences (Handley et al. 1994, 1999). The higher %N content in the wet site probably reflects the increased N availability in the soil due to higher rainfall. This is similar to what is reported elsewhere in southern Africa where an increase in soil N with increase in precipitation for areas below 850 mm of rainfall was found (Aranibar et al. 2004). This is within the range of rainfall sampled in the present study although the effect of site was lower than the effect of tree cover (described below).

The $\delta^{15}N$ of grass roots in the dry site with lowest rainfall, was different from the other two sites. The $\delta^{15}N$ is known to reflect the soil source and ecosystem N cycling (Handley et al. 1999, Robinson 2001). Higher values of $\delta^{15}N$ indicate higher loss of N from the system with a likely open N cycle that is also associated with N limitation (Nadelhoffer and Fry 1994, Handley et al. 1999) that in turn is influenced by rainfall (Handley et al. 1994, 1999). Therefore, comparatively lower $\delta^{15}N$ values in the wet and intermediate sites suggest likely smaller losses of N as result of hihger rainfall compared to the dry site that probably has an open N cycle and associated nitrogen limitation here. An open N cycle has been reported in arid areas with associated higher N losses which results in higher $\delta^{15}N$ in plants (Aranibar et al. 2004, Swap and Aranibar 2004). In all our study sites we used grasses only under *Vachellia* tree species and did not find any nodules in any of our study trees indicating the absence of the use of N fixed by rhizobia indicating an influence of the rainfall. This is also similar to findings from other parts of Africa where $\delta^{15}N$ of foliage indicated the absence of N fixation and rather seemed to reflect the rainfall of the sites (Handley et al. 1994).

Effect of trees

The presence of trees positively influenced the root characteristics of perennial grasses. The root % N (higher under trees), and C: N ratio (lower under trees) indicated higher N use under trees than outside. These effects were observed irrespective of the site. Tree effects on N and C are well established due to higher litter deposition and resultant higher N availability under-tree canopy than outside (Belsky et al., 1989; Ludwig et al., 2004b). It is also reported that trees have a nutrient mining property which enhances the nutrient availability to under-tree canopy grasses (Ludwig et al. 2001, Dinkelmeyer et al. 2003, Lehmann 2003, Sternberg et al. 2004). In another study, we experimentally showed that savanna trees are able to redistribute subsoil N to the under-tree canopy grasses throughout the year (Priyadarshini et al. 2014) which is consistent with the idea that facilitation rather than competition between trees and grasses may be operating at all the three sites.

Effect of trees and study site (rainfall)

We did not find any interactive influence of tree presence and the differences in rainfall of the three study sites on any of the grass root characteristics. In another study done during the wet to dry transitional season in two sites with differing rainfall in Kruger National Park but higher than in any of our study sites, it was found that root biomass was higher in the gaps outside-tree canopy than under trees, while at the higher rainfall site there were no differences in root biomass outside- and under-tree canopy (February and Higgins 2010). The findings of both this study as well as ours are not consistent with the hypotheses that there is an increase in root reserves with competition and resource limitation.

Conclusion

Water limitation and presence of trees did not result in increased root reserves of savanna grasses. We found a positive influence of trees on some of the root characteristics and no effect on others. The absence of influence of trees on grass root biomass, sugars and starch was in contrast to the underlying hypothesis on which we based this study. We acknowledge that our study represents a single season snapshot of a very dynamic process of root loss and proliferation in savanna grasses. However, it is expected that root reserves during dry season should be at their highest since the translocation of nutrients from senescing leaves and aboveground parts to roots and rhizomes would have occurred (McNaughton et al. 1998). It seems likely that tree-grass interactions in these three sites conformed to the stress-gradient

hypothesis as they fell in the drier rainfall range in South Africa through the facilitative influence of trees on grasses as shown in recent studies (Priyadarshini et al. 2014, 2015). Alternatively, it is possible that competition from trees may not have the impact as was previously perceived since grasses and trees may be using complementary water and nutritional resources.

Acknowledgements

APPENDIX 4.1

We did a post-hoc sample size calculation to ensure that type II statistical errors are unlikely. For this, we calculated the sample size that we would need if the ratio of means in the two canopy groups (outside – under tree) would be 2, so on an ln-scale, the difference in means Δ would be $\ln(2)$. For simplicity, we assume that a grass variable has a log-normal distribution with a coefficient of variation CV equal to 1 (so, standard deviation is equal to the mean representing substantial variability). On ln-scale the variance will be ln (2), and the standard deviation $\sigma = \sqrt{\ln(2)}$. To give an example, for the variable starch (analyzed on the logit-scale which is almost identical to ln-scale for values close to 0), a residual variance of 0.54 was obtained in the mixed model, which is smaller than the above assumed $\ln(2) = 0.69$. If the ratio of means (outside- over under-tree canopies or vice versa) would be 2 (so, difference on ln-scale $\Delta = 2$), using a z-test for a difference of means in independent samples (note that we used a more complex mixed model for the actual analysis), testing at $\alpha = 5\%$ significance level with a power $\beta = 80\%$, the required sample size would be:

$$n = 2\frac{\left(z_{\alpha/2}+z_\beta\right)^2}{(\Delta/\sigma)^2} = 2\frac{(1.645+0.842)^2}{\left(\ln(2)/\sqrt{\ln(2)}\right)^2} = 18 \text{ in each of the groups, groups being outside and}$$

under-tree canopy.

     For the variable starch, the actual sample size is 15 (15 outside- and 15 under-tree canopy, ignoring the three sites), close to the calculated sample size of 18. For root biomass the sample size was 36, much larger than the calculated sample size. Therefore, with the sample sizes in our study, the occurrence of a type II statistical error, if in reality the ln (2) difference exists, is unlikely.

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CHAPTER 5

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THE IMPORTANCE OF TREES IN HUMAN LAND-USE SYSTEMS IN AFRICAN DRYLANDS: AN ECOLOGICAL AND BIOGEOCHEMICAL PERSPECTIVE

K. V. R. Priyadarshini, Steven De Bie, Ignas M. A. Heitkönig, Herbert, H. T. Prins

ABSTRACT

The savanna biome, a mix of trees and grasses, supports a large fraction of the human population and sustains the highest densities and diversities of herbivores in the world. However, human-used savanna landscapes that are socio-ecologically important, have become increasingly treeless due to manifold reasons. In this paper, we review the key ecological role of trees in dry savanna landscapes emphasizing their importance for improved land-use and natural resource management. We limit this review to two human-use landscapes that dominate African savannas: Agroforestry and Rangelands that include silvo-pastoralism and mixed-game-livestock farming. Although trees were a part of these land-uses, data suggests that trees have become increasingly absent from these landscapes. We discuss the causes of tree loss and highlight the influences of large savanna trees in these systems on ecosystem functioning through nutrient and water redistribution in order to maintain land quality for animal and plant production.

Key Words: African Savannas, water and nutrient redistribution, agro-ecosystems, rangelands, silvo-pastoral systems, mixed-game-livestock land-use systems.

INTRODUCTION

Savannas are an important biome comprising nearly 20% of the Earth's terrestrial surface, and in Africa, almost 50% of the land area are savanna ecosystems (Scholes and Archer 1997). They support a large fraction of the human population (almost 40%, Maestre et al. 2012) and sustain some of the highest densities and diversities of herbivores in the world. The vegetation is characteristically a mix of trees and grasses. The maintenance of this structural integrity of savannas with trees in the landscape is critical for the functioning of this ecosystem (Scholes and Archer 1997, Jackson et al. 2002, Archer and Predick 2014). Presently, there is an alarming disappearance of large trees in almost all terrestrial ecosystems around the world including savannas that can have detrimental consequences to the ecosystem integrity and biodiversity of these ecosystems (Muchena et al. 2005, Manning et al. 2006, Lindenmayer et al. 2012, Matsika et al. 2012, Wessels et al. 2013).

Trees in savannas play a multifunctional role in the management of soil quality, and contribute to animal and human welfare (Manning et al. 2006, Verchot et al. 2007, Jose 2012). Trees influence savanna ecosystem functioning by their influence on water and nutrient cycles (Bernhard-Reversat 1982, Jackson et al. 2002, D'Odorico et al. 2007, 2010). However, these important functions of trees that have potential for better land management are often ignored (Ong and Leakey 1999, Manning et al. 2006). Instead, the role of trees in providing fodder, structural diversity for animal use, shade and so forth are more frequently invoked (Manning et al. 2006). Most human land-use areas in sub-Saharan African drylands, which are principally arid and semi-arid savannas, have tree cover ranging from 10-20 % (Zomer et al. 2009). However, many of these areas have a climatic potential for a higher tree cover and the present tree cover may not be sufficient to satisfy the human requirement of tree based products, for example: charcoal, fuelwood, or animal browse (Zomer et al. 2009). In this paper we review the key ecological role of trees in African drylands, both natural and human-used, emphasizing their importance for improved land-use and natural resource management.

Tree removal impacts ecosystem functioning by altering the soil characteristics, vegetation and wildlife habitats, and finally affecting the human communities that depend on these ecosystems (Ludwig and Tongway 2002, Kaur et al. 2005, Sangha et al. 2005, Manning et al. 2006, Lindenmayer et al. 2012, Carsan et al. 2014). Furthermore, stochastic rainfall patterns in combination with increasing intensity of livestock grazing prevents the establishment and recruitment of new trees, particularly in drylands (Muchena et al. 2005,

Zomer et al. 2009, Maestre et al. 2012). The importance of retaining trees in human-use landscapes is recognized and the direct ecosystem services that they provide, like fuelwood and fodder for animals, are being utilized by humans (Ong and Leakey 1999, Le Houérou 2006, Manning et al. 2006). Nevertheless, rapid decline in trees from human-use landscapes continues to occur (Zomer et al. 2009). In this paper, we highlight the importance of large savanna trees in two human land-use types that dominate African drylands: agroforestry and rangeland systems that include silvo-pastoral systems and mixed-game-livestock farming systems. Although trees were an integral part of these landscapes having ecological and socio-economic significance, data suggests that trees are becoming increasingly absent here (Walker 1993, Muchena et al. 2005, Le Houérou 2006, Manning et al. 2006, Verchot et al. 2007). Further, we highlight the importance of retaining savanna trees in these land-use systems for proper ecosystem functioning through nutrient and water redistribution in order to maintain land quality for animal and plant production.

TREE IMPACTS ON ECOSYSTEM FUNCTIONS: WATER AND NUTRIENT REDISTRIBUTION

Through its effects on soil moisture, rainfall is the major external driver for savannas (Scholes and Archer 1997). It is reported to be the largest dynamic factor that influences the plant-soil processes and can influence the ecosystem services provided by trees that are integral to the functioning of dry savannas (D'Odorico et al. 2010). In arid and semi-arid savannas, trees are reported to modulate and sustain evapo-transpiration, influence the effects of precipitation, and impact groundwater recharge (D'Odorico et al. 2007, 2010). Studies have shown that soils in the under-tree canopy have higher rates of mineralization and higher soil nitrogen content through likely increased nutrient inputs via litter-fall (Bernhard-Reversat 1982, Belsky et al. 1989, 1993a). Increased mineralization rates, decreased evapotranspiration and higher nutrient content of grasses under savanna trees provides better quality forage to herbivores (Belsky et al. 1989, Treydte et al. 2007, Ludwig et al. 2008). In Laikipia (Kenya), it was found that both native herbivores and cattle preferentially used grass under trees during drought due to higher quality of forage available there (Augustine et al. 2011). Therefore, the arrangement of trees in a landscape not only influences ecosystem functioning but also herbivore movement patterns which in turn have significant impacts on the ecosystem (Thompson Hobbs 1996). Thus, the relationships between trees and terrestrial ecosystem functioning is not only complex but also highly significant.

Trees and hydraulic redistribution

As shown in Fig. 5.1, trees play a crucial role in the eco-hydrology of savanna ecosystems (Lee et al. 2005, D'Odorico et al. 2007, 2010, Brooks et al. 2010). Trees modulate upward, downward and lateral flows of water. With their deep roots, trees are able to extract deep-soil or groundwater sources making this water available to shallow rooted plants (Lee et al. 2005, D'Odorico et al. 2010, Priyadarshini et al. 2015). Deep-soil water extraction is expected to be more pronounced in environments where topsoil undergoes rapid drying as in regions with coarse soils or with unpredictable and variable rainfall (D'Odorico et al. 2007). Studies show that trees increase infiltration rates through downward hydraulic-redistribution buffering the deep-soil water loss from climatic fluctuations and making this water a reliable water source to deep rooted plants (Eldridge and Freudenberger 2005, Lee et al. 2005). In a *Prosopis velutina* savanna, tree hydraulic-redistribution accounted for up to 50% of deep-water recharge and contributed almost equally to drought season transpiration (Scott et al. 2008). Some neo-tropical savanna trees, through extensive lateral rooting systems can transport water laterally up to 9 times the canopy size (Sternberg et al. 2004). Trees can also mobilize tightly bound immobile water in the soil and make them available to other plants and soil organisms (Brooks et al. 2010). Furthermore, through their water redistribution capacity, trees can sustain beneficial micro-organisms in the soil. Studies have shown that hydraulic-redistribution by trees during dry periods helps sustain the mycorrhizal community in the topsoil by preventing their desiccation thereby increasing the overall nutrient capture potential (Querejeta et al. 2003, 2007). Trees affect overall water budgets of an ecosystem by not only hydraulic-redistribution but also through the associated gas-exchange and transpiration. These processes are maintained without tree mortality during times of water stress largely because of hydraulic-redistribution (D'Odorico et al. 2007, Prieto et al. 2012).

With the use of stable isotope tracers, it was experimentally demonstrated that semi-arid savanna trees redistributed water from deep-soil to the topsoil during the dry season from where perennial grasses took it up (Priyadarshini et al. 2015). This suggests that dry season hydraulic-redistribution by trees can facilitate under-tree canopy perennial grasses by potentially preventing their desiccation and ensuring their long term survival. Additionally, dry season redistribution by savanna trees likely aids in reducing the loss of root storage, and maintaining photosynthetic potential for the upcoming growing season. The facilitative effects of trees on under-tree canopy grasses seems to increase with decreasing rainfall conforming to the "stress-gradient hypothesis" suggesting a positive influence of trees on
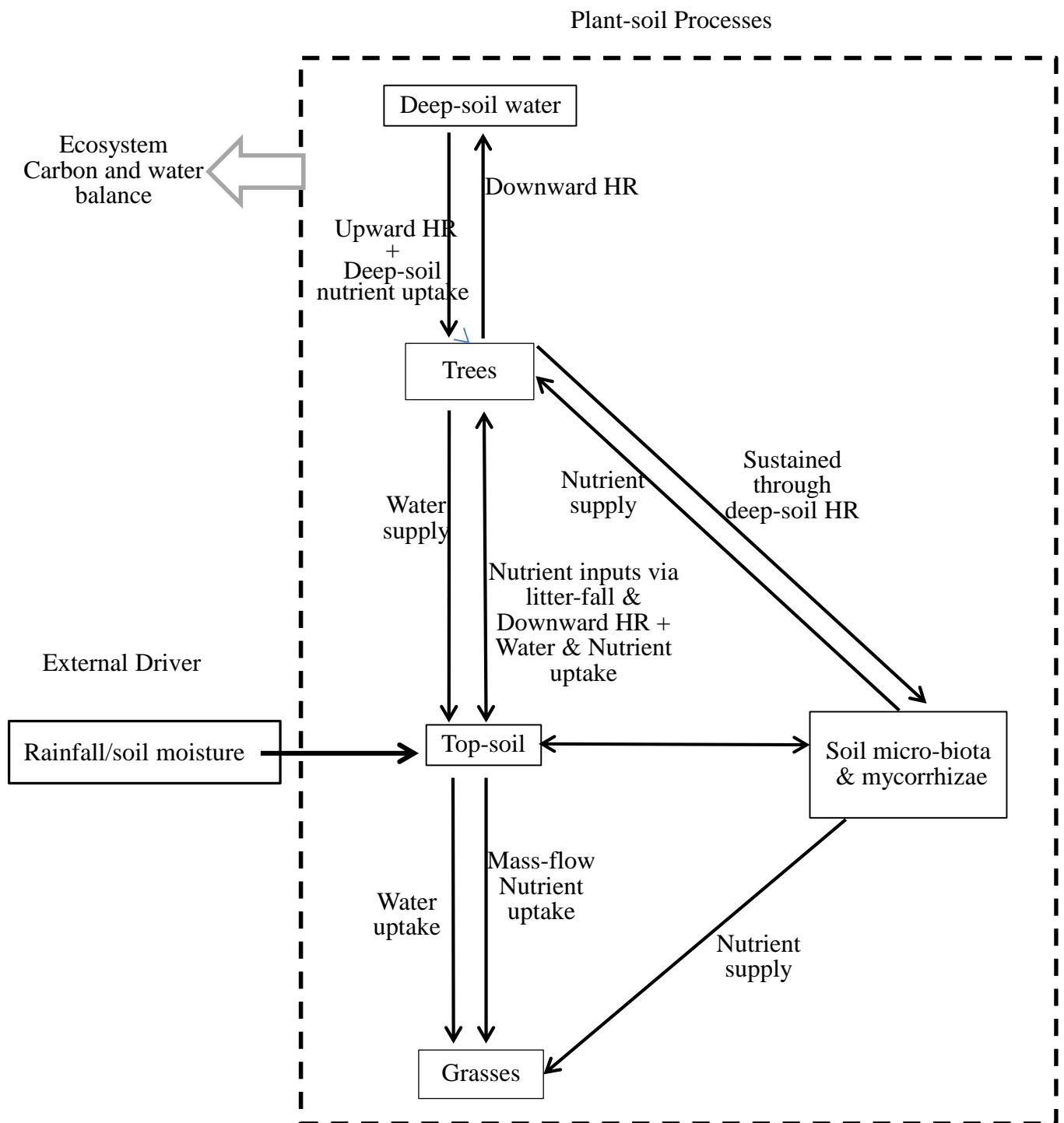
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Figure 5.1. Hydraulic-redistribution (HR) by trees and its influence on different components of the plant-soil system and the environment.

grasses at drier ends of the rainfall gradient (D'Odorico et al. 2007, Dohn et al. 2013, Moustakas et al. 2013). Hydraulic-redistribution by savanna trees is more common than previously understood since different types of savannas trees which are common and abundant in southern African savannas, hydraulically redistributed water (Priyadarshini et al. 2015). Therefore, the ecosystem impacts of tree removal on the hydrologic-cycle may be large and need to be investigated further. We summarize the critical role played by tree hydraulic-redistribution in the eco-hydrologic interactions in a tree-grass system:

1. Trees prevent dry season desiccation of under-tree canopy grasses and prevent loss of root reserves needed for early wet season growth.
2. Trees aid in the maintenance of rhizosphere micro-biota and mycorrhizal communities thereby increasing nutrient capture potential particularly of the plant-growth limiting elements such as potassium and phosphorus.
3. Trees maintain their roots in the topsoil through hydraulic-redistribution allowing them to capture nutrients from mass-flow during the wet season.
4. Increased downward hydraulic-redistribution by trees during precipitation events results in increased infiltration to the deep-soil creating a stable water source.

Trees and nutrient redistribution

Trees provide nutrient hotspots for the growth of plants under-tree canopy through their effects on mineralization rates, increased nutrient inputs via litter-fall (Belsky et al. 1989, 1993a), harbouring a unique suite of rhizosphere fungi (Bennett et al. 2009), and through their nutrient redistribution properties that can facilitate neighbouring under-tree canopy plants (Priyadarshini et al. 2014). As shown in Fig. 5.2, trees are key components of the nutrient cycles in savannas. Through their association with rhizobia and mycorrhizae, trees modulate the supply of nitrogen and phosphorus in the soil (Högberg 1986a, Newman and Ritz 1986). Experiments with ^{15}N tracers showed that savanna trees redistributed nitrogen from deep-soil to the topsoil enabling its uptake by the under-tree canopy grasses (Priyadarshini et al., 2014; Fig. 5.2). This phenomenon was not seasonally limited unlike hydraulic-redistribution and occurred throughout the year by different savanna tree types that are common and abundant in southern Africa indicating that deep-soil nitrogen-redistribution by savanna trees may be a common occurrence. Additionally, there is a possibility of increased contribution of deep-soil phosphorus, calcium and magnesium to plants as shown from strontium isotope data (McCulley et al. 2004).
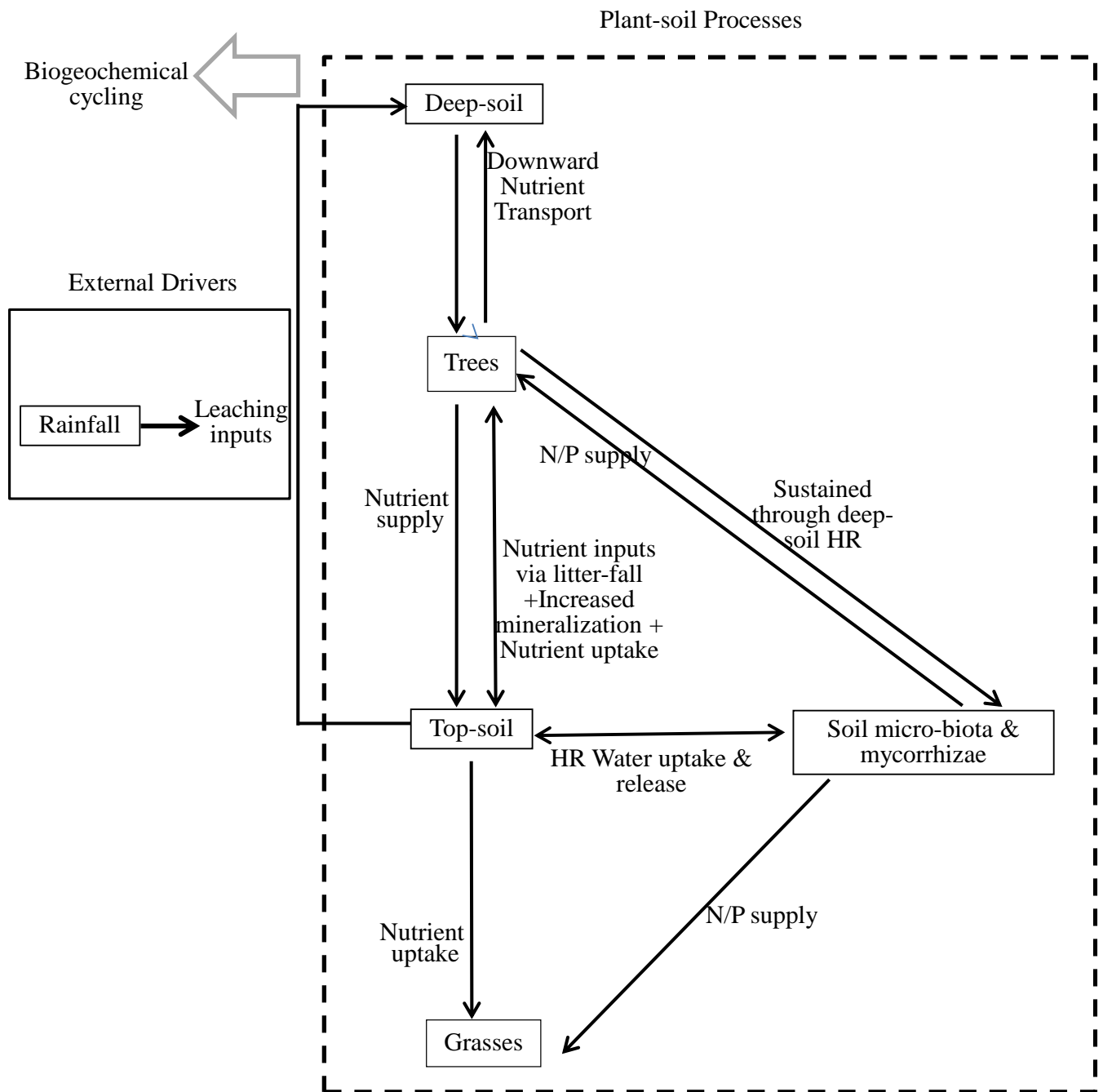
Figure 5.2. Nutrient redistribution by trees and its influence on different components of the plant-soil system and the environment. HR refers to hydraulic redistribution, N and P refer to Nitrogen and Phosphorus respectively.

The redistribution of nitrogen by trees in dry savannas can be potentially significant to the nitrogen cycle in these nitrogen-limited ecosystems. Due to their capacity for subsoil nutrient redistribution (Lehmann 2003, Priyadarshini et al. 2014), trees can make an important contribution to the biological cycling of nutrients by releasing them from the soil and integrating these otherwise unavailable nutrients to plants and other micro-biota, and into the biological nutrient cycles (Fig. 5.2). Therefore, loss of trees from terrestrial ecosystems, particularly savannas will result in the loss of a key function – nutrient redistribution, that is provided by trees (Manning et al. 2006). In summary the role of trees in nutrient redistribution is of significance for savanna ecosystems because:

1. Savanna trees redistribute deep-soil nutrients (and potentially other nutrients like phosphorus and potassium) making them available to shallow rooted neighbouring plants in the topsoil, consequently reducing inter-plant competition.

2. Nitrogen redistribution from deep-soil to the topsoil by savanna trees is not seasonally limited. Therefore, there is high likelihood of a reduction in nitrogen limitation for both trees and grasses in savannas.

3. Nitrogen redistribution may help reduce the external inputs of nitrogen through fertilizers in agricultural systems.

4. Rehabilitation of degraded lands through planting of trees will supply the topsoil with deep-soil nutrients like nitrogen and others like phosphorus potentially enhancing the colonization and survival rates of shallow rooted herbs and grasses.

TREES IN HUMAN-USE LANDSCAPES

Agricultural intensification, expansion and increased mechanization of agricultural activities, in addition to an increasing demand for fuelwood, are the major causes of declining trees in human-use landscapes (Muchena et al. 2005, Manning et al. 2006, Lindenmayer et al. 2012, Matsika et al. 2012, The Montpellier Panel 2013, World Economic Forum 2014). For example, a study in the communal lands of South Africa predicts that the woody biomass of the study sites will be exhausted in about 13 years unless there is about 15% reduction in fuelwood consumption (Wessels et al. 2013). It is predicted that global demand for fuelwood will rise 6 fold and prices will converge towards the price of industrial wood (Rauniker et al. 2010) increasing the probability of conflict (Adams 2003). Thus, the exploitation of remnant trees in human-use landscapes needs conservation attention. Integrating agro-forestry practices in cropland and rangeland management is one of the ways of sustainable food or

livestock production (Verchot et al. 2007, Thornton and Herrero 2014). In this section we highlight two such land-uses, agroforestry and rangelands that are used for animal production.

The inclusion of trees is a key feature of agroforestry systems and rangelands that include silvo-pastoralism and mixed-game-livestock farming. These land-uses are considered multifunctional land uses that promote sustainable exploitation of natural resources (Blench 2001, Herrero et al. 2010a, Jose 2012, Archer and Predick 2014, Binswanger-Mkhize and Savastano 2014) and are additionally environment friendly with reduced external inputs of fertilizers for increased biomass production (Verchot et al. 2007, Thornton and Herrero 2010). Here we discuss the ecological significance of trees in agroforestry and rangelands systems in Africa.

Agroforestry systems

Agroforestry is inclusive of trees in agricultural practices (Torres 1983, Sanchez 1995) and is promoted as a sustainable land-use practice that combines the best attributes of forestry and agriculture. Agroforestry is also a traditional farming system that is geographically extensive, for example: the *Faidherbia albida* systems in west and east Africa, the *dehesa* system in Spain, the *montado* system of Portugal, and other forms of agroforestry practices in South America and South Asia (Le Houérou 2006). Agroforestry is reported to play a role in carbon sequestration and mitigation of atmospheric accumulation of green-house-gases (Verchot et al. 2007). However, the contribution of agroforestry to natural resource conservation, namely soil nutrient and water resources, is often overlooked. Efficient resource utilization can be achieved through agroforestry practices (Tian et al. 2005, Carsan et al. 2014). The land quality can be maintained with agroforestry for long-term benefits than with monoculture crops (Prinsley 1992, Buresh and Tian 1998). For example, studies in India and Kenya show that agricultural utilization of rainfall under agroforestry was twice that of conventional annual cropping systems reducing the need for external irrigational inputs (Ong et al. 2002).

Figure 5.3 illustrates the major components of an agroforestry system. The differences from a natural savanna are the under-tree canopy characteristics, arrangement of trees in the landscape and the absence of large herbivores in agroforestry land-use. In natural savannas, the under-tree canopy is a dynamic and resilient mixture of perennials and annuals plants with different phenologies and potentially complementary resource use patterns (Ong and Leakey 1999, van Noordwijk and Ong 1999, Ong et al. 2002). In agroforestry, the under-tree
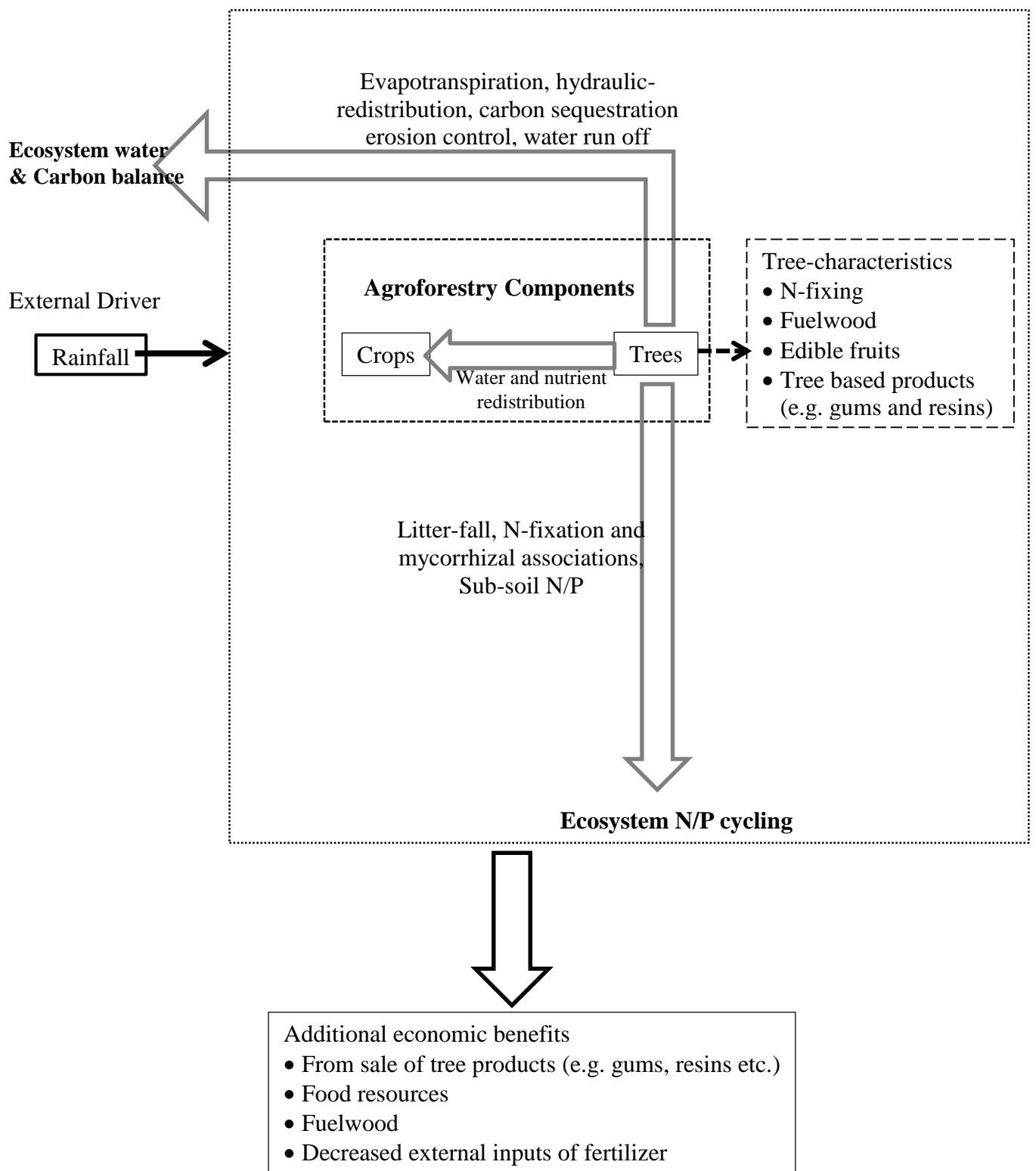
Figure 5.3. The ecological role of trees in agroforestry land-use system.

canopy is less plant-diverse with high yielding annuals that have high nutritional demands (Ong and Leakey 1999, Carsan et al. 2014) and trees are selected for characteristics that provide economic benefits to the farmer (Ong and Leakey 1999, Fig. 5.3). Furthermore, in irrigated and fertilized farms, the nutrient-redistribution capacity of the trees may be compromised since under these conditions, trees may be induced to use the topsoil resources bringing about competition with the crop plants (Lehmann 2003).

Mixed cropping with trees is declining in most parts of the world with increased mechanization and agricultural intensification (Ong and Leakey 1999, Zomer et al. 2009, The Montpellier Panel 2013, Pingali et al. 2014). Most agro-ecosystems are turning into monoculture croplands and much of the sustainability of agroforestry is lost (Prinsley 1992, Tilman 1999). For example, up to 30% of the east and west African Sahel is affected by human induced soil degradation, substantial increase in cropland areas devoid of trees, and increased mechanization (Tappan and McGahuey 2007). Increasing human population, rising demands for fuelwood, and rising labour requirements seem to be the major causes of removal of trees from most agroforestry systems (Tian et al. 2005, The Montpellier Panel 2013, Binswanger-Mkhize and Savastano 2014). Furthermore, agricultural intensification has resulted in unsustainable external inputs of water and nutrients leading to a decline in land quality and high levels of soil degradation (Tilman et al. 2002, The Montpellier Panel 2013, 2014, World Economic Forum 2014). Despite improved crop varieties, increased nutrient inputs, access to markets and technology, farmer income has not improved and soil degradation is a serious issue (Tilman 1999, Tilman et al. 2002, Carsan et al. 2014) exacerbated by the loss of trees in this land-use.

Trees in Agroforestry

The role of trees in agroforestry falls in to two categories: a tangible product output like fodder, timber, fuel, fruits etc., and "intangible" services like nutrient and water cycling, prevention of soil erosion, increasing the rates of soil water recharge and so on. The multiple contributions of trees in agroforestry are shown in Figure 5.3. Trees in agroforestry not only provide economic benefits but also promote the sustainable use of land, water and nutrient resources through the ecologically significant role they play in water and nutrient cycles (Fig. 5.1 and 5.2) similar to natural savannas. Intercropping with trees improves the efficiency of resource utilization (Tian et al. 2005, Le Houérou 2006, Verchot et al. 2007). For example, agricultural trials in agroforestry systems in Africa found that maize yields increased significantly on nitrogen-limited and degraded soils under agroforestry than conventional

farming (Verchot et al. 2007). Furthermore, modelling exercises in these same studies showed maintenance of maize yields even during dry years where conventional systems gave low yields (Verchot et al. 2007), showing that trees are important components for sustainable resource management in agroforestry (Sanchez 1995, Pate and Dawson 1999, van Noordwijk and Ong 1999, Le Houérou 2006, Carsan et al. 2014).

Most agricultural production in sub-Saharan Africa is rain-fed (UNDP 2000, Sivakumar et al. 2005). Land was traditionally left fallow for different periods allowing for soil nutrient recovery (Franzel 1999, Gaiser et al. 2011). Better soil management in agroforestry is attainable using improved fallow practices with the use of trees (Tian et al. 2005). Additionally, the loss of topsoil due to erosion and weed invasion is prevented resulting in better soil fertility that increase crop yields in the subsequent cropping phases (Buresh and Tian 1998, Ong et al. 2002, Tian et al. 2005, Binswanger-Mkhize and Savastano 2014). Traditional fallows that included trees are reported to suppress weeds, and soil borne pests and pathogens (Ogungbile and Manyong 2003). However, with an expanding human population and increasing scarcity for land, fallow periods are shortened or abandoned resulting in soil degradation preventing soil nutrient recovery leading to additional and unsustainable use of external inputs of nutrients (Franzel 1999, Tilman et al. 2002, Gaiser et al. 2011). Studies show that leaving the land fallow with nitrogen-fixing *Sesbania sesban* trees increased the maize yields as well as reduced the fallow time between cropping cycles (Sanchez 1995, Kwesiga et al. 1999, Tian et al. 2005).

The practice of fallows in small land-holder farming systems which was practiced in the past has drastically declined, draining the already nutrient limited soils with no means for external inputs by this farming community (Tian et al. 2005, Binswanger-Mkhize and Savastano 2014, World Economic Forum 2014). Reduced yields over short cropping cycles and various other social causes in addition to mechanization of agriculture seem to discourage the use of agroforestry practices in farmlands (Sanchez 1995, Ong and Leakey 1999, Zomer et al. 2009, Binswanger-Mkhize and Savastano 2014). Also, the range of trees that can successfully be incorporated into agroforestry practices are presently restricted and more trees that can provide both ecological services as well as economic benefits will need to be incorporated into agroforestry systems (Ong and Leakey 1999).

Rangelands: silvo-pastoral and mixed-game-livestock production systems

In their natural state rangelands consist of a mixture of grasses and woody plants with primary production that is dependent on the magnitude and seasonality of the rainfall (Walker

1993, Cumming and Du Toit 1999). Natural savanna rangelands have a higher diversity of native herbivores that are a mix of grazers and browsers, and show spatial seasonal movements in response to distribution of food, water and predators. This makes savanna systems highly responsive to the behaviour of animals and can have profound effects on the ecological functioning of this system by their influence on net primary production and nutrient cycling (Thompson Hobbs 1996, Cumming and Du Toit 1999). The primary use of rangelands is for livestock production as these lands are not economically viable for crop production. They differ from natural savanna rangelands in the vegetation composition, and are lower in plant and animal diversity (Walker 1993, Cumming and Du Toit 1999, Walker and Janssen 2002, Asner et al. 2004). In this paper we focus on the dry rangelands of Africa. With livestock demands expected to double by 2050, it becomes imperative that exploitation of African dry rangelands is done sustainably (Herrero et al. 2010a). Furthermore, rangelands of Africa are predicted to be highly vulnerable to global climate change as temperatures in Africa are predicted to increase higher than the global average whereas the rainfall is predicted to decrease (Herrero et al. 2012, Maestre et al. 2012).

Rangeland use and management for livestock production in Africa ranges from nomadic pastoralism, mixed subsistence farming relying mainly on livestock, mixed crop-livestock farming that relies mainly on farming and is termed agro-pastoralism, and mixed-game-livestock farming (Walker 1976, 1993). However, in virtually all of them, technological advancements like water provisioning, disease control and improved breeds, have led to over exploitation of rangelands (Walker 1993, Oba et al. 2000, Blench 2001, Walker and Janssen 2002). For this paper, we highlight two systems that include trees in the rangelands: silvo-pastoralism (Fig. 5.4) and mixed-game-livestock farming (Fig. 5.5).

Silvo-pastoral land-use systems

Silvo-pastoral systems use rangelands for livestock production that are inclusive of trees in land management. The characteristics of silvo-pastoral systems are livestock mobility, use of multiple livestock species, both of which allow exploitation of grazing resources that are unevenly distributed in time and space, and exploitation of multiple vegetation states, like woody perennials (Le Houérou 1980, Oba et al. 2000). This kind of nomadic pastoralism is fast declining in most parts of Africa (Le Houérou 1980, Prins 1992, Oba et al. 2000, Blench 2001) with global monetization resulting in decreased ratio between livestock and pastoralist numbers (Prins 1992). Furthermore, increasingly silvo-pastoralism is being replaced by agro-pastoralism which is principally a crop-livestock system where animals form an additional

source of income. This shift in pastoralism is occurring due to multiple reasons, some of which are food security, competition for resources and land, and political boundaries (Rass 2006, Herrero et al. 2012). For example, a switch from silvo-pastoralism to agro-pastoralism in the Sudano-Sahelian zone that traditionally supported nomadic and/or transhumant pastoralist population that depended on these Sahelian rangelands has occurred to meet food requirements (Le Houérou 1980, Breman and de Wit 1983, Nori et al. 2005). This has led to irreversible land degradation (Breman and de Wit 1983) and human conflict (Nori et al. 2005, Herrero et al. 2010a).

Rangeland management in silvo-pastoral systems has inclined towards increased biomass production emphasizing water provisioning and forage production, while trees are given little importance (Blench 2001, Cousins et al. 2010). The biomass production based assessment of rangeland condition has been questioned (Blench and Sommer 1999). With increasing effects of climate change and land degradation, an integrated rangeland management is advised that focuses on the functional integrity of grazing systems that include soil stability, eco-hydrology, erosion, and several other parameters (Herrero et al. 2010b). With the removal of trees from silvo-pastoral rangelands or conversion to agro-pastoralism that relies heavily on crops and crop residues as animal feed, a large part of functional diversity of savannas is eliminated (Blench and Sommer 1999, Manning et al. 2006, D'Odorico et al. 2010, Carsan et al. 2014). As illustrated in Figure 5.4, trees form a key component of silvo-pastoral land-use as in natural savannas (Fig. 5.1 and 5.2) and agroforestry systems (Fig. 5.3) described earlier. As in agroforestry, trees in this system are selected for characteristics that can provide economic benefits to the silvo-pastoral communities (Le Houérou 1980, 2006) but provide other ecosystem services as in natural savannas.

Mixed-game-livestock production systems

The difference between silvo-pastoral systems and mixed-game-livestock farming is the management of rangelands using wild herbivores in combination with livestock (Walker 1976, Cumming and Du Toit 1999). Early conservationists promoted this kind of rangeland exploitation on the premise of increased secondary productivity (per unit of animal biomass produced), multi-species utilization of resources and the perceived mimicking of natural savannas (Mossman and Mossman 1976, Walker 1976, Prins 1994, Carruthers 2008), particularly with cattle, since these do not utilize available food sources as fully as native ungulates making limited use of woody browse (Augustine et al. 2011). As shown in Figure 5.5, this kind of land use system may mimic natural savannas, particularly with the kind of
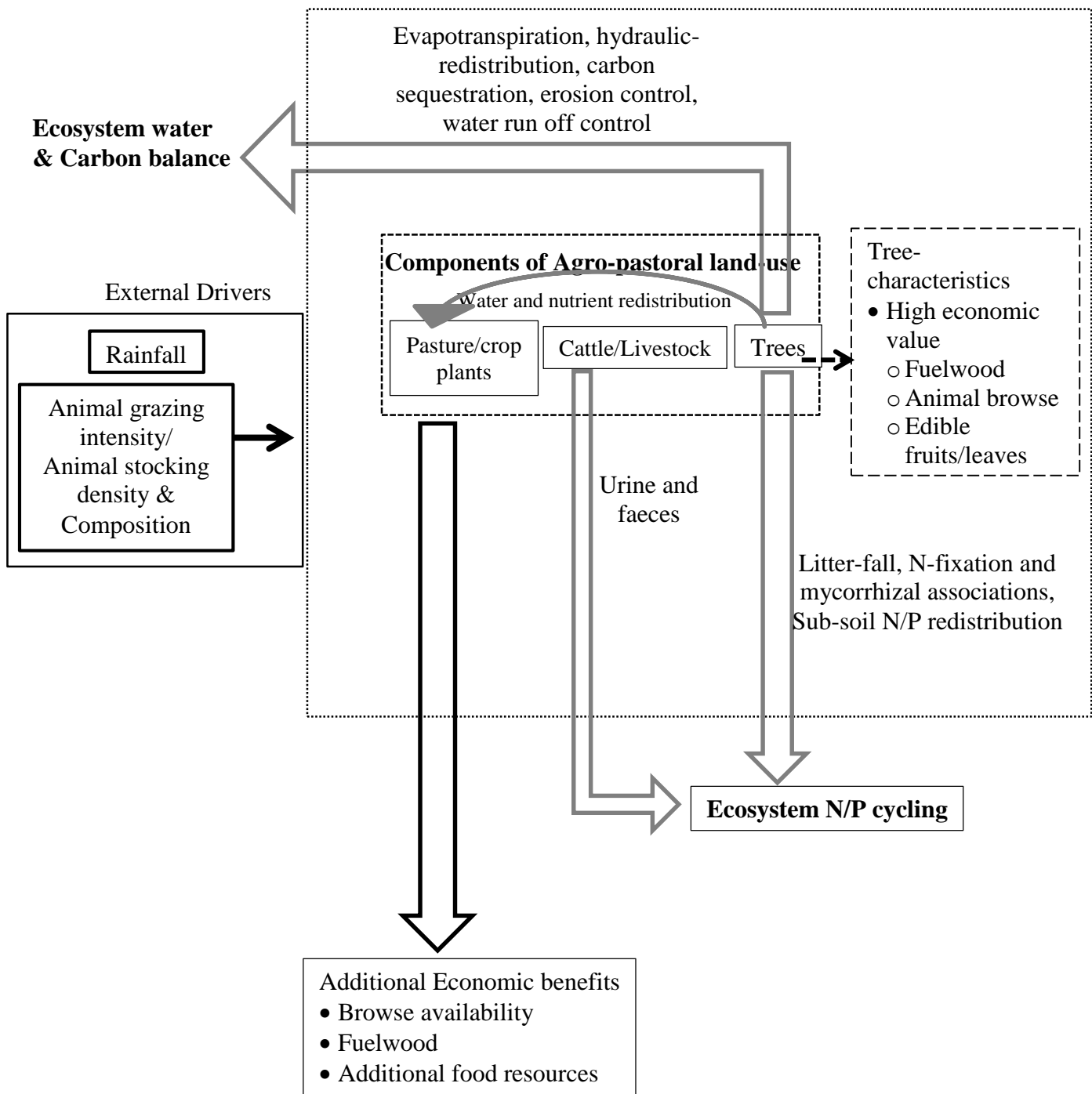
Evapotranspiration, hydraulic-redistribution, carbon sequestration, erosion control, water run off control

Ecosystem water & Carbon balance

External Drivers

Rainfall

Animal grazing intensity/ Animal stocking density & Composition

Components of Agro-pastoral land-use

water and nutrient redistribution

Pasture/crop plants

Cattle/Livestock

Trees

Tree-characteristics
- High economic value
  o Fuelwood
  o Animal browse
  o Edible fruits/leaves

Urine and faeces

Litter-fall, N-fixation and mycorrhizal associations, Sub-soil N/P redistribution

Ecosystem N/P cycling

Additional Economic benefits
- Browse availability
- Fuelwood
- Additional food resources

Figure 5.4. The ecological role of trees in silvo-pastoral land-use system

trees that are left on the landscape and to some extent the suite of wild herbivores that are reared on this land-use type. Furthermore, in South Africa, mixed-game-livestock farming has been shown to be economically profitable and at the same time, helped restore grazing areas and conserve wildlife (Carruthers 2008, McGranahan 2008).

Livestock-wildlife interactions are often viewed in terms of competition because herbivores with overlapping habitats and diets have obvious potential for competition. In a comprehensive review on competition between livestock and wildlife in Africa, Prins (2000) suggested that despite considerable resource overlap between wildlife and cattle, competition is largely asymmetrical and diffuse, with cattle having a competitive effect on some wildlife species, but wildlife often having little or no net competitive effect on cattle indicating that mixing wild herbivores with cattle is an economically viable option. A major economic benefit of mixing livestock with native ungulates in addition to game meat is the control of woody vegetation preventing woody plant encroachment as was found in Laikipia, Kenya (Augustine et al. 2011). The primary objective of conservationists to promote mixed-game-livestock farming is that managed rangelands will play a critical role in the conservation of Africa's large mammalian fauna (Prins et al. 2000). Mixed-game-livestock farming land-use systems are acknowledged to not only sustain nutrient heterogeneity through the rotational management of bomas and movement of native herbivores (Augustine et al. 2011) but also the structural heterogeneity through the inclusion of trees in the rangeland (Fig. 5.5) making it a sustainable form of rangeland land-use.

Nevertheless, the emphasis has continued (and will continue) to be on the monetary returns from animal production in addition to the increased demand for animal protein, tourism or hunting rather than maintaining ecosystem health (Carruthers 2008, Cousins et al. 2010). In parts of Africa where mixed-game-livestock farming is practiced, a large proportion of the land is under private management and management practices are tuned to increase animal production or better game viewing (Mkhabela 2003, Cousins et al. 2010). Tree removal is practiced on many of these farms to increase short-term grass production and improved game viewing for tourism (Mkhabela 2003, Smit 2004, McGranahan 2008). However, despite much research on woody and grass layers, the ecological basis for designing a sound land-management programme for mixed-game-livestock farming is still lacking. Changing densities of trees in mixed-game-livestock farming systems can have different consequences for both native flora and fauna (Archer and Predick 2014). Increased woody vegetation may favour browsing herbivores and decrease grazing herbivores (Smit and Prins 2015). Furthermore, increased woody vegetation decreases grass production
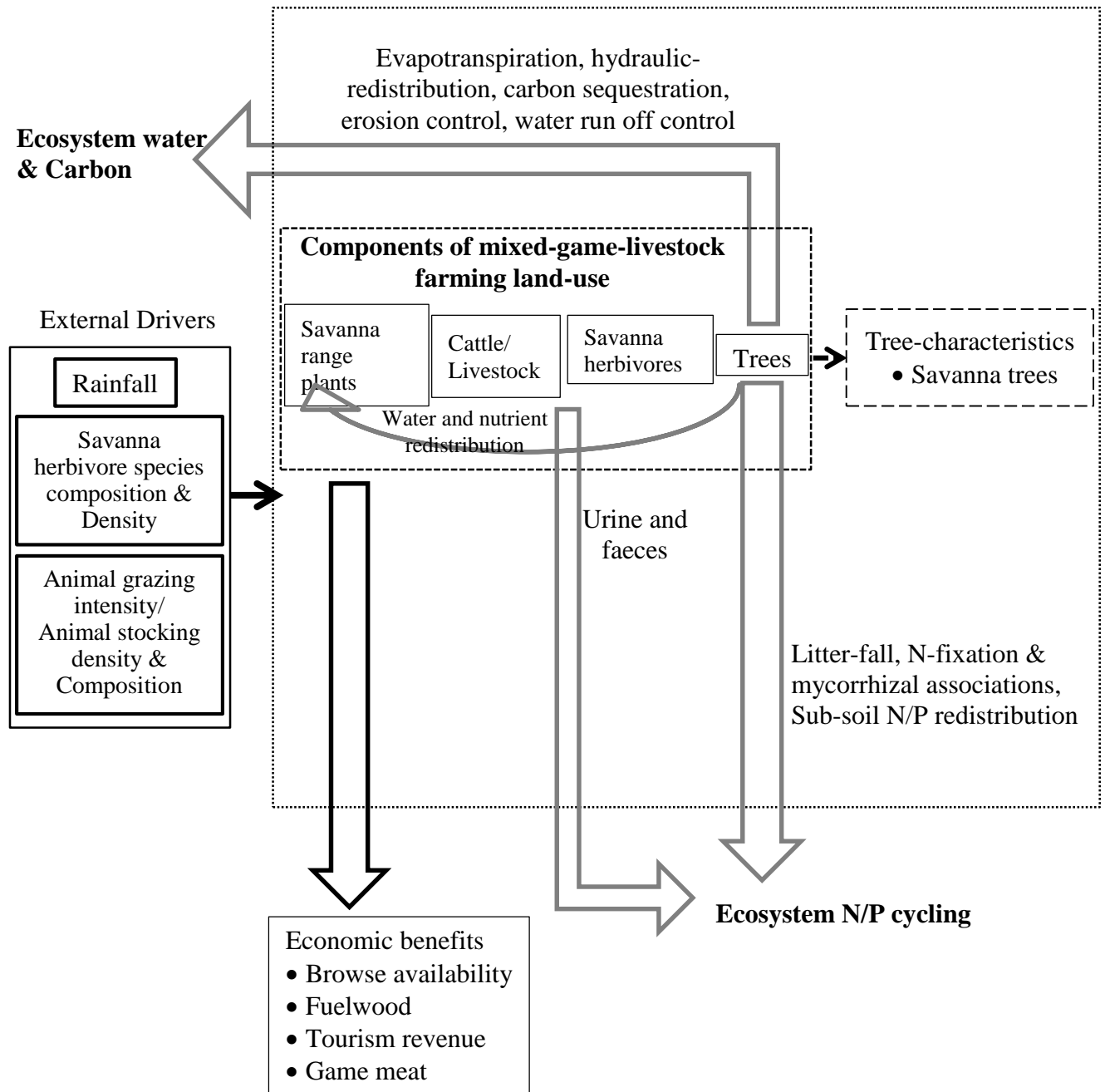
Figure 5.5. The ecological role of trees in mixed-game-livestock farming land-use system.

reducing the forage availability for grazing herbivores and areas (Scholes and Archer 1997). Therefore, any tree removal policy in mixed-game-livestock farming systems may need to carefully consider the impacts on the land keeping in view the rainfall, tree species and age, cattle or livestock stocking densities, types of wildlife species on the farms and ultimately, the probable effects on the natural functioning of rangeland in which trees play a crucial role (Walker 1976, 1993, Torres 1983, Smit 2004, Manning et al. 2006, Augustine et al. 2011).

Trees in rangelands

Similar to agroforestry, the multifunctional role of trees are important for better land management in rangelands. Additional to those described in agroforestry systems, the inclusion of livestock or wild herbivores is an added feature of both silvo-pastoral and mixed-game-livestock farming systems. Tree under-tree canopies are nutrient hot-spots because of nutrients deposited underneath trees by birds' nests on the trees, or by animals either browsing or resting in the shade (Belsky et al. 1993a, Dean et al. 1999). However, in both silvo-pastoral and mixed-game-livestock farming systems, range production for better animal yield is the final goal for land management (Walker and Janssen 2002, Carruthers 2008, Cousins et al. 2010). As in agroforestry and generally in savannas, the interactions between woody species and under-tree canopy grass is viewed to be competitive, with trees said to suppress grass growth (Scholes and Archer 1997, Ludwig et al. 2004a). Yet, in the drier range of arid and semi-arid savannas, grass biomass is higher under-tree canopy than outside, whereas in the higher rainfall regions, under-tree canopies have lower grass biomass than outside (Dohn et al. 2013, Moustakas et al. 2013). The forage quality of grasses under tree canopies is better with a higher nutrient content (Treydte et al. 2007, Ludwig et al. 2008) providing essential nutrition to both cattle and wild herbivores during the dry periods (Augustine et al. 2011). In parts of Africa, where rainfall is highly variable and drought is recurrent, multifunctional landscapes like silvo-pastoral land-use or mixed-game-livestock farming can have a considerable multidimensional value like contributing to biodiversity, ecosystem functioning, sustainable use of natural resources, biomass production: animal and plant, and provide economic benefits to human communities as illustrated in Figures 5.4 and 5.5 (Blench 2001, Jackson et al. 2012, Archer and Predick 2014, Binswanger-Mkhize and Savastano 2014).

It is reported that forage from trees provide essential nutrition to livestock in the Sahel and that removal of trees from this system drastically impacts grass production (Le Houérou 1980). In rangelands, trees have an added function in sustaining soil quality in the presence of

grazing (Figs. 5.4 and 5.5). They capture the nutrients deposited by animals that otherwise would be lost from the system. Trees facilitate the cycling of nutrients by horizontally and vertically transporting nutrients in the soil system. Tree characteristics between silvo-pastoral systems and mixed-game-livestock farming systems vary, with trees in the former land-use selected for direct benefits to the pastoral communities (Fig. 5.4), while in the mixed-game-livestock farming systems, trees are essentially savanna trees (Fig. 5.5), conforming to the premise that these systems may be a more sustainable form of land-use as it mimics natural savannas (Walker 1976, van Noordwijk and Ong 1999) at the same time providing additional revenue from game meat and tourism (Carruthers 2008). Furthermore, the suite of animals that these two systems harbour vary, with silvo-pastoral systems having largely livestock (Le Houérou 1980, 2006, Walker and Janssen 2002) whereas mixed-game-livestock farming systems possessing a suite of selected wild herbivores in addition to either cattle or livestock (Mossman and Mossman 1976, Walker 1976, Cousins et al. 2010). However, in many parts of Africa, silvo-pastoral systems also harbour wildlife (Cumming and Du Toit 1999), functioning much akin to mixed-livestock farming system, albeit with hardly any management interventions except the offtake of animal biomass.

Much work has been done in Australian rangelands to examine the long-term effects of removal of trees on rangeland production (Ludwig and Tongway 2002, Kaur et al. 2005, Sangha et al. 2005, Schmidt et al. 2010) whereas in Africa the emphasis has been on measuring tree influence on grass production for short periods. We did not come across any long-term studies in Africa that have quantified tree removal affects either on the grass community or on other land quality variables. However, tree suppression is a management practice in rangelands systems of South Africa, Botswana and Zimbabwe (*personal observation*). Long-term land cover studies of African farms and rangelands have shown decrease in tree cover and increase in bare soil (Zomer et al. 2009) leading to high levels of soil degradation (The Montpellier Panel 2014). In Australia, it was found that tree clearing increased productivity up to a short term of about 10 years. Beyond this time, not only did the pasture production decrease but tree clearing led to land degradation and loss of diversity among the pasture species (Kaur et al. 2005). Tree clearing also reduced soil nutrient availability to plants through its effects on pH (Sangha et al. 2005). Furthermore, a direct improvement in animal performance has not been demonstrated and rather implied as a consequence of better graze production (Teague and Smit 1992). In Bolivian dry rangelands, maintaining a low density of trees in rangelands has resulted in increased pasture production up to 3.5 times (del Pozo et al. 2004). However, such data are lacking for Africa, although the

contribution of the "intangible" services like increased soil fertility and nutrient cycling, provided by trees is well recognized (Torres 1983, Mkhabela 2003). Richter et al. (2001) compared heavily bush encroached bushveld with thorn-veld in the arid Northern Cape and Northwest provinces of South Africa and showed that grass species composition is not influenced with increasing tree density but grass density and grazing capacity decreased. Thus, in heavily bush encroached areas of arid and semi-arid savannas, tree clearing to some extent has a short-term positive influence on grass abundance through reduced competition for phosphorus (Kaur et al. 2005, Schmidt et al. 2010) and on the grazing capacity of the rangeland (Smit 2004). It is evident that the presence of low density scattered trees on rangelands positively influences the land-quality by reducing nutrient leaching, redistributing both water and nutrients, providing dry-season or drought time food for herbivores, reducing erosion and water run-off impacting soil-nutrient quality and water infiltration to sub-soil layers (Figs. 5.4 and 5.5).

CONCLUSION

It is clear that land degradation is a looming problem faced by the human population today. Adding to this are the impending impacts of climate change. Increasing temperatures, nutrients and CO_2, as well as changes in the precipitation patterns and land use are reported to be the key drivers of global environmental change. In particular, drylands are highly vulnerable to climate change (Maestre et al. 2012). The practice of agroforestry and rangeland management that includes trees, are reported to be climate smart and climate resilient systems buffering the effects of climate change to some extent (Verchot et al. 2007). The multiple services provided by trees, both ecologically and economically are substantial. However, trees are disappearing from human-use landscapes making these landscapes vulnerable to soil degradation and non-productive. In this paper we have focused purely on the importance of trees in human-used landscapes in African drylands and their influences on ecosystem functioning. However, we are not proposing that trees alone are the answer to all the existing problems related to land degradation but trees in these landscapes will support any other management interventions that may be needed for better land-use and natural resource management as well as food and animal production.

The benefits of agroforestry practices are well known and, both silvo-pastoral and mixed-game-livestock farming are ways of sustainably exploiting rangelands that otherwise are unsuitable for crop production. In both these systems, maintenance of trees in the

landscape is the key feature. It may be a simplified approach but successful implementation of agroforestry practices and its inclusion in rangeland management is a practical and a simple way to sustainably exploit African rangelands. However, this large goal cannot be achieved purely by using an ecological approach as the socio-economics and policies that govern management practices are highly complex in this region. Therefore, policies and protocols that promote the presence of scattered trees in African drylands are necessary. Furthermore, frameworks that can be implemented, easily operated by and economically beneficial to the communities that depend on these land-uses for their livelihood will be imperative for sustainable management of these landscapes (Tilman et al. 2002).

**SYNTHESIS: THE IMPORTANCE OF FACILITATIVE
INTERACTIONS FOR TREE-GRASS COEXISTENCE IN SAVANNAS**

INTRODUCTION

Terrestrial ecosystems support high plant diversity where different plant types coexist. Classical ecological theory proposes two principal mechanisms through which plant coexistence can occur – habitat and resource differentiation (Schoener 1974). Both these are based on the Gaussian principle of niche differentiation. The habitat differentiation mechanism proposes that plant species use different portions of the available habitats, or differ in the range of habitats that they occur in, where they may have a competitive advantage over other plant species. The resource differentiation mechanism proposes that plant species partition the limiting resources (e.g. nutrients, water) in such a way that each species is limited by a different component of the available resources, thus allowing coexistence. Yet, there are several examples where plants coexist in the same space using the same resources which the niche differentiation theory cannot explain. One such classic, much debated but less understood example is the co-occurrence of trees and grasses in savanna ecosystems (Scholes and Archer 1997, Rodriguez-iturbe et al. 1999, Higgins et al. 2000, Van Langevelde et al. 2003, Sankaran et al. 2004, Scheiter and Higgins 2007, Ward et al. 2013, February et al. 2013a).

It has been reported that both trees and grasses negatively influence the aboveground production of each other in savannas (Belsky 1994, Ludwig et al. 2004a, Riginos 2009, February et al. 2013b). Consequently, the premise of all models that explain tree grass interactions is based on competition (Scholes and Archer 1997, Jeltsch et al. 2000, House et al. 2003, Sankaran et al. 2004). However, trees ameliorating the under-tree canopy environment through reduced evapo-transpiration and enhanced mineralization effects have been reported from savannas, leading to higher grass aboveground biomass (Belsky et al. 1989, 1993a, Belsky and Canham 1994, Zou et al. 2005, Manning et al. 2006). In addition, improved forage quality of grasses with higher nitrogen content for herbivores is commonly found under tree canopies (Treydte et al. 2007, Ludwig et al. 2008, Augustine et al. 2011). Positive effects of trees on understory grasses have been documented (Belsky 1994, Belsky and Canham 1994, Ludwig et al. 2004b), but have been mostly underemphasized or ignored in evaluating tree-grass co-existence (Scholes and Archer 1997, Ludwig et al. 2004a). It is

suggested that coexistence is a balance of positive and negative interactions between plants (Holmgren et al. 1997, Callaway and Walker 1997, Bertness 1998). In this chapter, I synthesize the findings of my study, and discuss the role of positive interactions between trees and grasses, the current knowledge and the gaps where future research may be directed. The most significant finding of my study is that indirect positive influence of trees on grasses play an important role in supporting tree-grass co-existence in savannas.

Plant interactions range from being negative, neutral to positive. Positive interactions among plants, termed facilitation, occur when one plant enhances the growth, survival, or reproduction of a neighbouring plant (Callaway 2007). This is unlike competition which is a negative interaction that reduces growth, reproduction, and survival of both plants. Both facilitation and competition in plants have been suggested to co-occur and vary in time or space (Bertness and Callaway 1994, Holmgren et al. 1997, Callaway 1997, Callaway and Walker 1997, Kikvidze et al. 2006, Van Der Putten 2009). Studies suggest that high plant diversity and plant coexistence are a consequence of an array of inter-plant interactions. Competition as well as facilitation between plants play a key role in shaping the plant composition and community structure in an ecosystem. Plants impact ecosystem functioning through their influence on environmental resources, and consequently changes in environmental resources may in turn result in positive or negative interactions among plants (Tilman 1994, Chesson 2000, Fargione and Tilman 2002, Brooker 2006, Callaway 2007, Brooker et al. 2008, D'Odorico et al. 2010). Studies have shown that facilitative interactions in plants impact plant recruitment and plant community structure, indicating the growing importance of these positive plant interactions in plant ecology (Bertness and Callaway 1994, Callaway 1995, 2007, Holmgren et al. 1997, Brooker et al. 2008, Kikvidze and Callaway 2009). Although largely ignored in comparison to the role of competition among plants (unlike in animals where facilitation is recognized: Prins 2000, Odadi et al. 2011a, 2011b), facilitative plant interactions are increasingly being acknowledged as important and widespread in terrestrial vegetation (Brooker 2006, Callaway 2007, Brooker et al. 2008, Brooker and Callaway 2009).

FACILITATIVE EFFECTS OF TREES ON GRASSES AS A MECHANISM OF TREE-GRASS CO-EXISTENCE IN ARID AND SEMI-ARID SAVANNAS

The growth and developmental stage of trees, through associated changes in morphology and ecophysiology will influence tree-grass interactions. Therefore, results of studies carried out at the seedling or juvenile tree life stages cannot be extrapolated to large adult trees. At the

seedling or juvenile sapling stage, competition with grasses appear to suppress tree growth (Riginos 2009, February et al. 2013b, Barbosa et al. 2014) whereas, large trees suppress aboveground production of under-tree canopy grasses (Belsky 1994, Ludwig et al. 2004a). However, these appear to be influenced by season and amount of rainfall (Belsky 1994, Ludwig et al. 2001). Additionally, a meta-analysis of data from published literature indicates that aboveground grass production under-tree canopy is suppressed by about 20-25% in savannas (*Priyadarshini Unpublished data*) and there is yet no example that shows competitive exclusion of grasses from the under-tree canopy environment, except under heavy grazing pressure (Dean et al. 1995, Ward 2005, Kraaij and Milton 2006).

The ability of trees to use subsoil water and nutrients has been well studied in agro-ecosystems (Buresh and Tian 1998, Lehmann 2003). The phenomenon of hydraulic-lift and hydraulic-redistribution by trees in natural ecosystems is also well established (Ludwig et al. 2003, Neumann and Cardon 2012, Prieto et al. 2012), but nutrient redistribution is less studied. In order to understand whether nutrient and water redistribution by trees could be a mechanism that allows tree-grass co-existence, I evaluated these processes in different functional types of savanna trees in Chapters 2 and 3. I used the natural abundance of stable isotopes ^{15}N, ^{2}H and ^{18}O, and an experiment using enriched stable isotope tracers ^{2}H$_2$O and ^{15}NH$_4$ to track the redistribution of water (^{2}H$_2$) and nutrients (^{15}N) and their uptake by under-tree canopy grasses.

Seasonal shifts in tree-grass water relations: Facilitation, resource partitioning, and competition in tree-grass interactions

The variation in natural abundance of ^{2}H in plant water showed that there were clear seasonal differences in use of water-sources by trees and grasses (Chapter 2). The enriched ^{2}H tracer results together with the natural variation in ^{2}H and ^{18}O stable isotopes provided evidence for facilitative effects. Facilitation happened in the dry season through hydraulic-redistribution of deep-soil water by trees to the under-tree canopy grasses via the topsoil. This was shown by all the studied tree types. There was overlap in use of water-sources with grasses and trees using topsoil water during wet and the transitional dry to wet seasons. However, competition between tree and grasses most likely occurred only in the dry to wet transitional seasons due to water limitation in the soil. Although trees and grasses had overlapping water sources in the wet season, water limitation was no longer an influencing factor due to sufficient rainfall. Water-resource partitioning was observed during the dry and the transitional wet to dry

seasons, with grasses using water from the topsoil and trees using subsoil water. Studies that show evidence for such a clearly dynamic water resource-use are rare (Kikvidze et al. 2006, Callaway 2007) and my study demonstrated this for three common and abundantly found African savanna trees.

Most studies focus solely on aboveground biomass of grasses as a response indicator of tree competition on grasses. Since reduced aboveground grass biomass was observed, facilitative effects of tree hydraulic-redistribution on understory grasses were inferred to be insufficient (Ludwig et al. 2004a, Callaway 2007). However, there are significant ecological benefits as suggested by several studies on dry season water facilitation by trees to under-tree canopy plants (Ryel *et al.,* 2003; Prieto *et al.,* 2012; Neumann and Cardon 2012; Sardans and Peñuelas 2014). The most notable advantages of hydraulic-redistribution from trees to the understory grasses in savannas is the prevention of desiccation, and maintenance of root resource-reserves, which aid photosynthetic activity in perennial C_4 grasses for the upcoming growing season. Additionally, hydraulic-redistribution helps maintain the mycorrhizae that mediate both water and nutrient transfer during the dry season (Querejeta et al. 2007). Therefore, the facilitation via hydraulic-redistribution by trees to grasses potentially influences survival and reproduction of these grasses, thus enabling tree-grass coexistence in savannas.

The impacts of hydraulic-redistribution are manifold ranging from prolonging root lifespan, influencing plant interactions, influencing soil biota, to ecosystem level regulation of water movement (D'Odorico et al. 2010, Neumann and Cardon 2012). However, hydraulic-redistribution is not the same as hydraulic-lift which is solely the upward movement of water along a vertical pressure gradient created due to the effects of transpiration and results in the supply of water to the leaves in the tree canopy for photosynthesis (Caldwell and Richards 1989, Prieto et al. 2012). Hydraulic-lift is a diurnal phenomenon while hydraulic-redistribution is a much more complex process with some occurrence of biological control by the trees on the outflow of water into the surrounding soil (Peñuelas and Filella 2003, Prieto et al. 2012). In my study, I show the extreme seasonality of hydraulic-redistribution which has not been described so clearly yet. Hydraulic-redistribution is the primary means by which hydraulic failure is prevented in trees (Norton and Hart 1998, Domec et al. 2004, 2006, Prieto et al. 2012). Hydraulic failure is a process by which gas emboli get trapped in the tree water transport system that prevents upward transport of water for photosynthesis in the leaves of trees, as a result of water stress. This failure leads to tree

mortality. Although trees that have evolved under conditions of water stress have a higher resistance to hydraulic failure (Maherali and Pockman 2004), studies indicate that most trees including those in savannas are highly vulnerable to hydraulic-failure with increase in drought stress (Breshears et al. 2005, Choat et al. 2012). The redistribution capacity in trees is influenced by the extent to which a tree species can resist hydraulic failure through a process termed cavitation resistance (is the measure of the water stress that a tree can withstand). Therefore, understanding hydraulic-redistribution and factors that influence this process is needed. Under changing climatic conditions with predictions on increased frequencies of droughts in savannas (Maestre et al. 2012), hydraulic redistribution becomes a key phenomenon that may support the long-term survival of trees in savannas.

My PhD study shows evidence that dry season hydraulic-redistribution is much more widespread in savannas than previously recognized. The tree species that I studied occur abundantly and are widespread in southern African savannas and all of them exhibited hydraulic redistribution. Tree mediated hydraulic-redistribution of water is a potentially significant regulator of the hydrologic-cycle in these water limited ecosystems. Empirical and modelling estimates of the average amount of water moved by hydraulic-redistribution by trees range from 0.04 mm of water per day to 3.2 mm of water per day. Even this small amount of redistributed water is ecologically significant for plant survival, maintenance of the major functional roots in plants, sustaining mycorrhizae and other soil biota (Neumann and Cardon 2012). With looming climate change that may possibly result in increased tree densities in savannas (Bond and Midgley 2000, Kgope et al. 2010, Buitenwerf et al. 2012) and changes in frequencies of drought and rainfall intensity particularly in arid and semi-arid areas (Feng et al. 2013), it is necessary to measure the magnitude of water-redistribution by trees in savannas.

The major constraint was measuring the magnitude of water-redistribution by the trees as detailed in Chapter 2. I only qualitatively measured and identified the extreme seasonality of water-redistribution. The determination of the quantitative extent of this redistribution remains a challenge. To have a measure of the quantitative extent of water redistributed by tress is needed since this will potentially have large ecosystem impacts as trees have a large influence on ecosystem level water cycling (D'Odorico et al. 2003, 2010, Neumann and Cardon 2012). In my study, all the different tree types I studied (see methods sections of chapter 2 and 3) are widespread and abundant in southern African savannas and were similar in their redistribution characteristics.

The phenomenon of hydraulic-redistribution is much more complicated than previously understood (Prieto et al. 2012). The complex nature of source-sink system within a plant and in the plant-soil interface, creating water potential gradients along which the water moves depend on multifarious abiotic and biotic factors that are not clearly understood and can potentially influence plant interactions (Dawson 1993, Scholz et al. 2002, Prieto et al. 2012). It seems that just a water potential gradient between the soil and plant environment may not be sufficient. In my study, hydraulic-redistribution was limited to the dry season alone. However, hydraulic-lift is most likely a year-round phenomenon as seen in *Vachellia tortilis* (Ludwig et al. 2003). This distinction is presently absent in tree ecohydrology, although there is evidence to suggest that extent of soil dryness influences hydraulic-redistribution (Burgess et al. 2000b, Peñuelas and Filella 2003, Prieto et al. 2012). Furthermore, most trees in almost all biomes have a large resistance to water stress resisting outflow of water (Choat et al. 2012, Prieto et al. 2012). There are studies that have shown that plants can have multiple sources of water apart from water from the soil, particularly through direct foliar uptake (Limm et al. 2009, Goldsmith et al. 2013). This has so far not been examined for trees or grasses from drier regions. Additionally, trees can tap stored water when needed (Phillips et al. 2003). Some of the questions that arise from my PhD study are:

1. Does hydraulic-lift to the canopy at all times result in hydraulic-redistribution to the surrounding soil and neighbouring plants?

2. A follow up question is that since there is higher resistance to outflow from the tree to the soil than inflow from soil to tree roots (Prieto et al. 2012), what are the micro-environmental soil conditions (that are potentially influenced by the climatic conditions) under which outflow of water from the trees to soil (hydraulic-redistribution) occur?

3. Since any increase or decrease in tree densities will influence the ecosystem ecohydrology (D'Odorico et al. 2010), what are the ecosystem impacts of increase or decrease in tree densities on the hydrologic cycle in savannas?

Soil biota and tree mediated nitrogen supply in savannas as a means of tree-grass coexistence

The nitrogen dynamics in the rhizosphere are extremely complex and even basic processes like uptake and release by plants are not fully understood (Jackson et al. 2008). Nitrogen is an essential plant nutrient and although it is abundant in the atmosphere, it is a highly limited plant resource in terrestrial ecosystems. Using the natural variation in foliar ^{15}N and nitrogen content, I showed in Chapter 3 that trees and grasses in a semi-arid savanna were using

mycorrhiza-supplied nitrogen in all seasons except in the wet season. In the wet season, both trees and grasses switched to microbially-fixed nitrogen. The $^{15}NH_4$ tracer experiment that I carried out, provided evidence for subsoil nitrogen-redistribution by trees to the under-tree canopy grasses via the topsoil in all seasons. Furthermore, I concluded that it is highly unlikely that trees and grasses depended on mineralized soil nitrogen as deduced from the natural variation in foliar ^{15}N of grasses and trees, and the reported seasonal variation in mineralization rates in the Kruger Park region (Coetsee et al. 2008). The results taken together with the results from Chapter 2 (Priyadarshini et al. 2015) show that the subsoil nitrogen-redistribution by trees is independent of water-redistribution indicating active uptake of nitrogen by plants as reported elsewhere (Gebauer and Ehleringer 2000, Glass 2005, Masclaux-Daubresse et al. 2010) but so far is overlooked for savanna plants.

Most significantly, my study questions the notion that soil inorganic nitrogen availability is limiting plant growth and survival in savannas. I show that mineralized inorganic nitrogen may not be important and that trees and grasses used largely mycorrhiza supplied or microbially fixed nitrogen and question the established nutrient model. Most savanna literature emphasises the role of mineralized inorganic plant-available nitrogen (Scholes and Walker 1993, Scholes and Archer 1997, Scholes et al. 2003b). The findings of my study conforms to the findings of a study carried out in the more arid Kalahari transect that plants may not be limited by nitrogen (Wang et al. 2010). This is also the case in humid savannas (Abbadie et al. 1992, Aranibar et al. 2004). There are only a few studies that identify the importance of biogenic nitrogen in savannas (Abbadie et al. 1992, Craine et al. 2009b).

As in Chapter 2, in Chapter 3 as well the major constraint and the biggest challenge was measuring the magnitude of nitrogen-redistribution by the trees. I qualitatively measured that nitrogen redistribution occurred in all the tree types that I studied, that too throughout the year. However, the quantitative extent of nitrogen-redistribution by savanna trees and the ecological significance of this phenomenon to tree-grass interactions evaded explanation. As I show in Chapter 3, there is increasing evidence that plants do not completely depend on mineralized inorganic nitrogen (Abbadie et al. 1992, Aranibar et al. 2003, Hawkes 2003, Priyadarshini et al. 2014). My study identified the importance of soil micro-organisms and subsoil nitrogen redistribution by savanna trees. However, some questions arise from my study regarding nitrogen dynamics in savannas and its role in facilitating tree-grass coexistence. For example:

1. What are the contributing fractions of different sources of nitrogen, both biotic and abiotic for trees and grasses in savannas?

2. What is the magnitude of deep soil nitrogen redistributed by trees to grasses and what is the ecological significance?

3. What are the implications of deep soil nitrogen-redistribution by trees at the ecosystem scale, particularly since the levels of nitrogen are increasing in the atmosphere globally (Vitousek et al. 1997)?

4. What is the role of dry season hydraulic-redistribution to microbial and mycorrhizal maintenance and nutrient transfer between trees and grasses in savannas?

5. As nitrogen and phosphorus cycles in plants are linked (Vitousek et al. 2002), what are the implications to phosphorus dynamics?

Studies elsewhere have reported that plants can be opportunistic in the form of nitrogen that they use including the direct uptake of organic amino acids (McKane et al. 2002, Jackson et al. 2008, Wang and Macko 2011). This has not been shown in savanna plants. It is evident that the nitrogen cycle is highly mediated by plants and in particular by trees due to their longer life spans and extensive root systems (Sternberg et al. 2004), altering the soil properties through litter deposition (Belsky et al. 1989, 1993a, Moyo et al. 1998, Ludwig et al. 2004b), and redistributing subsoil nitrogen (Priyadarshini et al. 2014). Therefore, plant plasticity in using different forms of nitrogen and the role of soil biota could greatly influence nitrogen cycling in savannas as well as the interactions among plants.

I show in Chapter 4 also that trees enhance the under-tree canopy nitrogen content. I examined the influence of competition from trees and water limitation on the root storage characteristics of perennial grasses by comparing under-tree canopy areas and outside in Chapter 4. This study was done in three sites of different rainfall across South Africa. The underlying hypothesis on which I based this investigation was that competition from trees and water limitation in the environment will result in increased storage in roots of grasses under trees. I found that although there were no differences in the root biomass, starch, and sugar content, the root nitrogen content was higher and C:N ratios were lower in grasses under-tree canopy than outside-tree canopy, indicating the positive influence of trees on under-tree canopy nitrogen content. This was likely through potentially higher amounts of litter fall and consequently, higher turnover of mineralized nitrogen (Bernhard-Reversat 1982, Belsky et al. 1989, Moyo et al. 1998), or alternatively through facilitative influence of subsoil water and nitrogen-redistribution (Ludwig et al. 2003, Priyadarshini et al. 2014,

2015). Therefore, my results suggest a positive interaction between trees and grasses in dry savannas indicating that trees may be playing an important facilitative role here.

Studies on competitive effects on storage characteristics for grasses are few and most studies focus on defoliation effects in combination with water stress that showed increased allocation to the roots (Jaramillo and Detling 1988, Danckwerts and Gordon 1990, Danckwerts 1993, Oosthuizen and Snyman 2003). On the contrary, the findings from Chapter 4 on root storage characteristics under and outside-tree canopies across an aridity gradient, indicate largely neutral (no change in starch, sugars or root biomass) and positive (increase in nitrogen content) effects on root characteristics of under-tree canopy grasses. The ecological importance of root storage in plants is well documented of which the most important are growth and survival in times of abiotic stress in addition to withstand defoliation, enable rapid recovery, reproduction, and to withstand competition (Chapin et al. 1990, Lemaire and Millard 1999). Therefore, to understand the role of storage in perennial grasses in savannas and competition with trees, further investigation is needed. My study was exploratory in order to understand the extent of storage in perennial grasses exposed to water stress and competition from trees. It is suggested that facilitative interaction in plants potentially have legacy effects that could reflect the evolutionary history of these perennial grasses that most likely are adapted to water and competitive stress (Craine 2006, Van Der Putten 2009, Wiens et al. 2010). These aspects are not yet understood fully. An assumption in Chapter 4 was that there is "tree posed" competitive stress on the understory grasses. However, my results indicate otherwise suggesting a facilitative influence of trees on some of the grass root characteristics (Priyadarshini et al. 2016).

Functional role of trees in savannas

The importance of the functional role of trees is well established and it would not be inappropriate to call them keystone structures for savannas (Manning et al. 2006). Trees influence savanna ecosystem functioning by their impacts on water and nutrient cycles (Bernhard-Reversat 1982, Caylor et al. 2005, D'Odorico et al. 2007, 2010) and through their capacity for water and nutrient redistribution from deep-soil to topsoil as show in Chapters 2 and 3 (Priyadarshini et al. 2014, 2015). However, these important functions of trees that have potential for better land management have been ignored in practice (Rao et al. 1998, Ong and Leakey 1999, Manning et al. 2006). In Chapter 5, I provide a review of the functional role of trees in two land-use types in arid and semi-arid regions of Africa: agroforests and rangelands

that include silvo-pastoral systems and mixed-game-livestock farming systems where trees are an integral part of these land-uses. These land-uses have significant ecological and socio-economic implications for Africa. Although both increases and decreases in tree densities are occurring in savannas worldwide, the trend is of decreasing number of trees in human-used savanna landscapes. I evaluated the causes for the loss of trees in these land-uses and highlight the functional role of trees in these land-use systems, and therefore, the importance of trees for sustainable land and natural resource management.

The increasing disappearance of trees in human-use lands is the principal cause leading to soil degradation and ultimately land degradation. Making agro-ecosystems mimic natural systems has been an important issue and has been the topic of a special issue of the journal "*Agroforestry Systems*" (Lefroy et al. 1999). At least 3 papers highlight the facilitative role of trees in agro-ecosystems emphasizing better nutrient and water capture (Ong and Leakey 1999, Pate and Dawson 1999, van Noordwijk and Ong 1999) and consequently better land management. Furthermore, the two land-use types described in Chapter 5 of my PhD study (agroforestry systems and rangelands that include silvo-pastoral and mixed-game-livestock farming systems) are reported to not only mimic natural systems but also buffer the human communities depending on them against the vagaries of climatic fluctuations (Ewel 1999).

Dryland ecosystems that include arid and semi-arid savannas and land-uses within this land classification category are highly vulnerable to climate change (Maestre et al. 2012). Already, agricultural production in many parts of the developing world are facing the effects of climate change with reduced crop yields (Verchot et al. 2007). It is clear that agricultural intensification has resulted in the loss of tree cover and soil degradation (Zomer et al. 2009, The Montpellier Panel 2014). In large parts of Africa, the past few decades have witnessed increased urbanization, improved infrastructure and access to markets has led to increased mechanization in agriculture, land irrigation and improved access to both organic and inorganic manure but has not necessarily resulted in either enhanced agricultural production or famer income (Tilman 1999, Binswanger-Mkhize and Savastano 2014). Both intensified agroforestry with the inclusion of trees on farms, and diversified agroforestry (as in silvo-pastoral or mixed-livestock-game ranching) can contribute to increased yield per unit land that potentially can have economic benefits to the land users that practice them. Most importantly these practices have the potential to reduce land conversion or deforestation (Steenwerth et al. 2014) as I illustrate in Chapter 5.

The knowledge on the facilitative role of trees for better land management had been in practice in the past in most parts of the developing world (Altieri 2004). However, with increased agricultural intensification and associated consumption demands of a rising human population, these practices have disappeared leading to soil degradation (The Montpellier Panel 2014). Agricultural intensification seems to emerge as the single biggest cause for the loss of tree cover and soil degradation (Zomer et al. 2009, The Montpellier Panel 2014). Although global food production has increased with better crop varieties (Tilman 1999, Tilman et al. 2002), unregulated agricultural practices with increased use of fertilizers, pesticides and irrigation has affected the hydrology (Gleeson et al. 2012) and resulted in nutrient overload to both the fresh water and marine ecosystems (Tilman 1999). Trees in agro-ecosystems make a contribution to "climate smart" or "climate resilient" agriculture (Howlett et al. 2011, Luedeling et al. 2011, Steenwerth et al. 2014). Therefore, much of the future research will need to be directed at sustainable farming practices that are economically profitable and acceptable at the farmer level (Pannell 1999, Tilman et al. 2002). Presently, successful adoption of sustainable farming practices such as maintaining scattered trees in agricultural landscapes, remain the biggest challenge (Prinsley 1992, Pannell 1999, Tilman et al. 2002, Giller et al. 2009).

BIOTIC INFLUENCE ON WATER AND NITROGEN DYNAMICS ON PLANT INTERACTIONS IN SAVANNAS

My study shows that nutrient and water cycling in savannas are biotically influenced through the capacity of redistribution of trees and that this process is much more common than previously acknowledged. Some biotic and abiotic influences, mainly those on woody cover in savannas, namely rainfall, fire and herbivory (Van Langevelde et al. 2003, Sankaran et al. 2005) have been well discussed in savanna ecology. However, apart from herbivory, the focus on biotic influence on tree-grass interactions as well as on water and nutrient dynamics is comparatively less explored. There seem to be both direct and indirect effects of biotic factors on plant interactions in savannas. My study shows that trees are a significant biotic influence on water and nutrient cycling facilitating subsoil resources to shallow rooted under-tree canopy grasses thereby impacting tree-grass interactions in savannas. The influence of large herbivores in savannas on vegetation and nutrient cycling has also been shown (McNaughton 1988, Thompson Hobbs 1996, van der Waal et al. 2011). For example, ungulate influence on tree establishment; wild herbivores positively influenced tree establishment but had a negative effect on seed production (Goheen et al. 2010). Wild

herbivores have been shown to create nutrient hotspots though urine and faeces deposition that influence vegetation communities and nutrient cycling (McNaughton 1988, Thompson Hobbs 1996, van der Waal et al. 2011). However, the role of soil biota is less studied and may have a much larger role to play in plant coexistence (van der Heijden et al. 2003, Bardgett 2005, Van Der Putten 2009). The results from Chapter 3 indicate that the role of mycorrhizae and microbially fixed nitrogen in nutrient transfers and uptake in savannas, in addition to subsoil nitrogen-redistribution by trees, shows a significant biotic influence on nitrogen cycling in savannas. It has also been shown that cyanobacterial crusts in the soil not only capture but retain nitrogen for longer making it available to the plants which otherwise would be lost to the environment (Hawkes 2003). This significant biotic influence on the nitrogen cycle may be playing an importance role in maintaining plant coexistence, and thus diversity in savannas.

Increase in the foliar nitrogen content of both trees and grasses during the wet season (Chapter 3, Priyadarshini et al. 2014) indicated increased nitrogen transfer to both trees and grasses from the soil biota, suggesting an important role of soil biology and savanna seasonality. Mycorrhiza also improve the efficiency of phosphorus capture and transportation (Newman and Ritz 1986) which is reported to be the most limiting nutrient in savannas (Ludwig et al. 2001, 2004b, Augustine et al. 2011). It is recognized that 95% of all terrestrial plants have associations with mycorrhiza (Smith and Read 2010) but this aspect is ignored in savannas and emphasis is given to mineralization of nitrogen that reportedly becomes available to plants just after the rains. My study shows that trees and grasses in semi-arid savannas do not depend on mineralized nitrogen for their nitrogen requirements (Chapter 3, Priyadarshini et al. 2014).

Trees were thought to take up the mineralized nitrogen through rapid synchronous root and leaf development making them better competitors for this resource than grasses (Scholes and Archer 1997, Archibald and Scholes 2007). However, measurements of net mineralization in Kruger National Park show that this occurs only in the latter part of the wet season (Coetsee et al. 2008). At the onset of first rains, the microbial uptake of mineralized nitrogen is highly rapid making mineralized nitrogen unavailable to plants (Bardgett 2005, Jackson et al. 2008). Additionally, soil microbial crusts have been found to be important in nitrogen supply through atmospheric nitrogen fixation making it available to plants (Aranibar et al. 2003, Hawkes 2003). Therefore, future studies or models with regard to nitrogen dynamics in savannas may need to consider the role of soil biota, particularly since the association of many African savanna trees with both ecto- and endo-mycorrhizae has been

demonstrated (Högberg 1982, 1986b, 1989, Högberg and Piearce 1986). The general perception that all nitrogen fixing trees in savannas possess nodules is a misconception (Högberg 1986a). I examined all the putative nitrogen fixing trees in my study in different study sites across South Africa for nodules and found that these did not occur in any of the trees. In an elegant study, Cramer et al. 2007, showed in a glasshouse pot experiment that nitrogen fixing African acacias have the capacity to switch on and off their nodulating character and nodulate only with competition or nutrient limitation. Chapter 3 (Priyadarshini et al. 2014) of my study demonstrates that tree ecophysiology via subsoil nitrogen redistribution, in combination with soil micro-organism mediated nitrogen supply to plants, may aid tree-grass coexistence in savannas.

Hydraulic-redistribution is reported to maintain microbial and mycorrhizal activity, thus enabling nutrient transfer during the dry periods (Querejeta et al. 2007). It is likely that the redistribution of subsoil nitrogen by trees (Priyadarshini et al. 2014) may provide this essential nutrient to both the mycorrhiza and the under-tree canopy grasses, thereby influencing the nitrogen cycle.

CONCLUSION

My PhD study identified major ecophysiological processes that occur in savannas. Importantly, the redistribution capacity of trees to supply grasses with subsoil water and nitrogen. Overall, this study highlights the importance of facilitative interactions in savannas that until now have been overlooked. I also show that soil organisms play a significant role in savanna nitrogen dynamics. Further, I discuss the application of knowledge thus gathered for land management in arid and semi-arid tropics in detail. A simple Gaussian model of niche or habitat differentiation may not be a functional explanation of plant coexistence; rather there is increasing evidence of the role of biotic interactions which my study illustrates.

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SUMMARY

Terrestrial ecosystems support a high plant diversity where different plant types coexist. However, the mechanisms that support plant coexistence are not entirely clear. Savanna ecosystems that are nutrient and water limited are characterized by the coexistence of trees and grasses. Tree-grass interactions in savannas are typically viewed as being competitive and are based on the Gaussian principle of niche or habitat differentiation. Trees and grasses are reported to suppress the growth of each other and the interactions are viewed as competition. However, tree-grass mixtures persist in a range of rainfall conditions in savannas. I examined tree-grass interactions to understand the ecological processes that may sustain tree-grass coexistence in dry savannas (< 800 mm of rainfall) of southern Africa. Specifically, I investigated water and nitrogen resource-use patterns of trees and grasses, and the effects of competition between trees and grasses on resource storage in perennial grasses were examined. Furthermore, I reviewed the functionality of trees in two common human land-use types in African drylands and presented an ecological perspective of the role of trees in these land-use types.

Seasonality of plant available water imposes intense water limitation to plants in savannas. Yet, trees and grasses coexist. The water relations between trees and grasses are poorly understood. In Chapter 2, I identified the principal water-sources for trees and grasses in different seasons using the natural variation in H and O stable isotope composition of source waters. There was water-source use partitioning as well as overlap as indicated by the seasonal differences in the stable isotope composition of water in trees and grasses. Trees and grasses used water from the topsoil after rainfall indicating overlap of water-sources. Trees used groundwater or subsoil water when there was no water in the topsoil, indicating partitioning of water-use. Grasses always used water from the topsoil. I confirmed hydraulic-redistribution in all the studied tree species and water transfer to grasses via the topsoil by labelling deep-soil (2.5 m depth) with a deuterium (^{2}H) tracer. However, this occurred only in the dry-season. Results indicated possible shifts in tree-grass interactions during different periods of the year. Furthermore, dry-season hydraulic-redistribution indicated potential facilitation affects by trees to their understory grasses.

A key question in savanna ecology is how trees and grasses coexist under nitrogen limitation. In Chapter 3, I investigated the sources of nitrogen for trees and grasses in a semi-

arid savanna using natural abundance of foliar $\delta^{15}N$ and nitrogen content. Additionally, I used ^{15}N tracer additions to investigate the redistribution of subsoil nitrogen by trees to grasses. Foliar $\delta^{15}N$ values were consistent with trees and grasses using mycorrhiza-supplied nitrogen in all seasons and a switch to microbially-fixed nitrogen during the wet season. The use of mineralized soil nitrogen by trees and grasses seemed highly unlikely based on seasonal variation in mineralization rates in the Kruger Park region. The foliar $\delta^{15}N$ values were similar for all the studied tree species differing in the potential for nitrogen-fixation consistent with the absence of nodules indicating the lack of rhizobially fixed nitrogen. The tracer experiment showed that nitrogen was redistributed by trees to understory grasses in all seasons. Redistribution of nitrogen by trees and subsequent uptake of this tree redistributed nitrogen by grasses from the topsoil was independent of water redistribution. Although there was overlap of nitrogen sources between trees and grasses, dependence on biological sources of nitrogen coupled with redistribution of sub-soil nitrogen by trees could be contributing to the co-existence of trees and grasses in semi-arid savannas.

An important plant response to competition and resource limitation is an increase in root reserves. In Chapter 4, I investigated the root characteristics of perennial grasses in the presence and absence of trees as a proxy of competition in South African savannas in three sites that differed in rainfall. I based this investigation on the hypothesis that competition from trees and water limitation will result in increased storage in roots of grasses under trees. However, I found no significant effect of variation in rainfall of the different study locations on root characteristics of grasses. Furthermore, there was no significant influence of tree presence on most root characteristics, with the exception of nitrogen-content. The root nitrogen content showed an increase with rainfall and tree presence through potentially higher mineralization rates and nitrogen availability in the under-tree canopy environment. The study sites occurred in the drier rainfall range in South Africa. Therefore, it is likely that trees and grasses in these dry savannas might have a positive relationship conforming to the stress-gradient hypothesis. Alternatively, grasses and trees might be using complementary water and nutritional resources.

The mix of trees and grasses is critical for the functioning of the savanna biome, which supports a large fraction of the human population and sustains the highest densities and diversities of herbivores in the world. Both, increases and decreases in tree densities have been reported from savannas globally, which are attributed to human activities and climate change. Changes in tree densities could drastically impact ecosystem functioning and lead to

land degradation and large economic losses. Consequently, the sustainable and heterogeneous nature of various savanna land-use types is compromised. In Chapter 5, I illustrated the significant role of trees in dry savannas (< 800mm rainfall) based on nutrient and water-redistribution capabilities of savanna trees and presented an ecological perspective of the role of trees in two human land-use types in African drylands: agroforests and rangelands which include silvo-pastoral systems and mixed game-livestock farming systems. I evaluated the causes for the loss of trees in these land-use types highlighting the role of trees for better land and sustainable natural resource management.

In Chapter 6, I synthesized the conclusions of all the preceding chapters highlighting the importance of facilitative interactions in tree-grass coexistence in savannas that are mostly overlooked. A simple Gaussian model of niche or habitat differentiation may not be a holistic and functional explanation of plant coexistence but rather the role of biotic interactions that include symbionts like mycorrhizal fungi will influence not only the competitive ability of plants but also facilitation, may be more pragmatic. Plant-plant interactions are complex and a multitrophic approach may be necessary to understand the functioning of these interactions and their roles in ecosystems.

SAMENVATTING

Terrestrische ecosystemen bevatten een hoge diversiteit aan planten, met veel verschillende soorten planten die naast elkaar kunnen bestaan. De mechanismen die voor deze coëxistentie zorgen zijn echter niet geheel duidelijk. Savanne ecosystemen die zijn beperkt in voedingsstoffen en water worden gekenmerkt door een uniek ecologisch kenmerk: de coëxistentie van bomen en grassen. Boom-gras interacties in savannes worden typisch beschouwd als competitief en zijn gebaseerd op het principe van niche- of habitatdifferentiatie. De competitie tussen bomen en grassen komt doordat ze elkaars groei onderdrukken. Ondanks deze competitie komen in savannes met verschillende regenvalomstandigheden, bomen en grassen naast elkaar voor. Deze studie onderzocht boom-gras interacties om de ecologische processen die boom-gras coëxistentie in droge savannes (<800 mm neerslag) van zuidelijk Afrika onderhouden, beter te begrijpen. Ik onderzocht de patronen in gebruik van water en stikstof door bomen en grassen en de gevolgen van concurrentie tussen bomen en grassen op het opslaan van voedingsstoffen in meerjarige grassen. Daarnaast onderzocht ik, met een ecologisch perspectief, de rol van bomen in twee soorten landgebruik in Afrikaanse droge gebieden, waarbij ik de functionaliteit van bomen in deze types landgebruik samen heb gevat.

Seizoensgebonden beschikbaarheid van water zorgt voor een enorme invloed van waterbeperking voor planten in savannes. Toch, komen in deze gebieden bomen en grassen naast elkaar voor. Er is dan ook nog maar weinig bekend over de waterrelatie tussen bomen en grassen. In hoofdstuk 2, werden de belangrijkste water-bronnen voor bomen en grassen in verschillende seizoenen geïdentificeerd met behulp van de natuurlijke variatie in H en O stabiele isotoop samenstelling van verschillende waterbronnen. Seizoensgebonden verschillen in de stabiele isotopensamenstelling van water in bomen en grassen gaf aan dat er zowel overlap als verdeling van waterbronnen plaatsvond. Bomen en grassen gebruikten water uit de bovengrond na regenval, wat aangeeft dat er overlap van waterbronnen is. Bomen verschoven naar water dieper in de grond als er geen water in de bovengrond was, wat een indicatie van verdeling van waterbronnen was. Grassen gebruikten altijd water uit de bovengrond. Door het labelen van diepe bodem (2,5 m diepte) met een deuterium (^{2}H) tracer, werd de herverdeling van water in alle onderzochte boomsoorten en verplaatsing van water naar grassen via de bovengrond bevestigd. Dit gebeurde echter alleen in het droge seizoen.

Deze resultaten geven aan dat er mogelijk verschuivingen in de boom-gras interacties plaatsvinden tijdens verschillende periodes van het jaar. Bovendien, gaf de herverdeling van water in het droge seizoen aan dat bomen mogelijk een faciliterende rol spelen voor de waterhuishouding van de grassen die eronder groeien.

Een belangrijke vraag in savanne ecologie is hoe bomen en grassen naast elkaar bestaan onder stikstof beperking. In hoofdstuk 3 werden de bronnen van stikstof voor bomen en grassen in een semi-droge savanne onderzocht met behulp van natuurlijke overvloed aan blad- δ^{15}N en stikstofgehalte. Daarnaast werd toevoeging van ^{15}N tracer gebruikt om de herverdeling van ondergrondse stikstof door bomen naar grassen te onderzoeken. Blad-δ^{15}N waarden waren consistent, waarbij bomen en grassen in alle seizoenen gebruik maakten van mycorrhiza-geleverde stikstof en wisselden naar microbiotisch-gebonden stikstof tijdens het natte seizoen. Op basis van seizoensgebonden variatie in de mineralisatiesnelheid in de Kruger Park regio, leek het gebruik van gemineraliseerde bodem stikstof door bomen en grassen zeer onwaarschijnlijk. De blad- δ^{15}N waarden waren vergelijkbaar voor alle onderzochte boomsoorten die wel verschilden in hun potentie om stikstof te fixeren in overeenstemming met de afwezigheid van knobbels die wijzen op het gebrek aan stikstof gebonden door rhizobium-bacteriën. Het tracer experiment toonde aan dat stikstof werd verdeeld door bomen naar de eronder groeiende grassen in alle seizoenen. Deze herverdeling van stikstof door bomen en latere opname van deze herverdeeld stikstof door grassen uit de bovengrond was onafhankelijk van de herverdeling van water. Hoewel er overlap was van stikstof bronnen tussen de bomen en grassen, kan de afhankelijkheid van biologische bronnen van stikstof, in combinatie met een herverdeling van de ondergrondse stikstof door bomen, bijdragen aan de co-existentie van bomen en grassen in halfdroge savannes.

Een belangrijke reactie van planten op concurrentie en beperkingen in de beschikbaarheid van grondstoffen is een toename in wortelreserves. In hoofdstuk 4, werden de wortelkenmerken van meerjarige grassen onderzocht in drie sites die verschillen in neerslag. Ze werden onderzocht in de aan- en afwezigheid van de bomen als een proxy voor concurrentie in Zuid-Afrikaanse savannes. Dit onderzoek was gebaseerd op de hypothese dat de concurrentie van bomen en waterbeperking zal leiden tot een verhoogde opslag in wortels van grassen onder bomen. Er werd echter geen significant effect van variatie in neerslag op wortelgroei kenmerken van grassen gevonden in de onderzochte gebieden. Bovendien werden, behalve stikstofgehalte, de meeste worteleigenschappen niet significant beïnvloed

door de aanwezigheid van bomen. Het stikstofgehalte in wortels nam toe met neerslag en de aanwezigheid van bomen. Dit is waarschijnlijk toe te schrijven aan de hogere mineralisatiesnelheden en beschikbaarheid van stikstof in de omgeving onder de boomkronen. De studie locaties lagen echter in het drogere deel van Zuid-Afrika. Daarom is het waarschijnlijk dat bomen en grassen in deze droge savannes een positieve relatie hebben als gevolg van de stress-gradiënt hypothese. Als alternatief, zouden grassen en bomen ook complementaire water- en voedingsbronnen kunnen gebruiken.

De combinatie van bomen en grassen is essentieel voor het functioneren van het savannebioom, dat een groot deel van de menselijke bevolking steunt en de hoogste dichtheden en diversiteit van herbivoren ter wereld onderhoudt. Zowel stijgingen als dalingen in de boomdichtheden zijn gemeld uit savannes wereldwijd, die worden toegeschreven aan menselijke activiteiten en klimaatverandering. Veranderingen in de boomdichtheden kunnen een drastische invloed hebben op het functioneren van ecosystemen en kan leiden tot aantasting van het land en grote economische verliezen. Bijgevolg is dat de duurzame en heterogene aard van de verschillende soorten landgebruik worden aangetast. In hoofdstuk 5, wordt de belangrijke rol van bomen in droge savannes (<800 mm neerslag) op basis van voedingsstoffen en water-herverdeling door savanne bomen geïllustreerd. Hierin geef ik een ecologisch perspectief van de rol van de bomen in twee soorten landgebruik in Afrikaanse droge gebieden: agroforests en rangelands die silvo-pastorale systemen en gemengde vee-wildhoud systemen omvatten. De oorzaken voor het verlies van de bomen in dit soort landgebruik wordt geëvalueerd en de rol van bomen voor beter landgebruik en duurzaam beheer van natuurlijke grondstoffen worden besproken.

Hoofdstuk 6 vat de conclusies van de voorgaande hoofdstukken samen waarin het belang van facilitaire interacties in de boom-gras coëxistentie in savannes, die meestal over het hoofd wordt gezien, wordt benadrukt. Een eenvoudige model van niche- of habitatdifferentiatie is misschien niet een allesomvattende en functionele beschrijving van plantaardige coëxistentie en misschien is een model met de rol van biotische interacties inclusief symbionten, parasieten of roofdieren, die niet alleen het concurrerend vermogen van planten, maar ook facilitatie zullen beïnvloeden, veel pragmatischer. Plant-plant interacties zijn complex en een multitrofe benadering kan nodig zijn om het functioneren van deze interacties, en hun rol in ecosystemen, beter te begrijpen.

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BIOGRAPHY

K.V. R. Priyadarshini (Priya) was born on the 25th of May 1972 in New Delhi, India and had a childhood spent in different parts of the country. She completed high school from the central Indian city of Nagpur, after which moved south-east to the port city of Visakhapatnam and pursued a B.Sc in Life Sciences and an M.Sc in Environmental Sciences at Andhra University. She then undertook a survey on the olive ridley sea-turtles along the northern coast of Andhra Pradesh with WWF-India under a fellowship programme jointly funded by WWF-India and Council for Advancement of People's Action and Rural Technology (CAPART), Ministry of Rural Development, Government of India. Post this survey, she joined the Wildlife Institute of India (WII), Dehradun to work on a WII and United States Fish and Wildlife Service collaborative project on conservation of the Indian wolf, and pursued a PhD with Saurashtra University, Rajkot, on ecological aspects of the Indian blackbuck *Antilope cervicapra*. She then joined Wageningen University to do a second PhD under the mentorships of Prof. Herbert Prins and Prof. Steven de Bie, where she studied the resource ecology of savanna trees and grasses in South Africa. Presently, she resides in Kota Kinabalu, Sabah, Malaysia with her husband Yoganand Kandasamy and is working on commencing research on applied ecology to aid land and soil management in tree plantations.

Publications:

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PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)
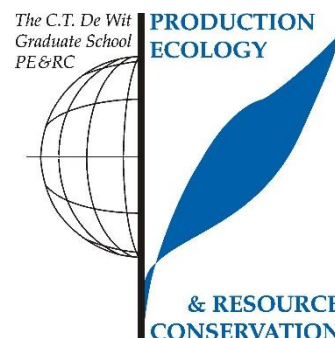
Review of literature (6 ECTS)

- Tree grass interactions in savannas, stable isotope ecology, ecophysiology

Writing of project proposal (4.5 ECTS)

- Resource use by trees and grasses in savannas: implications to tree-grass interactions (2009)

Post-graduate courses (9.1 ECTS)

- Ecophysiology of plants; Experimental Plant Sciences (2007)
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- Stable isotope ecology; SIRFER and Ehleringer lab, University of Utah, Salt Lake City, USA (2010)
- Introduction to R for statistical analysis; Biometris (2012)

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