WOOD RESPIRATION IN SAVANNAS

Mpilo Zenzele Khumalo

UNIVERSITY OF THE
WITWATERSRAND,
JOHANNESBURG

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DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the degree of the Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

(Signature of candidate)

15th day of December 2020 in Johannesburg

ABSTRACT

This dissertation investigates respiration by woody tissues in African savannas. Woody tissues are the major component of the biomass in savanna ecosystems. Since wood is made up of long-chain carbon molecules, and when alive is growing or maintaining its cells and thus respiring, it is an active and important component of the carbon cycle at organism, ecosystem and global scales.

The wood respiration flux was measured using a LiCor 8100A respirometer on ten common tree species (*Combretum apiculatum*, *Sclerocarya birrea*, *Senegalia nigrescens*, *Spirostachys africana*, *Burkea africana*, *Ochna pulchra*, *Strychnos pungens*, *Terminalia sericea*, *Philenoptera violacea*, and *Vachelia nilotica*) at three South African savanna sites: Skukuza, Wits Rural Facility, and Nylsvley Nature Reserve. Simultaneously, several factors that could potentially influence wood respiration rates were measured: (1) stem temperature; (2) stem size (height and diameter); (3) woody tissue nitrogen content, (4) woody tissue densities; (5) season of the year; (6) bark and sapwood thickness; and (7) fraction healthy leaves present during measurements (representing tree phenology).

The highest wood respiration rates were observed during the warm and wet growing season (October to March), and the lowest during the cooler dry season (April to September). Sapwood volume was found to be the best basis for expressing the wood respiration rate (rather than bark area, for instance). Species respire at different rates per unit sapwood volume. I found that the wood respiration rate is significantly associated with stem temperature and season of the year, and weakly related to the time of day. Wood respiration has a non-linear relationship to bark temperature: during the growing season, it increases with temperature up to maximum around 35 to 45 °C and declines at higher temperatures. During the dormant season, wood respiration rates increased with temperature, levelling off but not declining at high temperatures.

Using known allometric relationships and the relationships I established between respiration rates and continuously measured environmental variables, I scaled-up wood respiration from the scale of measurement (a chamber area of 0.01 m^2) to the sum of wood respiration fluxes from a hectare of savanna at the Skukuza flux site, which has long term measurements of ecosystem CO_2 exchange and soil respiration. I also scaled up the other main savanna ecosystem CO_2 fluxes (soil respiration, leaf respiration by trees and grasses, fire emissions, and respiration by insect and mammal herbivores). The sum of all these fluxes is the Total Ecosystem Respiration (TER), which I compared to the ecosystem respiration (R_{eco}) as measured ‘top-down’ by eddy covariance. I found that TER estimates were on average 42% larger than R_{eco}. It is unclear whether this difference results from an overestimation of one or more fluxes in the TER, or an underestimation of R_{eco}. I found that on average TER > Net Primary Production (NPP) > R_{eco}, suggesting that Skukuza is a small source of CO_2, which agrees with long-term Net Ecosystem Exchange (NEE) measured at this site.

Soil respiration amounted to about 84% of CO_2 efflux from this site, leaf respiration (almost equally divided between grasses and trees) 10%, fire 3%, and wood respiration only 1 – 2%, and respiration by herbivores amounted to just 1%. All these fluxes, except those from fires, peak during the wet and warm growing season.

Keywords – savanna, respiration, carbon, wood, ecosystem, autotrophic

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LIST OF ABBREVIATIONS AND SYMBOLS

Name	Abbreviation/Symbol
Aboveground Net Primary Production	**ANPP**
Akaike Information Criterion	**AIC**
Autotrophic Respiration	R_a
Carbon	**C**
Carbon dioxide	CO_2
Confidence Intervals	**CI**
Construction Autotrophic Respiration	$R_{a, c}$
Degrees of freedom	**df**
Dry biomass	**DM (kg DM)**
Eddy covariance	**EC**
Ecosystem Respiration	R_{eco}
Fraction Absorbed Photosynthetically Active Radiation	**FAPAR**
‘Function of’	f
Photosynthetically Active Radiation	**PAR, MJ**
Emissions of carbon dioxide from fires	R_{fire}
Gross Primary Production	**GPP**
Heterotrophic Respiration	R_h
y-intercept of any relation	β_0
Leaf Area Index	**LAI**
Leaf Autotrophic Respiration	$R_{a, leaf}$
Linear Mixed-Effects Model	**LMM**
Litter respiration	R_{litter}
Maintenance Autotrophic Respiration	$R_{a, m}$
Microbial respiration	$R_{microbe}$
Nitrogen	**N**
Net Ecosystem Exchange	**NEE**
Oxygen, in its di-oxygen atmospheric molecular form	O_2

Root Respiration	**R_{root}**
Estimated slope of any relation	**β**
Soil Respiration	**R_{soil}**
Standard deviation	**SD**
Standard error	**SE**
Stem Area Index	**SAI**
Total Ecosystem Respiration	**TER**
Water	**H_2O**
Wood Autotrophic Respiration	**$R_{a, wood}$**

LIST OF UNITS

Name	Symbol	Use
Degrees Celsius	**°C**	Temperature
Grams	**g**	Mass
Grams of carbon per megajoule	**gC/MJ**	Radiation Use Efficiency (ε)
Grams of carbon dioxide per square meter per year	**$gCO_2/m/y$**	Carbon stocks/fluxes
Grams per square meter	**g/m^2**	Litterfall
Gigatonnes of carbon per year	**GtC/y**	Carbon stocks/fluxes
Kilograms per square kilometre	**kg/km^2**	Biomass
Megajoule	**MJ**	Energy
Meters above sea level	**m.a.s.l.**	Altitude
Meters, centimetres, millimetres	**m, cm, mm**	Length
Micromoles of carbon dioxide per square meter per second	**$\mu mol\ CO_2/m^2/s$**	Carbon dioxide fluxes
Micromoles of carbon dioxide per cubic meter per hour	**$\mu mol\ CO_2/m^3/h$**	Carbon dioxide fluxes
Micromoles of carbon dioxide per cubic meter per year	**$\mu mol\ CO_2/m^3/y$**	Carbon dioxide fluxes
Milligrams per cubic meter	**mg/m^3**	Concentration
Grams per cubic meter	**g/m^3**	Density
Parts per million	**ppm**	Concentration
Petagrams of carbon per year (10^{15} gC/y)	**Pg C/y**	Global carbon fluxes
Square meters per hectare	**m^2/ha**	Tree basal area
Tonnes (metric, i.e. Mg) per hectare	**t/ha**	Biomass stock

Chapter 1: Introduction to ecosystem respiration

Rationale

Our knowledge about the carbon cycle of savanna ecosystems is incomplete. This is both surprising and worrisome. The amount of carbon dioxide (CO_2) respired by woody tissues has seldom been measured for savannas, despite wood being the largest biomass component in savannas (Sankaran et al., 2005). Reasons for this include; (1) lack of access to the necessary equipment in savanna-containing countries, often because this kind of equipment is expensive, (2) few qualified people to carry out this kind of research, and (3) difficulties encountered with temporal and spatial upscaling of respiration measurements (Sprugel et al., 1995).

Wood respiration is one of the important CO_2 effluxes in high-biomass ecosystems like forests, and thus potentially savannas. Global phenomena such as woody plant encroachment, deforestation, afforestation, biodiversity loss, global warming and climate change can be systematically linked to changes in the number of woody tissues, their composition and function. For example, afforestation and woody encroachment, or alternately deforestation or loss of woody cover have implications to the micrometeorology of ecosystems, which could upscale to influence the regional or even global climate (Scholes et al., 2015). Wood plays a key role in the terrestrial carbon cycle, as both a major carbon sink and stock (second only to soil carbon) and possibly as the source of an important flux (wood respiration). Since there is a well-known link between the carbon cycle and the global climate, it is crucial to understand processes such as wood respiration. Other autotrophic and heterotrophic respiration processes from savannas have been measured or can be derived from known predictive equations. Soil respiration is often the biggest source of CO_2 in systems like savannas (Chen et al., 2003), as measured using small chambers under and between canopies. Emissions of CO_2 from wildfires can be considered as an accelerated respiration process and have been extensively studied in savannas (Cachier et al., 1995; Hao et al., 2012; Lehsten et al., 2009).

Carbon enters ecosystems through the process of photosynthesis and is stored or sequestered there in biomass and soil organic carbon. Once we know exactly the rate at which it leaves ecosystems (i.e. respiration, including decomposition, which is mostly microbial respiration at work), we can work out whether savannas are carbon sinks or sources, a matter of great importance for the future evolution of the atmospheric CO_2 level that drives climate change. For instance, we can use an understanding of respiration dynamics to predict whether savannas will shift from carbon sinks to sources, when that may occur and what the drivers of such a shift may be.

Literature on wood respiration

Respiration (sometimes termed 'biological oxidation') is defined as a process whereby living organisms use oxygen (O_2) to break down organic molecules (in the form of carbohydrates, or with a carbohydrate backbone, such as proteins) (Amthor, 2000; Edwards and Hanson, 2003; Thornley, 1977; Vries and Penning, 1975; Weigl et al., 1951). This definition takes into account both physiological and biochemical processes of respiration but excludes purely physicochemical processes such as photo-degradation. It also excludes breakdown as a result of fire; a process that is important in savannas and highly analogous to biologically-mediated respiration. Respiration results in the release of energy in the form of adenosine triphosphate (ATP), which is used to synthesise new tissues and to maintain existing living tissues (Vries and Penning, 1975). The by-products from the respiration process are water (H_2O) and CO_2 and in the case of decomposition of organic molecules containing elements in addition to C, O and H, those elements in inorganic form (Singh and Gupta, 1977). Thus, decomposition is a key process making nutrients re-available for uptake by organisms. In photosynthetic organisms, respiration ('autotrophic respiration')[a] can be thought of as the reverse process of photosynthesis[b] (Hadden and Grelle, 2016; Ryan et al., 1994b, 1996; Vose and Ryan, 2002).

There are three viewpoints for the existence and the importance of respiration, especially in plants. ***View 1*:** The growth-and-maintenance-respiration paradigm (GMRP) argues that the growth of new tissues and maintenance of existing tissues are two

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[a] **Respiration:** $C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ H_2O + 6\ CO_2 + \textit{energy (ATP)}$

[b] **Photosynthesis:** $6\ H_2O + 6\ CO_2 + \textit{radiant energy, 400—700nm} \rightarrow C_6H_{12}O_6 + 6\ O_2$

fundamentally distinct processes, even though they share some biochemical reactions (Amthor, 2000). The assumption is that respiratory energy can either contribute to the ‘growth’ or ‘maintenance’ of tissues**.** ***View 2*****:** The growth-maintenance-and-wastage-respiration paradigm (GMWRP) extends the GMRP by assuming that some respiration may occur without benefit to a plant (Amthor, 2000; Thornley, 1977). This respiratory heat energy or CO_2 loss by a plant is conventionally termed ‘wastage’ (Amthor, 2000). ***View 3*****:** The general paradigm (GP) acknowledges that respiration has significant relationships with many other biochemical processes or pathways, not just growth, maintenance and wastage (Amthor, 2000). In this dissertation, I lean more towards the general paradigm as it takes into consideration every aspect of respiration. Future studies (e.g. one linking growth rates with respiration) can focus on a single component of wood respiration and thus chose any other paradigm.

In the carbon cycle of terrestrial ecosystems, including savannas (Figure 1.1), carbon is assimilated into the ecosystem through photosynthesis; a flux termed Gross Primary Production (**GPP**) (Woodwell and Whittaker, 1968). A portion of this flux is returned to the atmosphere almost immediately, through photorespiration (inefficiencies in the assimilative pathway itself). Another portion is returned after a delay of hours to months, and from all tissues, not just photosynthesising cells, in the form of maintenance respiration ($\mathbf{R_{a,\,m}}$) and growth respiration ($\mathbf{R_{a,\,c}}$) (Ryan et al., 1994b). The assimilated carbon that remains after respiration results in biomass accumulation (plus other pathways, such as root exudates and volatile organic carbon emissions, which are usually considered small, but can in some circumstances be substantial (Hanson et al., 2000; Otter et al., 2002)). This is called Net Primary Production (**NPP**) (Lovett et al., 2006; Roxburgh et al., 2005). In the process of biomass growth, about one-quarter of the carbon used is emitted as construction respiration ($R_{a,\,c}$) (Lambers et al., 1983). The live biomass has an ongoing maintenance requirement, which results in a small, continuous but time-varying autotrophic respiration flux, a large part of which is potential respiration from woody tissues ($\mathbf{R_{a,\,wood}}$) since although they are metabolically relatively inactive, constitute a large fraction of the living tissues. Some biomass is consumed by herbivores, which then liberate its embodied energy to supply their own needs, generating heterotrophic respiration ($\mathbf{R_h}$) in the process (Heusner, 1985; Zhou et al., 2009a). Some biomass dies and forms litter (much of this is not apparent, because it occurs belowground as fine root turnover), which eventually becomes transformed into soil organic matter. The decomposition of these dead carbon pools by invertebrates and microbes, including the consumption of root exudates and the carbon spent by the plant in subsidising root symbionts such as mycorrhizae and nitrogen-fixing bacteria, is the largest component of heterotrophic respiration. This component is conventionally measured as it emerges from the soil surface (soil respiration $\mathbf{R_{soil}}$) (Hanson et al., 2000; Lloyd and Taylor, 1994; Makhado and Scholes, 2011; Raich and Potter, 1995). Because of how R_{soil} is measured, the soil respiration flux conventionally includes $\mathbf{R_{litter}}$ and $\mathbf{R_{root}}$ in addition to $\mathbf{R_{h,\ microbe}}$ and $\mathbf{R_{h,\ soil\ invertebrates}}$. In savannas, a portion of the undecomposed or partly decomposed aboveground biomass is consumed by fire ($\mathbf{R_{fire}}$) (Figure 1.1) (Higgins et al., 2000; Shea et al., 1996). It is also important to note there are lateral movements of carbon (such as resulting from harvest and transport of carbon-based materials, transport overland by floods, leachates, soil erosion, wind-carry, and intersystem movement of herbivores) which can interfere with carbon budget closure at a site. These fluxes are typically relatively small, and exports are assumed to be approximately balanced by imports (Kirschbaum et al., 2001). The sum of all the autotrophic, heterotrophic and fire respiration terms is called 'ecosystem respiration' ($\mathbf{R_{eco}}$, sometimes denoted as $\mathbf{R_e}$ Archibald et al., 2009; Houghton, 1996; Lavigne et al., 2012). In an ecosystem at steady state (i.e. climax, where it is no longer a net accumulator of biomass), assimilation should exactly balance ecosystem respiration, i.e. GPP = $|R_{eco}|$. Note that by convention, the fluxes *out* of the atmosphere (into the vegetation) are given a negative sign, while those into the atmosphere are given a positive sign. Globally, undisturbed terrestrial ecosystems are not quite at steady state at present. Rather, as a whole (but not necessarily individually) they are sinks of carbon of the order of 3% of global terrestrial GPP (Hadden and Grelle, 2016; Houghton, 1996). It is thought that this is the consequence of a combination of factors, including the rising atmospheric CO_2, increasing N deposition, changing climate, and recovery from past vegetation disturbance in some regions of the world (Field et al., 1998; Hadden and Grelle, 2016).

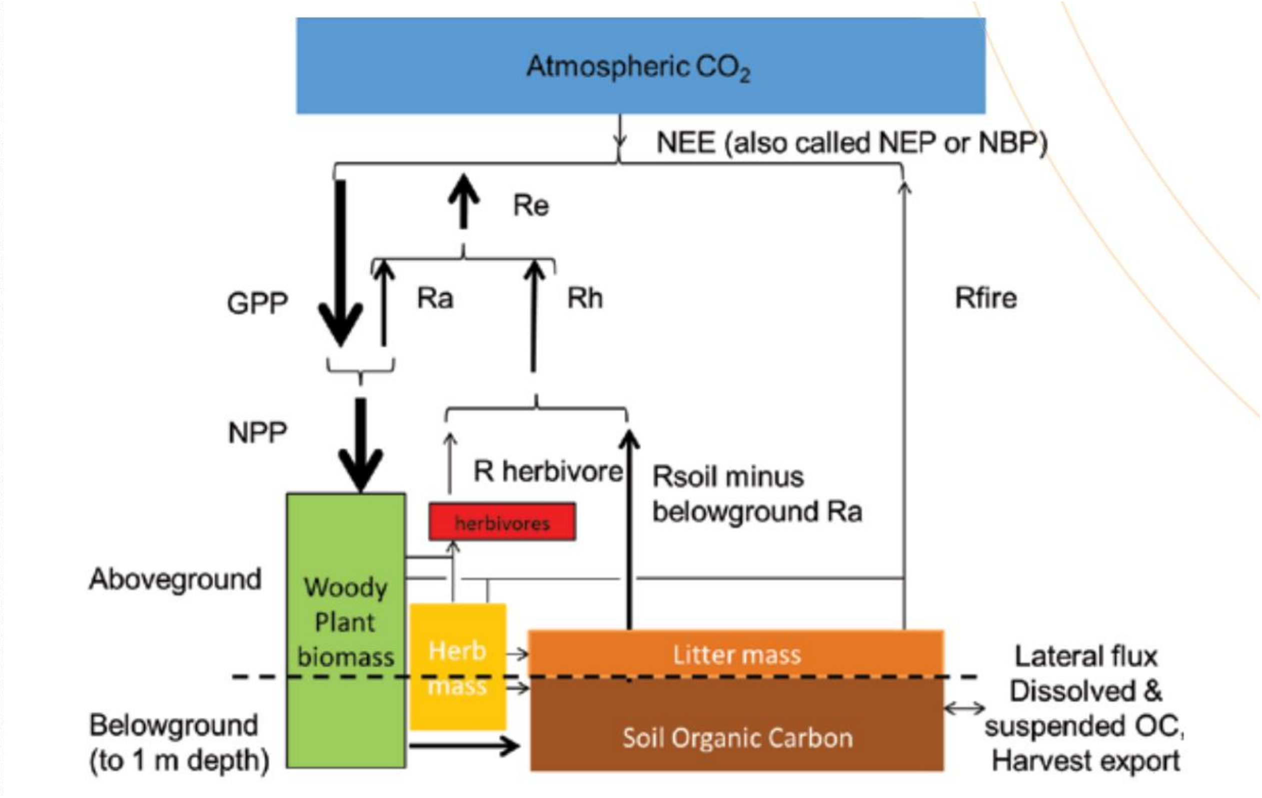

Figure 1.1 *A typical terrestrial carbon cycle: The width of the arrows represents the relative magnitude of the fluxes. The size of blocks represents the relative magnitude of stocks. Fluxes from the ground to the atmosphere are conventionally given a positive sign, and fluxes from the atmosphere into the terrestrial ecosystem are given a negative sign. Source:(Kgope et al., 2015).*

Carbon assimilation

Gross Primary Production (GPP)

Gross primary production (GPP) is the total amount of organic carbon that is fixed (i.e. converted from gaseous CO$_2$ to a solid carbohydrate form) in an ecosystem by photosynthesis per year (Field et al., 1998; Kirschbaum et al., 2001; Lovett et al., 2006; Smithson, 2002). Since this is a flux from the atmosphere to the ground, it is conventionally given a negative sign in carbon budget studies. Global terrestrial GPP is estimated at ~120 Gt C/y Smithson, 2002; Steffen et al., 1998). GPP is conventionally estimated from satellite observations of the Fraction Absorbed Photosynthetically action radiation (FAPAR), Photosynthetically Active

Radiation at canopy level (PAR, MJ), and an assumed constant but ecosystem-specific Radiation Use Efficiency, ε (gC/MJ) (Running and Zhao, 2015).

$$\mathrm{GPP} = \mathrm{FAPAR} \times \mathrm{PAR} * \varepsilon$$

GPP is also commonly inferred from eddy covariance (EC) flux measurements, which measures Net Ecosystem Exchange (**NEE**), the sum of GPP and R_{eco}. If you have NEE, and an estimate of R_{eco}, you can back out GPP (Archibald et al., 2009; Falge et al., 2002; Räsänen et al., 2017). The key problem here is the accurate estimation of R_{eco}, which is the main subject of chapter 3 of this thesis.

Net Primary Production (NPP)

Net Primary Production (NPP) is the sum of GPP and respiration by plants (i.e. autotrophic respiration R_a[c], noting that they have opposite signs) (Bronson and Gower, 2010; Kirschbaum et al., 2001; Lovett et al., 2006).

$$NPP = GPP + Ra$$

NPP once corrected for losses associated with volatile organic carbon and root exudates, is reflected in the increase in the sum of below ground and aboveground biomass growth over a period of time, provided the biomass is protected from herbivory and fire, and the biomass shed as litter is accounted for (Chen et al., 2003; Kirschbaum et al., 2001; Lovett et al., 2006). NPP is a key measure of ecosystem health and productivity (Field et al., 1998). Global terrestrial NPP is estimated at ~60 GtC/y (Smithson, 2002). This means global NPP is about half of global GPP (this ratio ranges between 30% and 70%), and R_a is the other half of GPP – an approximation which is widely used in estimating either NPP from GPP or vice versa.

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[c] Fluxes from the atmosphere to land are conventionally assigned as negative while those from land to atmosphere are assigned as positive (e.g. GPP is negative, R_a is positive)

Carbon effluxes from ecosystems

Autotrophic respiration (R_a)

The amount of carbon respired by the plants in an ecosystem is called autotrophic respiration (R_a) (Edwards and Hanson, 2003; Martínez-García et al., 2017; Ryan et al., 1997). The aboveground components of R_a in savannas include respiration from tree leaves (where ‘tree’ includes all woody plants, such as shrubs), tree branches, tree stems, tree fruiting bodies, grass and forb stems, grass and forb leaves and fruiting bodies (Chen et al., 2003). The two major components of belowground R_a are coarse root R_a and fine root R_a (Chen et al., 2003; Makhado and Scholes, 2011; Malhi et al., 1999). A complication comes in with respiration by fungal mycorrhizae and bacterial root symbionts, since technically that is heterotrophic respiration, but functionally these organisms are part of the plant rooting system (Hanson et al., 2000). Most savanna species have such associations, and they may consume a large fraction of the assimilated carbon (Hartnett et al., 2004; Walker et al., 2003). Studies have found that in most terrestrial ecosystems, R_a comes from belowground (Chen et al., 2003; Hadden and Grelle, 2016; Yang et al., 2014). There is also potentially a small contribution to ecosystem R_a from bark-living lichens and photosynthetic soil crusts.

Heterotrophic Respiration (R_h)

Heterotrophic respiration (R_h) is the release of CO_2 by microbes, invertebrate and vertebrate animals, resulting from metabolic processes (Zhou et al., 2009a). In savannas this component can be separated into two main parts: that by herbivores, and that by microbes.

- *R_h by herbivores*

This component reflects the metabolism of herbivores (mainly large mammals and insects in savannas). This flux can be derived from herbivore biomass and empirical relationships between basal metabolic rate and body size and between basal metabolic rate and respiration rate (Darveau et al., 2002; Heusner, 1985). It is one of the smallest fluxes in the global carbon cycle and is often not accounted for in whole-ecosystem carbon budget studies (Archibald et al., 2009; Chen et al., 2003), but African savannas are relatively herbivore-rich ecosystems, both in terms of vertebrates and invertebrates (Hempson et al., 2017), so I include this respiratory flux in my analysis out of interest.

- *R_h by microbes*

This component reflects the metabolism and degradative processes mediated by heterotrophic microbes. In savannas, these microbes include fungi, bacteria and archaea (Hanson et al., 2000; Mikan et al., 2002; Stotzky, 2016). The microbes are more abundant below than above ground (Beverly and Franklin, 2015; Hu et al., 2001), though they can also occur on bark and leaf surfaces, there the $R_{h,\ microbial}$ flux gets confused with wood and leaf respiration respectively (Anderson, 2014; Stotzky, 2016). Aboveground, microbes are responsible mostly for the decomposition of litter (dead plant matter). This '*litter respiration*', I will for simplicity assume is a form of heterotrophic microbial respiration, even though it includes photo-degradation, and small components of invertebrate respiration (Araujo et al., 2012).

Soil Respiration (R_{soil})

Soil respiration (R_{soil}) is the release of CO_2 by roots (R_a), soil microbes (R_h) and the non-microbial soil biota (vertebrate and invertebrate herbivores and detritivores) (Lloyd and Taylor, 1994; Makhado and Scholes, 2011).

Soil respiration is one of the biggest fluxes in savannas and the second-largest terrestrial carbon flux globally (Kirschbaum et al., 2001; Makhado and Scholes, 2011). Factors known to influence the rate of soil respiration in savannas are soil water content, soil temperature and the productivity of the vegetation (often proxied by the soil organic carbon content) (Lloyd and Taylor, 1994; Makhado and Scholes, 2011; Mikan et al., 2002). This flux is normally measured using chambers connected to infrared gas analysers (Chen et al., 2002; Hibbard et al., 2005; Makhado and Scholes, 2011; Wang et al., 2005; Xu et al., 2000; Zhou et al., 2009b), but some researchers have used other techniques (Xu et al., 2000). The soil surface litter is usually not removed before the measurement is taken, thus this term includes R_{litter}. Teasing apart R_{root} from $R_{microbe}$ can be done by applying microbial biocides, or by excluding roots from the measurement area, or by isotopic tracer techniques (Beverly and Franklin, 2015; Hanson et al., 2000). Each of these methods has their advantages and drawbacks such as improved accuracy of components of respiration, but also the introduction of error propagation.

Ecosystem Respiration (R_{eco})

Ecosystem respiration (R_{eco}) is the amount of carbon respired by the whole ecosystem (Archibald et al., 2009; Brændholt et al., 2018; Chen et al., 2003; Hadden and Grelle, 2016; Malhi et al., 1999). It can be estimated from the NEE at night-time, when photosynthesis is zero (assuming no CAM plants are present), as measured by eddy covariance (EC) (Archibald et al., 2009; Bolstad et al., 2004; Falge et al., 2002; Merbold et al., 2009; Räsänen et al., 2017). The daytime R_{eco} is then extrapolated from the night-time estimate, either by multiplying by the ratio of daylight hours to night-time hours or more commonly, by using a temperature function driven by the diurnal course of air temperature (Archibald et al., 2009; Lavigne et al., 2012; Moffat et al., 2007).

Among the several problems with measuring R_{eco} by the night-time, EC method is that frequently the turbulence assumptions necessary for valid EC measurements are not met at night, and CO_2 either accumulates or drains off the landscape, undetected (Archibald et al., 2009; Moffat et al., 2007). R_{eco} reflects all respiration processes occurring within an ecosystem and is often compared to the Total Ecosystem Respiration (TER), which is the same thing, but measured ‘bottom-up’ as the sum of individual fluxes (Hadden and Grelle, 2016; Yuste et al., 2005). TER is the summation of all respiration processes, which are measured independently, using different techniques, at shorter time scales and with footprints smaller than that of a flux tower (Chen et al., 2003; Hadden and Grelle, 2016; Makhado and Scholes, 2011; Martínez-García et al., 2017; Xu et al., 2000). By contrast, flux tower measurements are referred to as ‘top-down’.

Fire Emissions (R_{fire})

Savannas burn relatively frequently (once every 1 to 5 years is typical), mostly ignited by people (Archibald et al., 2012; Biggs, 2003). Savannas fires are highly seasonal, occurring almost exclusively during the dry season (Biggs, 2003; Govender et al., 2006; Hoffa et al., 1999). Their occurrence, assuming an ignition source, depends on two main factors; (1) availability of adequate combustible fuel (i.e. aboveground dead biomass, ‘packed’ in a way that permits self-sustaining fire propagation) and (2) weather conditions (mostly humidity, air temperature and wind speed) (Biggs, 2003; Higgins et al., 2000; Shea et al., 1996; Trollope and Potgieter, 1985). Biomass burning in savannas plays a pivotal role in cycling carbon and is one of the biggest sources of aerosols and trace gases that are responsible for cloud formation (Cachier et al., 1995; Hao et al., 2012). The emission of carbon and other elements from fires can be estimated from concentration measurements taken in the smoke plume, or by measuring the loss of fuel. The area burned is determined by measuring fire scars on remotely sensed data (Archibald et al., 2010; Cachier et al., 1995; Hao et al., 2012; Lentile* et al., 2006). Fires occur too fast for most typical infrared gas analysers mounted on EC towers to accurately estimate the emission fluxes (Archibald et al., 2009).

Net Ecosystem Exchange (NEE)

Net Ecosystem Exchange (NEE) is synonymous with Net Ecosystem Production (NEP) (Archibald et al., 2009; Chapin et al., 2006; Hadden and Grelle, 2016; Kirschbaum et al., 2001; Randerson et al., 2002; Ryan, 1991a). NEE at very large scales is called Net Biome Production (NBP) and differs from NEE by the inclusion of relatively rare disturbance events, and having most of the lateral transfers of carbon within the measurement footprint. NEE was first defined in 1968 by Woodwell and Whittaker as the difference between GPP and R_{eco}, (but it is the sum of GPP and R_{eco}, recalling that they bear different signs).

$$NEE = GPP + R_{eco}$$

NEE in a ‘steady-state’ ecosystem is zero (i.e. NEE = 0). A net ecosystem carbon sink has NEE < 0 and a net carbon source has NEE > 0 (Archibald et al., 2009; Räsänen et al., 2017). This flux is what eddy covariance flux towers measure (Archibald et al., 2009; Chen et al., 2003; Falge et al., 2002; Hadden and Grelle, 2016; Räsänen et al., 2017), they do so imperfectly when the turbulence assumptions are violated or when carbon dioxide is gained or lost by lateral processes below the plane of measurement (Burba, 2013; Rannik et al., 2016).

Wood respiration in terrestrial ecosystems

Plant respiration processes generally respond to factors that are also known to affect photosynthesis (Archibald et al., 2009). Wood respiration ($R_{a,\ wood}$) rates are expected to be affected by species, phenological state (and thus the season of the year), plant size or age, the relative physiological activity level of the tissue (often indexed by its nitrogen content, which reflects the enzymatic concentration), tissue density, tissue volume and tissue temperature. Chapter 2 of this dissertation goes in details about these potential drivers in relation to wood respiration.

Wood respiration studies have been done mainly in natural forests and forest plantations of Eurasia and North America (Bolstad et al., 2004; Brændholt et al., 2018; Ryan et al., 1997, 1995, 1994a; Sprugel, 1990; Yang et al., 2014). Temperature is a major determinant of wood respiration. The wood respiration rate has often been found to have an exponential relationship to tissue or air temperature (The exponent of this relationship is frequently expressed as the 'Q_{10}', which is the ratio of the respiration rate at some reference temperature, typically around 20° C, and that at a temperature 10°C cooler, and is classically assumed to have a value around 2). Some studies have also found other forms of relationships (Reichstein et al., 2003; Ryan et al., 1994b; Trumbore et al., 2013, p. 10; Wang et al., 2005, p. 10; Xu et al., 2000, p. 10; Yang et al., 2019; Zhou et al., 2009b, p. 10). Tree species have been found to respire at different rates depending on their typical stem diameter, tissue nitrogen content and sapwood fraction (Asao et al., 2015; Hilman et al., 2017; Levy and Jarvis, 1998; Patterson et al., 2018; Rodríguez-Calcerrada et al., 2015; Ryan et al., 1997; Stockfors and Linder, 1998; J. Y. Yang et al., 2012). Wood respiration rates have also been found to be highly seasonal; with high rates observed during the growing season (Beringer et al., 2007; Chan et al., 2018; Stockfors and Linder, 1998; Vose and Ryan, 2002; Wieser and Bahn, 2004; Zha et al., 2004).

Most CO_2 effluxes are measured at short time scales (a few minutes) and over small footprints. Wood respiration has been measured using small chambers since the early studies in the 1960s (Woodwell and Whittaker, 1968) up to the current study (Chapter 2). It has also been measured from whole trees (Pérez-Priego et al., 2015). Even whole tree measurements need upscaling to reach ecosystem scale. Upscaling is necessary because ecologists and policymakers are interested in understanding what is happening within an entire landscape rather than one individual tree or species, let alone one small chamber. It is also essential to understand what happens over an entire year, rather than just over the seconds or hours of the actual measurement. This means that most CO_2 efflux measurements have to be re-calculated at relevant scales, using unbiased algorithms (Cheng et al., 2010; Lavigne et al., 2012; Meir and Grace, 2002; Wu, 1999). This is a common challenge for natural scientists. Chapter 3 of this dissertation goes in detail about the upscaling of savanna CO_2 effluxes.

Aims and objectives of this study

The first aim of this thesis was to quantify wood respiration rates by several common Southern African savanna species ($R_{a, wood}$), and to understand the factors that influence those rates (Chapter 2). The second aim was to upscale wood respiration and compare it to other respiration fluxes at ecosystem scale (Chapter 3).

Objectives and key questions

Objective 1: Measure $R_{a, wood}$ and quantify its relationship to potential drivers such as bark temperature, season or time of the year, sapwood nitrogen content, sapwood volume, tree size, and species.

- ***Key question:*** Which factor(s) significantly predict $R_{a, wood}$ in savannas?

Objective 2: Upscale $R_{a, wood}$ from chamber measurements (µmol $CO_2/m^2/s$ measured at a scale of 0.01 m^2) to ecosystem-scale (g $CO_2/m^2/y$, expressed at a scale of 1 ha; the use of m^2 is a SI formalism since this is the base unit of length dimensions; the actual scale of ecosystem quantification has a length dimension of about 100m, and thus an area of 1 000 m^2).

- ***Key question:*** How can $R_{a, wood}$ be upscaled in savanna ecosystems?

Objective 3: From literature and chapters 2 and 3; collect all relevant information about respiration processes in savannas to scale tree-scale effluxes to an ecosystem level.

- ***Key question:*** Which components of savannas respires most CO_2? During which parts of the year?

- ***Key question:*** After calculating TER, is it equal to R_{eco}? What might be missing or double-counted?

Structure of this dissertation

Chapter 2 and chapter 3 of this dissertation have been written in a free-standing format for submission to a scientific journal for publication. Chapter 2 is focused on objective one of this thesis and has been nominally prepared and formatted for submission to the '*New Phytologist*' journal. Chapter 3 is focused on objectives two and three and has been prepared and formatted for submission to '*Global Change Biology*'. The chapters are presented as they will be submitted, except that some few changes might occur following review and that in the thesis all the references are to be found in a single consolidated references section at the end.

Chapter 2: Drivers of wood respiration in southern African savannas

This chapter is written as a stand-alone paper, intended for submission to *New Phytologist*.

M.Z. Khumalo[1, 2]

[1]School of Animal, Plants and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

[2]Global Change Institute, University of the Witwatersrand

Author for correspondence:

Mpilo Z. Khumalo

Email: mpilozenzele0@gmail.com

Summary

- The amount of CO_2 emitted by woody tissues (wood respiration) was previously unquantified in African savannas, despite wood being the largest component of biomass in these geographically extensive ecosystems.
- This study measured wood respiration from ten dominant savanna species located at three sites in South Africa and determined the main factors that control its variation.
- Measurements were taken using the LiCor 8100A system during four seasons: early-dry, late-dry, early-wet, and late-wet. Each species-sample comprised trees varying in diameter, phenology, wood nitrogen content, sapwood volume and wood density.
- The respiration rates were in the order of 0.03 – 12.85 µmol $CO_2/m^2/s$ relative to bark area, or 0.96 – 365.28 µmol $CO_2/m^3/s$ relative to sapwood volume. Sapwood volume was a better predictor of wood respiration ($R^2 = 80\%$) than was bark area ($R^2 = 59\%$).
- Bark temperature and season of the year are the major significant drivers ($p < 0.001$) and time of day was a minor driver ($p = 0.008$) of wood respiration rates. The effect sizes are $\beta = 0.12$ for temperature, $\beta = 0.58$ for season of the year and $\beta = -0.0001$ for time of day.
- Wood respiration during the growing season rises to a maximum rate between 35 - 45 °C and then falls at higher temperatures. During the dormant season, the wood respiration rate levels off at high temperatures but does not fall at even higher temperatures.
- Once temperature, seasonality and time of day were accounted for, species differences remained, which were related to sapwood density ($p = 0.01$, $R^2 = 0.6$) but not to wood nitrogen content or phenology.

Keywords: temperature, season, time of day, species, sapwood, volume, density.

Introduction

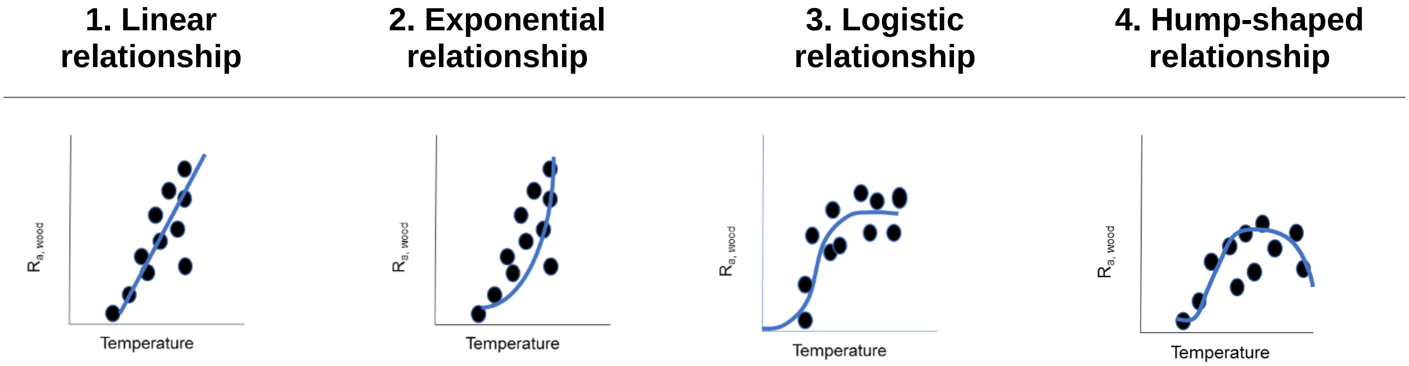
Ecologists, when explaining the terrestrial carbon fluxes to lay people, sometimes make the analogy of ecosystems ‘breathing in’ through photosynthesis and ‘breathing out’ through respiration. The problem is that we generally know a great deal more about the ‘breathing in’ part (carbon assimilation) than the ‘breathing out’ part, and this is certainly true for savannas. There are some estimates of whole savanna ecosystem respiration (Archibald et al., 2009; Chen et al., 2003; Kutsch et al., 2008; Räsänen et al., 2017), and some of the soil respiration in savannas (Chen et al., 2002; Makhado and Scholes, 2011; Rochette et al., 1997), but virtually none on respiration by the largest component of the biomass, wood ($R_{a,\ wood}$). Respiration is a more important determinant of whether an ecosystem is a carbon sink or source than photosynthesis (Hadden and Grelle, 2016; Houghton, 1996).

Reliable equipment to measure soil respiration (e.g. the LiCor 8100-A soil flux system, LI-COR Biosciences, Lincoln, Nebraska, USA) now exists. It can be relatively easily adapted to measure $R_{a,\ wood}$. The upscaling of chamber measurements to the whole ecosystem remains a challenge, but one for which the conceptual tools exist. Therefore this paper sets out to fill the information gap regarding wood respiration in savannas, for three different savanna ecosystems in southern Africa.

Respiration is a metabolic process whereby a living organism breaks down carbohydrates using oxygen (O_2) to produce energy (Kozlowski, 1992; Lambers et al., 1983; Vries and Penning, 1975). The energy is produced in the form of adenosine triphosphate (ATP) which is used to synthesise new tissues for growth and repair, and to keep living tissues alive (Ryan, 1990; Vries and Penning, 1975). This process releases CO_2 and water (H_2O) as by-products (Amthor, 2000; Vries and Penning, 1975). Respiration can be expressed as the reverse process to photosynthesis [$C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ H_2O + 6\ CO_2 + \textit{energy (ATP)}$] (Weigl et al., 1951). However, unlike photosynthesis, respiration occurs in all plant tissues, throughout the day and the year (Ryan et al., 1994b, 1994a, p.). Net wood respiration ($R_{a,\ wood}$) has been found to come from three components: (1) woody tissue respiration (CO_2 efflux) to the atmosphere, (2) bark photosynthesis (CO_2 influx), and (3) xylem-sap CO_2 dissolution (which can either be an efflux or influx depending on the rate of CO_2 diffusion) (Hilman and Angert, 2016; Wang et al., 2019). For this research, I used an opaque chamber to ensure that I measured only $R_{a,\ wood}$ efflux to the atmosphere, uncontaminated by a photosynthesis signal (Wang et al., 2019).

Although wood respiration has never to our knowledge been measured in African savannas, it has been extensively studied in natural and planted forests in North and South America and Eurasia (e.g. Bosc et al., 2003; Brændholt et al., 2018; Ryan, 1990; Ryan et al., 1995; Xu et al., 2000, p. 10; Yang et al., 2014). These studies have inspired some of the key questions I aim to answer in this current research.

Biological processes (including $R_{a,\ wood}$) are known to be positively and often non-linearly responsive to temperature (Arrhenius, 1889). The commonly found relationship between $R_{a,\ wood}$ and temperature is an exponential increase in wood respiration with an increase in temperature (Maier et al., 1998; Stockfors, 2000). This is often expressed in the form of a temperature quotient (Q_{10}, relating an increase in the rate of a biological process following a 10 °C increase in temperature, with typical values between 1.6 and 3.5 for $R_{a,\ wood}$) (Davidson et al., 2006; Tjoelker et al., 2001). Savannas are on average much warmer than the forests in which $R_{a,\ wood}$ has been measured in the past. Does a simple exponential relationship still apply, or is there a levelling-off or even decline at high temperatures? It could be expected that $R_{a,\ wood}$ in savannas will have one of the following relationships with temperature:



Most studies have found that $R_{a,\ wood}$ is highly seasonal (Araki et al., 2010; Ceschia et al., 2002; Chan et al., 2018; Ryan et al., 1997; Wieser and Bahn, 2004; Zha et al., 2004). Rates reach a maximum during the active growing season (which in savannas is both warm and wet). Apart from the direct temperature controls, this has been attributed to an increased level of various energy-consuming physiological activities in the plant, such as tissue synthesis and growth, repair and maintenance (Kozlowski, 1992; Lambers et al., 1983; Vries and Penning, 1975). Low rates are observed during dormant seasons (in southern Africa savannas, the dry but still warm months of the Austral winter), during which it is suggested that only maintenance respiration occurs (Amthor, 1984; Bosc et al., 2003; Ryan, 1990; Ryan and Waring, 1992).

Savannas differ from a temperate and boreal seasonal forest in that the seasonality in savannas is principally induced by dryness, not by low temperatures (Archibald et al., 2009). Some research has suggested that $R_{a,\ wood}$ measured during the growing seasons is influenced by high sap flow (reflecting the transpiration stream and low stomatal conductance) during this season (Teskey and Mcguire, 2002). It has been recently confirmed that the transpiration rate does not necessarily influence $R_{a,\ wood}$ directly (Bužková et al., 2015). Savannas are characterised by distinct wet and dry seasons, so it will be interesting to see how $R_{a,\ wood}$ changes in relation to season, controlling for both hydration and temperature.

$R_{a,\ wood}$ would be expected to vary with time of day, given that temperature varies diurnally. Once the temperature is controlled for, there may be a residual time-of-day effect, which could, for instance, be due to the variation in photosynthesis in response to irradiation levels (Bowman et al., 2005; Edwards and Hanson, 1996; Fan et al., 2017; Teskey and Mcguire, 2002; Wang et al., 2019; Zha et al., 2004; Zhu et al., 2012).

$R_{a,\ wood}$ has been found to positively correlated with tree growth rate (Ceschia et al., 2002; Damesin et al., 2002; Lavigne and Ryan, 1997; Maier, 2001; Rowland et al., 2018; Ryan et al., 1994a; Stockfors and Linder, 1998; Zha et al., 2004). Tree growth rates are highly dependent on the nitrogen (N) status of the trees, where trees with high N content grow faster than those with low N. $R_{a,\ wood}$ has also been found to have a positive relationship with chemically bound wood N content (Ceschia et al., 2002; Maier, 2001; Maier et al., 1998; Reich et al., 2008; Ryan et al., 1996). This is because high N bound in tissues is indicative of faster metabolism by those tissues, which corresponds to faster rates of CO_2 production and release by these tissues (Reich et al., 2008).

Some studies have looked at the effect of tree size (stem diameter) on $R_{a,\ wood.}$ They find a weak correlation, generally negative, or no correlation (Bosc et al., 2003; Carey et al., 1997; Cavaleri et al., 2006; Ceschia et al., 2002; Damesin et al., 2002; Fan et al., 2017; Hadden and

Grelle, 2016; Ryan et al., 1994a). Large-diameter stems may contain a relatively smaller fraction of respiring tissue since only the sapwood volume is thought to respire (Stockfors and Linder, 1998). Many studies base their whole-tree extrapolations on sapwood volume (Edwards and Hanson, 1996; Lavigne and Ryan, 1997; Maier et al., 1998; Ryan, 1989; Ryan et al., 1995, 1994a); but some studies argue that $R_{a,\ wood}$ relates better to surface area than to underlying sapwood volume since the major respiring tissues are the cambium and phloem situated just beneath the bark (Lavigne and Ryan, 1997; Woodwell and Whittaker, 1968). Which predictor works best in savannas?

Different tree species could be expected to respire at different rates, even once the above factors have been taken into consideration. Respiration could logically be affected by several things: (1) phenological status (e.g. deciduous, semi-deciduous and evergreen) (Asao et al., 2015; Rowland et al., 2018) (2) wood density in bark and sapwood (the amount of space between cells of woody tissues that drives the amount and rate of gaseous diffusion and positively correlates with transpiration) (Lavigne et al., 2004), (3) phenology (whether or not there were leaves or fruits present on the tree during data collection) (Gielen et al., 2003; Patterson et al., 2018; Rodríguez-Calcerrada et al., 2015), and (4) amount of nitrogen in the tissue (which is an indicator for metabolic activities such as growth and tissue maintenance) (Maier et al., 1998; Vries and Penning, 1975).

Site elevation has been found to significantly affect the rates of $R_{a,\ wood}$ (Robertson et al., 2010). It is unclear if this effect is independent of temperature, hydrature and species. Drought, and factors like photosynthetically active radiation (PAR) and leaf area index (LAI) may also be indirectly linked to $R_{a,\ wood}$ (Cavaleri et al., 2006; Rowland et al., 2018). This study will explore some of these possibilities.

Aim

This research aims to (1) measure $R_{a,\ wood}$ from a variety of common savanna tree species with a range of ecophysiological traits, in several savanna sites, during various seasons of the year and at different times of the day; and (2) derive a predictive model for $R_{a,\ wood}$ from a set of potential drivers, including bark temperature, season, stem diameter, species, sapwood thickness, wood N content and wood density.

Hypotheses

- ***Hypothesis 1:*** Species respire at significantly different rates, and these differences are explained by their differing wood nitrogen content, sapwood volume and wood density.
- ***Hypothesis 2:*** Trees with thick sapwood will respire at greater rates than those with thin sapwood, regardless of stem diameter, and especially during the dry season.
- ***Hypothesis 3:*** The temperature response curve of wood respiration in savanna trees, measured over the full environmental range, is neither linear nor continuously exponentially rising, but increases with temperature below a certain point and then levels off or declines at the highest experienced temperatures.
- ***Hypothesis 4:*** Wood respiration rates are higher in the wet season than the dry, all other factors being equal.

Materials and methods

A pilot study was undertaken in 2017 at the Skukuza flux tower site (■ in Figure 2.1), in the southern part of the Kruger National Park, in South Africa. The full study was conducted at three savanna sites situated in Limpopo and Mpumalanga provinces of South Africa (Figure 2.1) which have different bedrock, soils, vegetation, and microclimates.

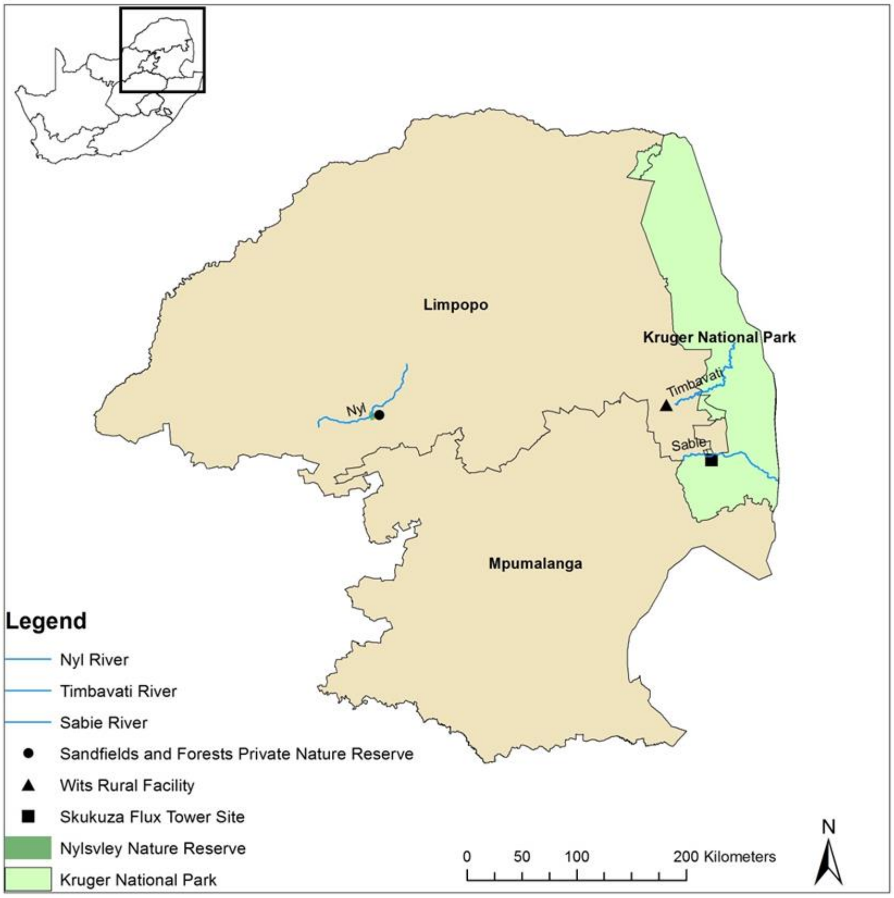


Figure 2.1: *Location of the three study sites.*

Skukuza Flux Tower Site, Kruger National Park (KNP)

This site is situated at 25.0167° E, 31.4833° S, 365 m.a.s.l. in a semi-arid savanna ecosystem with a catenal separation of broad-leaf and fine-leaf savanna types (■ in Figure 2.1) (Biggs, 2003; Scholes et al., 2001). The site has measured Net Ecosystem Exchange using the eddy covariance technique since the year 2000 (Archibald et al., 2009; Makhado and Scholes, 2011; Scholes et al., 2001). Mean annual rainfall is 550 mm with a standard deviation of 160 mm (Makhado and Scholes, 2011; Scholes et al., 2001). The dry season typically extends from May to October and the wet season from November to April. During the wet season, which coincides with the austral summer, midday air temperatures can reach 44 °C or more; the bark temperature can be higher. During the dry season, air temperatures can drop at night to below freezing point (Scholes et al., 2001), but daytime temperatures are typically warm.

The underlying bedrock is Archaean granite and gneiss, forming a gently undulating landscape with a distinctive catena (Scholes et al., 2001). The coarse-sandy uplands are dominated by broad-leafed *Combretum apiculatum* trees, while the clay-loamy bottomlands are dominated by fine-leafed *Senegalia nigrescens* (previously known as *Acacia nigrescens*) trees (Scholes et al., 2001).

Averaging over both vegetation types, the tree layer accounts for about 20 t/ha of aboveground biomass. Trees can reach heights of 8 – 10 m (Archibald et al., 2009; Makhado and Scholes, 2011; Nickless et al., 2009; Scholes et al., 2001). The herbaceous layer is dominated by C4 grasses like *Panicum maximum*, *Digitaria eriantha*, *Eragrostis rigidior*, and *Pogonarnthria squarrosa.* The herbaceous layer aboveground biomass varies within and between years, but typically amounts to 1 – 2 t/ha and reaches heights of 0.5 – 1 m, (Scholes et al., 2001). This site experiences continuous herbivory by about 15 indigenous species of large mammalian herbivores and a wide variety of insects. The grass layer burns about once every three years (Biggs, 2003, p. 3; Govender et al., 2006; Hempson et al., 2017; Scholes et al., 2001).

Sandfields and Forests Private Nature Reserve (NNR)

This site is located at 24.6461° E, 28.7539° S,1100 m.a.s.l., northeast of the Nylsvley Nature Reserve (NNR) (● in Figure 2.1) (Coetzee et al., 1976; Scholes and Walker, 1993). NNR is one of the most intensely studied savanna ecosystems in South Africa because it was the main study site of the South African Savanna Biome Programme between 1974 and 1992 (Scholes and Walker, 1993). The site experiences three distinct seasons: (1) a dry warm season from May to July; (2) a dry cool windy season from August to October; and a wet season from November to April (Coetzee et al., 1976; Scholes and Walker, 1993). It receives, on average, 620 mm of rainfall annually (Scholes and Walker, 1993). Minimum dry season temperature is -3.2 °C and maximum wet season temperature is 38.5 °C (Scholes and Walker, 1993).

This site is on metamorphosed sediments (Waterberg quartzites), producing an almost flat landscape with very sandy and nutrient poor soils (Coetzee et al., 1976; Scholes and Walker, 1993). The vegetation consists of broad-leaved trees such as *Burkea africana* and poorly-unpalatable grasses such as *Eragrostis pallens* (Coetzee et al., 1976; Scholes and Walker, 1993). Other common trees on the site include *Combretum imberbe*, *Terminalia sericea*, *Ochna pulchra*, *Strychnos pungens* and *Vachellia tortilis,* while other common grasses include *P. maximum*, *E. gummiflua*, and *Themeda triandra* .

Wits Rural Facility, Limpopo, South Africa

Wits Rural Facility (WRF) is situated 24.5642° E, 31.1111° S, 550 m.a.s.l., on the western boundary of the KNP (▲ in Figure 2.1) (Shackleton, 1999; Shackleton and Scholes, 2011). It is underlain by granites with dolomitic intrusions here and there. The soils are mainly coarse-sandy (Shackleton, 1999). The seasonality is the same as Skukuza: dry from May to October and wet from November to April. The mean annual rainfall is 670 mm (Shackleton, 1999; Shackleton and Scholes, 2011). The site has relatively fewer very large browsers (giraffe occur, but not elephants) than Skukuza, and fire frequency is lower. WRF is similar but slightly richer in species than Skukuza. The mean tree canopy height reaches 6 – 7 m (Shackleton and Scholes, 2011).

Study species

Respiration measurements were taken from 10 common (usually dominant) savanna tree species, which varied from site to site with some deliberate overlaps. The number of stems measured was 36 at KNP, 12 at NNR, and 13 at WRF (Table 2.1).

Table 2.1: *List of all study species and their characteristics from three study sites.*

Species	Phenological functional type	Number of trees at each site		
		KNP	NNR	WRF
Combretum apiculatum	Deciduous	11	-	-
Sclerocarya birrea	Deciduous	14	-	4
Senegalia nigrescens	Deciduous	7	-	-
Spirostachys africana	Semi-deciduous	4	-	-
Burkea africana	Deciduous	-	3	-
Ochna pulchra	Deciduous	-	3	-
Strychnos pungens	Evergreen	-	3	-
Terminalia sericea	Deciduous	-	3	3
Philenoptera violacea	Semi-deciduous	-	-	3
Vachelia nilotica	Deciduous	-	-	3
	Subtotal :	36	12	13
	Total :	61		

These species were chosen because (1) they are the dominant woody species in each study area (an important issue for upscaling measurements at a later stage); (2) they vary in wood densities and wood nitrogen contents; and (3) have different growth strategies (fast growers and slow growers).

Study design and protocol

Data were collected during four visits to each site between April 2018 and June 2019. The campaigns were timed to coincide with different growing seasons: (1) **early dry season** from April to June; (2) **late dry season** from July to October; (3) **early wet season** from November to December; and (4) **late wet season** from January to March. KNP was only visited during the dry seasons, but WRF, with the same environment as KNP, was measured in wet and dry seasons. Measurements were taken over three to four days at each site; throughout the daylight hours (the presence of dangerous wildlife precluded night-time measurements).

The protocol was as follows:

1. *Preparation*

A day before taking measurements, two respiration collars (10 cm wide and 5.5 cm tall sections of PVC pipe, cut into a slight concave on the tree-ward side) were stuck on each tree using silicone sealant, one facing north and the other facing south (Figure 2.2). This positioning of the collars ensured that the bark temperature varied over the maximum range throughout the day.

2. *Temperature*

Bark temperatures were measured inside each respiration collar using a non-contact high precision infrared thermometer (Flus IR-833, D: S = 30:1), before and after every wood respiration measurement. The average of the before and after measurements were recorded as the bark temperature during $R_{a,\ wood}$ measurements.

3. *Wood respiration*

$R_{a,\ wood}$ rates were measured using a soil CO_2 flux system LiCor 8100A (LI-COR Biosciences, Lincoln, Nebraska, USA), equipped with a 10 cm diameter closed chamber. Respiration was measured at each collar three to four times each day (early morning, late morning, midday and afternoon), and over the seasons to include cold, cool, warm and hot temperatures. The LiCor 8100 measures the accumulation of CO_2 within the chamber headspace, using an Infrared Gas Analyser, and fits a linear function over a specified period to determine the respiration rate. Each measurement took about three minutes, consisting of three replicates (each consisting of one sample per ten seconds) with purge/resting periods between each replicate. The chamber head has a self-closing mechanism to counter problems of over-pressurisation when closing the chamber.

4. *Tree dimensions*

Stem circumferences were measured using a tape measure above and below the respiration collars (Figure 2.2), which were averaged and converted to stem diameter (m) assuming a circular stem. Tree height was estimated using a 2 m high ranging rod as a reference. Canopy cover and tree health (estimated % green leaves present at each sample period) were recorded.

5. *Wood density and nitrogen content*

Wood core samples (from bark to heartwood) were taken from the same general region where the respiration collars were placed, using a Haglöf 5.15 mm diameter tree corer (Figure 2.2), after respiration sampling was completed for a season. Bark and sapwood thicknesses were recorded from the newly-extracted core. The cores (bark and sapwood separated) were weighed, oven-dried (at 60 °C for three weeks), reweighed for wood density, crushed and milled for further analysis. Oven dry mass and core dimensions occupied by this mass were used to determine bark, sapwood and wood density of each tree,

$$\rho = \frac{dry\ sample\ mass}{wood\ corer\ volume}$$

The milled samples were analysed for nitrogen content by iThemba labs at the University of the Witwatersrand, Johannesburg using a Flash HT Plus elemental analyser coupled to a Delta V Advantage and corrected against an in-house standard (Merck Gel and urea).

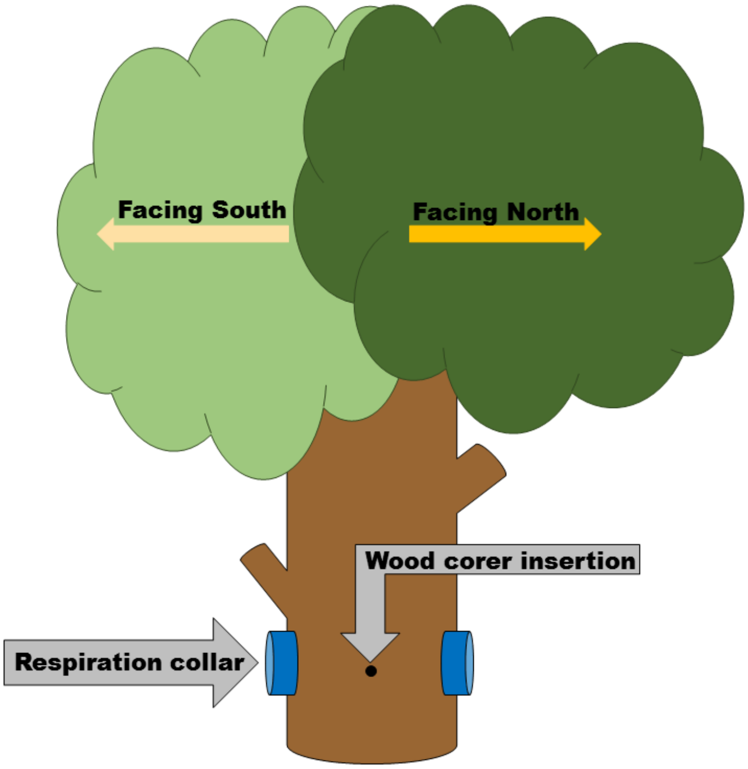


Figure 2.2: *A schematic showing the placement of respiration collars and the point where the wood core was taken.*

Statistical analysis

$R_{a,\ wood}$ data were captured by the Li-8100A version 4.0.0 software, transferred to a spreadsheet, and imported to R version 3.6.2 (R Foundation for Statistical Computing, Vienna, Austria) for all statistical analyses.

All datasets were tested for normality and homogeneity using various methods (histograms, Q-Q plots, Shapiro-Wilk tests, and Leven's tests). If variables were determined to be not normally distributed, they were transformed by taking the natural logarithm before analysis. All data were assessed for significance at $\alpha = 0.05$ and $\alpha = 0.001$.

The dates of data collection within each year (expressed as the Julian day, with 1 January=1) were converted a continuous season variable by representing the year as 0° (1 January) to 360° (31 December), to obtain a trigonometrical range from -1 (mid-dry season in

July) to +1 (mid-wet season in December) using the R base functions ***strptime()*** and ***strftime()***.

The sapwood volume sampled by the chamber was calculated using three geometrical assumptions (see Appendix A). After comparing the approaches, the ‘cylinder assumption’ was selected (i.e. the sapwood volume sampled is the sample ring area multiplied by the sapwood thickness) as it is the most frequently used in literature. A summary of descriptive statistics and how outliers were handled can be found in Appendix A.

Linear mixed-effects models (LMMs) were fitted as a first analytical step. LMMs were chosen because they can deal with the unbalanced sampling design, repeated measures per tree, and the complexity of our hierarchically nested study design (Harrison et al., 2018; Zuur et al., 2009). These models were evaluated using the ***lmer()*** function from the **lme4.0** package (version 1.1-21) (Bates et al., 2015) and the **lmerTest** package (version 3.1-1) (Kuznetsova et al., 2017). I separated the dataset into a *‘training dataset’* (90% of the original dataset) and a *‘test dataset’* (10% of the original dataset) using a stratified K-fold method. The *training dataset* was used to run the models and the *test dataset* was used to cross-validate these models (i.e. assess for bias/goodness of fit and accuracy).

Two full models of wood respiration were fitted (one for respiration per sapwood volume and one for respiration per bark surface area as a response variable), with temperature, time of year (season) and time of day as fixed effects (Equation 1 and 2). Both these models had three random effects, hierarchically nested, as TreeID, species and site (Equation 1 and 2).

$$\text{Respiration } f \text{ surface area OR } f \text{ sapwood volume } \cong \text{ Temperature} + \text{OR} \times \text{Temperature}_{\text{Squared}} + \text{OR} \times \text{Season} + \text{OR} \times \text{Time of day} + \left(1 \,\middle|\, \frac{\frac{\text{Site}}{\text{Species}}}{\text{TreeID}}\right)$$

Subsequently, models with all combinations of these factors (including and excluding interaction terms) were fitted and compared using the Akaike Information Criterion (AIC). The model with the best explanatory power (lowest AIC) was chosen. The random-effects assumed only differences in the intercept (i.e. the mean value) between sites, species, and TreeID, meaning that individual species were assumed to have different baseline respiration rates, but all showed the same response to temperature. Fixed effects were first standardised (i.e. scaled and cantered using the algorithm (x – mean)/SD before analysis, as advised by Harrison et al., 2018. This did not improve the explanatory power of these variables unstandardised fixed effects were used in subsequent analyses. Collinearity and interaction between predicting terms were checked for and was found to be very small and not significant. The KNP study site was only sampled during the early dry season (mainly due to logistics) which caused an underestimate in the models (see *Figures: A3a, A3b, A4a, A4b* in *supplementary results* of Appendix A), so further analysis was conducted with and without this site (which had relatively few observations). In this chapter, the results mainly exclude the KNP site.

Mixed-effects modelling cannot account for non-linearities in the response of respiration to temperature and season. Because the response variable is logged, and a linear model is then fitted, the linear mixed effect model essentially assumes an exponential relationship between temperature and respiration and a linear relationship between season and respiration. This is justified by what has been found elsewhere in the literature (Davidson et al., 2006; Patterson et al., 2018), but I was specifically interested in whether there was a limit to the temperature-respiration relationship at very high temperatures. To assess the temperature-respiration functional form, I added $(\text{temperature})^2$ as a fixed effect in the mixed models. This allowed the mixed-effects models to show that temperature has a second-order polynomial relationship with respiration. To confirm these findings, I categorised the dataset into ‘active’ vs ‘dormant’ seasons and simultaneously ran a General Additive Model (GAM) between temperature and respiration. To assess the ‘true’ relationship between season and time of day with respiration, I ran polynomial regression models with normalised respiration (i.e. respiration values divided by species mean for the day).

The models of wood respiration expressed per unit per bark surface area model had the lowest AIC (Table 2.2); however, the respiration per sapwood volume model was able to explain more than 80% of the variance while the respiration per bark surface area model only explained about 59% (Figure 2.3).

Table 2.2: *Results from the model selection of two models: wood respiration as a function of* (f) bark surface area and wood respiration f *sapwood volume.*

Model	df	AIC	Diff
$R_{a, wood} = f$ bark surface area	9	2536.6	0.00
$R_{a, wood} = f$ sapwood volume	9	2556.1	19.56

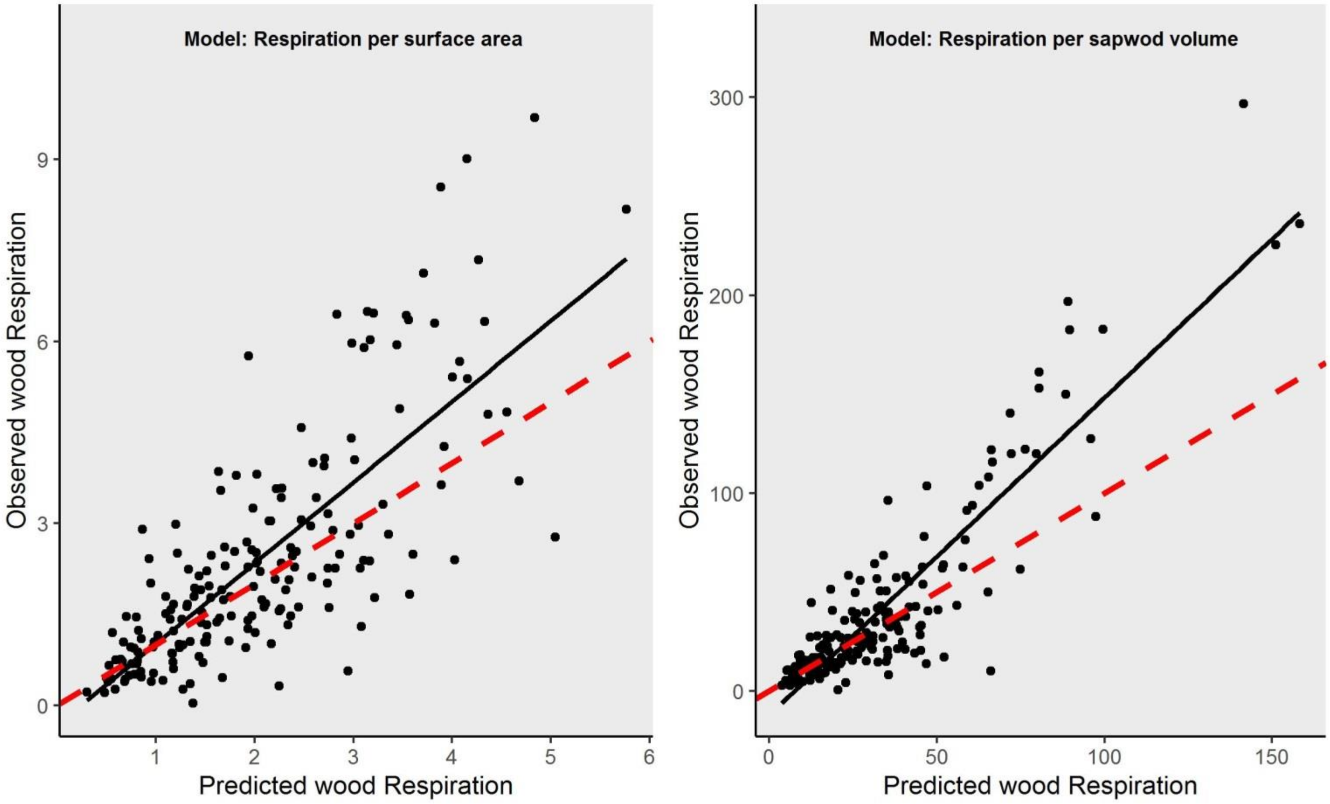


Figure 2.3: *Model validation for mixed effects models: (1) Respiration ƒ bark surface area $R^2 = 0.59$, $p < 0.001$, slope = 1.33 and intercept = -0.32; (2) Respiration ƒ sapwood volume $R^2 = 0.80$, $p < 0.001$, slope = 1.61 and intercept = -12.25). The dashed red line (--) represents the 1:1 line for comparison.*

Since the AIC difference between the models was not large and sapwood volume has more explanatory power, I chose the respiration per sapwood volume model as the best-fitting model for wood respiration.

The sapwood volume-based model was used to predict the response of respiration to across a range of temperatures for each species in the dataset, to predict respiration throughout different times of the day, and to predict the response of respiration to changes in seasons throughout the year. To assess wood respiration rates among savanna species, I ran a test on the species-specific intercepts of the random effects model output. I ran linear and polynomial models with intercept as a response, and wood density, nitrogen content, phenological functional type, and stem diameter as predictor variables. Again, I used model selection and the AIC to assess which was the best model.

This chapter presents results from the respiration as a function of (f) sapwood volume model. Results from the model of wood respiration as a function of bark surface area (which mostly show similar trends as the sapwood model) are presented in Appendix A. All graphics were created using the graphics packages **ggplot2**, **ggpubr** and/or **cowplot** (Wickham, 2009). See Appendix A for a link to an R-markdown document that describes how I did all analysis, which was produced to ensure the reproducibility and reliability of my findings.

Results

Wood respiration showed a relationship with temperature and season (Figure 2.4) different from the classical assumptions of an exponential form for the former, and the latter being accounted for by the temperature effect. This led to various in-depth analyses.

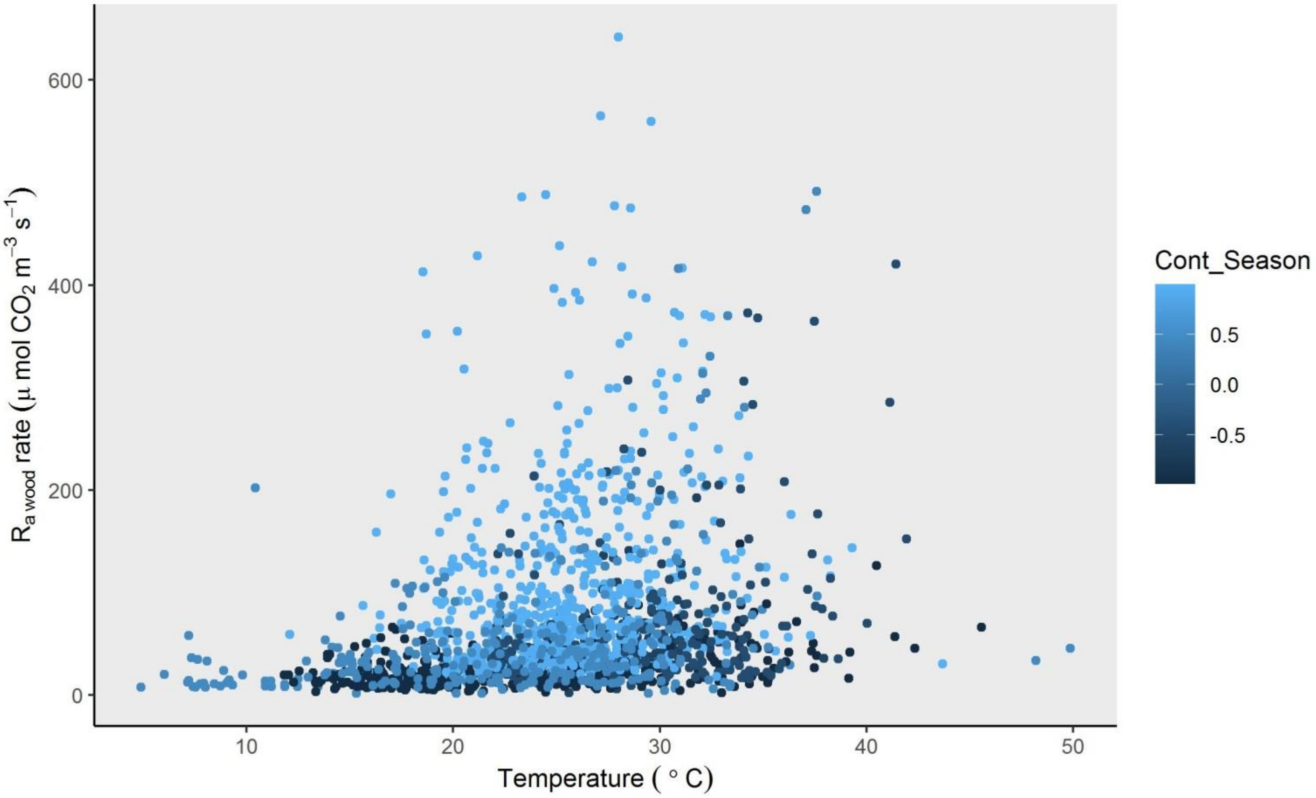


Figure 2.4: *Wood respiration ƒ sapwood volume from dry season (-1) to wet seasons (+1) and from cool temperature (5 °C) to warm temperatures (50 °C).Each dot representing an individual sample.*

Savanna species respire at different rates (Figure 2.5 and 2.6), accounted for to a high degree (80%) on the several factors presented in the LMM results and multiple regression models. $R_{a,\ wood}$ rates as a function of (*ƒ*) surface area (Figure 2.5) and $R_{a,\ wood}$ rates *ƒ* sapwood volume (Figure 2.6) differ among species. Some species respire more per surface area (e.g. *P. violacea*) and others respire more per sapwood volume (e.g. *V. nilotica*). There is also a clear seasonal pattern in respiration in all species. See more descriptive statistics in Appendix A.

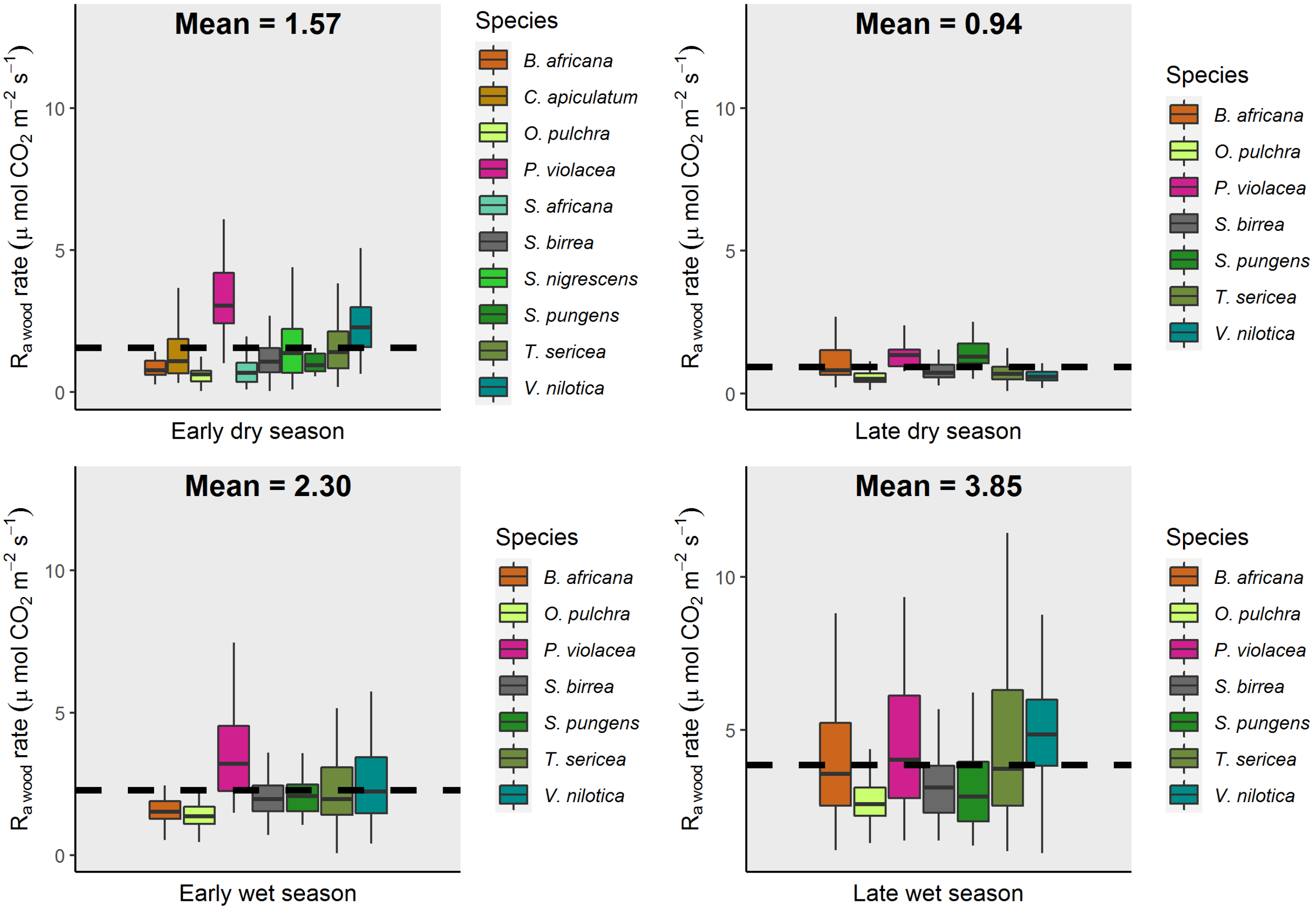


Figure 2.5: *Wood respiration ($R_{a,\ wood}$) rates per surface area among savanna species measured in four distinct seasons. The black thick-dashed lines (**--**) represent the mean $R_{a,\ wood}$ rates for each season.*

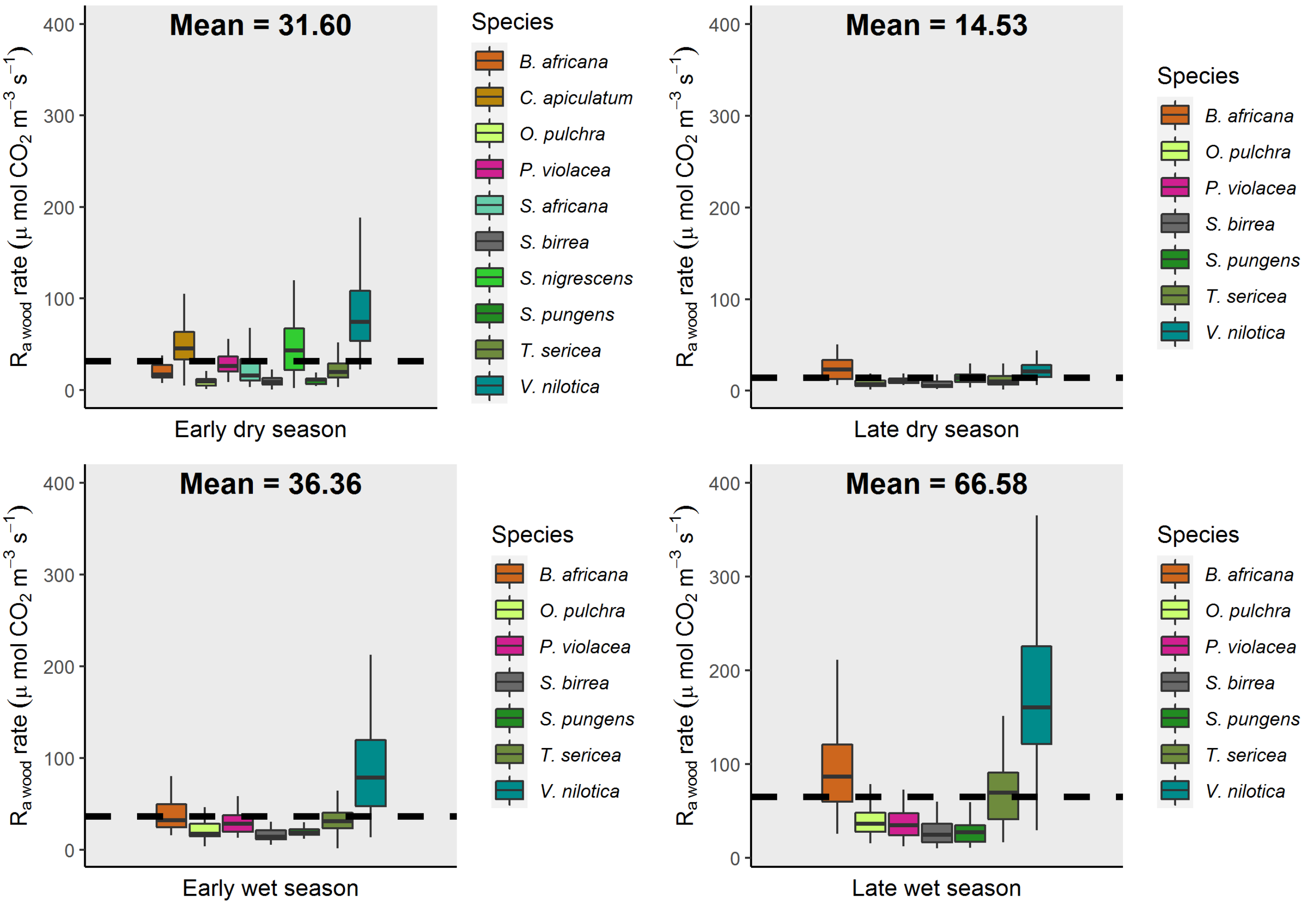


Figure 2.6: *$R_{a,\ wood}$ rates per sapwood volume among savanna species measured in four distinct seasons. The black thick-dashed lines (**--**) represent the mean $R_{a,\ wood}$ rates for each season.*

Results from the model of $R_{a,\ wood}$ = *ƒ* sapwood volume

The mixed-effects model showed that temperature, season of the year and time of day were significant predictors ($p < 0.001$) of wood respiration rates. A model that included these factors without an interaction term had the lowest AIC (Table 2.3).

Table 2.3: *Wood respiration is best explained by a sapwood model that includes additive effects of temperature, season, and time of day. This model had the lowest AIC value (2 556) compared with the next best model which excluded time of day.*

Model	df	AIC	Diff
logRespiration ~ Temperature + Temperature_squared + Season + Time of day	9	2556	0
logRespiration ~ Temperature + Temperature_squared + Season	8	2561	5
logRespiration ~ Temperature + Season + Time of day	8	2584	23
logRespiration ~ Temperature + Season	7	2587	3
logRespiration ~ Temperature * Season	8	2588	2
logRespiration ~ Season + Time of day	7	3041	453
logRespiration ~ Season	6	3150	109
logRespiration ~ Temperature + Temperature_squared	7	3514	364
logRespiration ~ Temperature + Temperature_squared + Time of day	8	3516	2
logRespiration ~ Temperature	6	3583	67
logRespiration ~ Temperature * Time of day	8	3583	1
logRespiration ~ Temperature + Time of day	7	3584	1

All fixed effects in this model are significant predictors of wood respiration ($p < 0.001$) but time of day, while significant, has a weak coefficient (Table 2.4).

Table 2.4: *Parameter estimates for the respiration ƒ sapwood volume model*

Parameter	Coefficient	SE	CI_low	CI_high	t-value	*p*
(Intercept)	1.11391	0.23017	0.66279	1.56503	4.83958	< 0.0001
Temperature	0.12289	0.01202	0.09934	0.14644	10.22758	< 0.0001
Tempsquared	-0.00130	0.00024	-0.00176	-0.00083	-5.48770	< 0.0001
Season	0.57448	0.01590	0.54332	0.60565	36.13133	< 0.0001
Time od day	-0.00013	0.00005	-0.00023	-0.00003	-2.64907	< 0.008
Random effects	(variance)					
Site	$8.926*10^{-08}$ ($2*10^{-07}$%)					
Species	$2.185*10^{-01}$ (37.0%)					
Tree individual	$1.199*10^{-01}$ (20.3%)					

N = 1675;
Groups = 25 trees, 8 species and 2 sites
df = 1668; $p < 0.001$

The effects of temperature

Air temperature in savanna environments

Air temperature follows a common seasonal pattern in southern African savannas, as briefly sketched in the methods section of this chapter. At the Skukuza EC flux tower (KNP), air the multiyear average of daily maximum and minimum temperature ranges from 5.6 °C (night-time, mid-winter) to 32.6 °C (daytime, mid-summer) (39 years of data from Scholes et al., 2001) (Figure 2.7). Near the Nylsvley Nature Reserve (NNR), the ranges are from 4.0 °C (mid-winter) to 29.2 °C (mid-summer) (7 years of data from Scholes and Walker, 1993) (Figure 2.7), and at Wits Rural Facility (WRF), air temperature ranges from 6.5 °C (mid-winter) to 31.6 °C (mid-summer) (data from June 2016 to September 2020) (Figure 2.7). These temperatures were useful in understanding the measured daily, monthly and annual wood respiration rates as lowest temperatures seem to almost always occur between May and September.

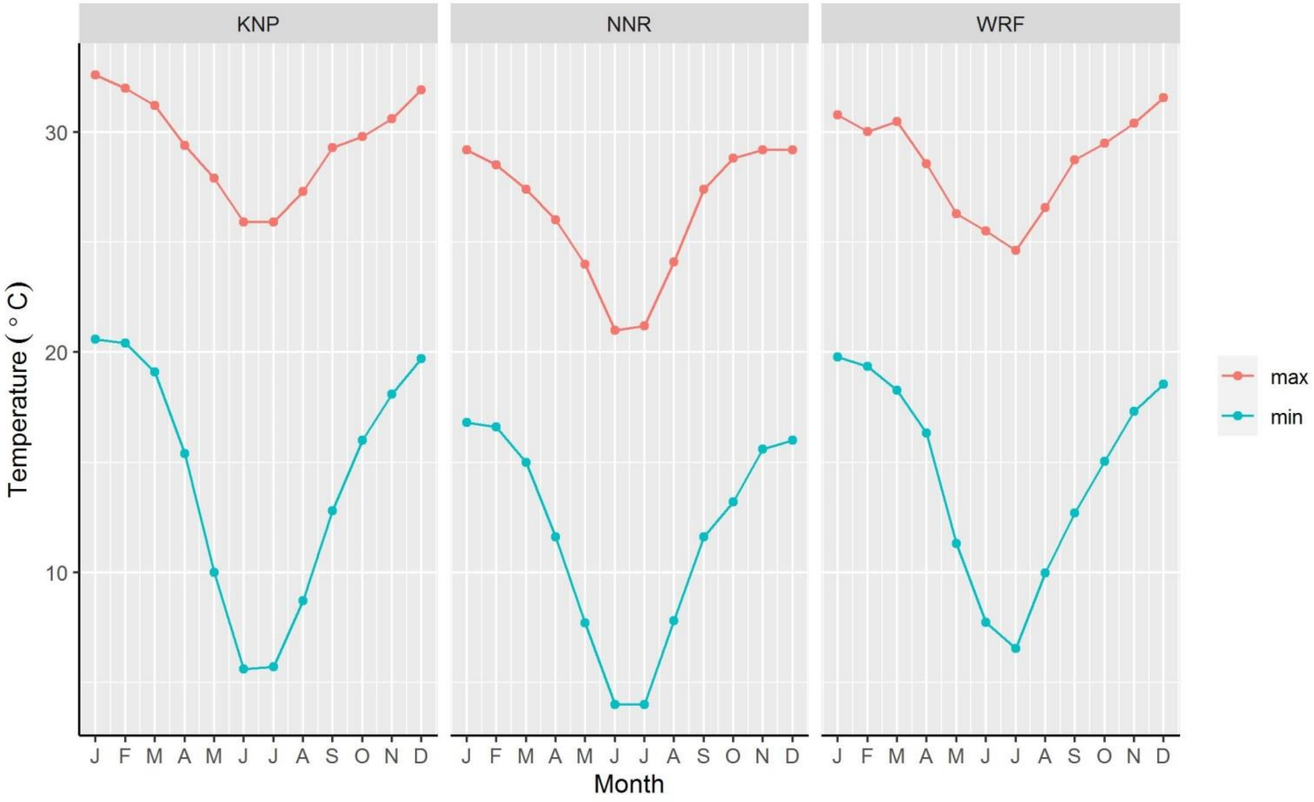


Figure 2.7: *Long-term air temperature (mean minimum and mean maximum) at each study site (KNP, NNR and WRF), showing the general seasonal trend. Data may also be requested from (https://www.csir.co.za/smart-places).*

The effect of bark temperature on wood respiration

Predictions by the respiration *ƒ* sapwood volume model show that bark temperature is significantly associated with the rate of wood respiration ($p < 0.001$, $\beta = 0.12$) (Figure 2.8). When season of the year and time of day were kept constant (i.e. mid wet season, season=+1 and time of day = 11H40, the time of day when the most measurements were taken), respiration increased with temperature up to a maximum of about 150 µmol $CO_2/m^3/s$ between 35 - 45 °C and thereafter starts decreased while temperature increased (Figure 2.8).

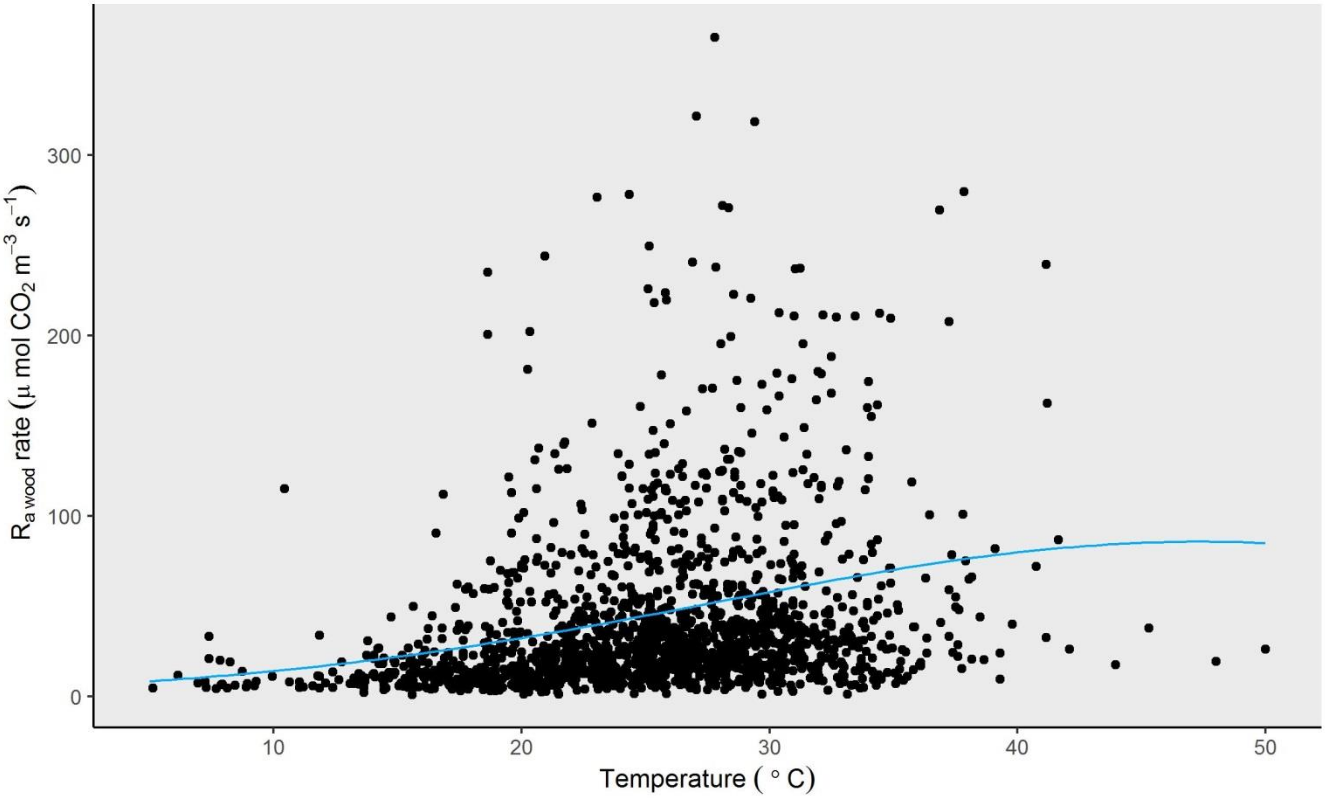


Figure 2.8: *The relationship between bark temperature and wood respiration rates as predicted by the respiration ƒ sapwood volume model, when season is kept constant at mid-wet (+1) and time of day is kept at 11H40.*

Results from the GAM analysis of temperature effects on wood respiration

The general additive model (GAM) results confirmed the above results and added further details regarding the temperature-respiration relationship. Respiration increases with increasing temperatures to an optimum but decreases at high temperatures during the predominantly wet season (when plants are physiologically active) ($p < 0.001$, $R^2 = 0.03$, $\beta = 115.2$) (Figure 2.9). However, during the predominantly dry season respiration levels off (rather than decreases) at high temperatures ($p < 0.001$, $R^2 = 0.15$, $\beta = 47.4$) (Figure 2.9). *V. nilotica* respires more than all other species, both in the active and dormant seasons (Figure 2.9).

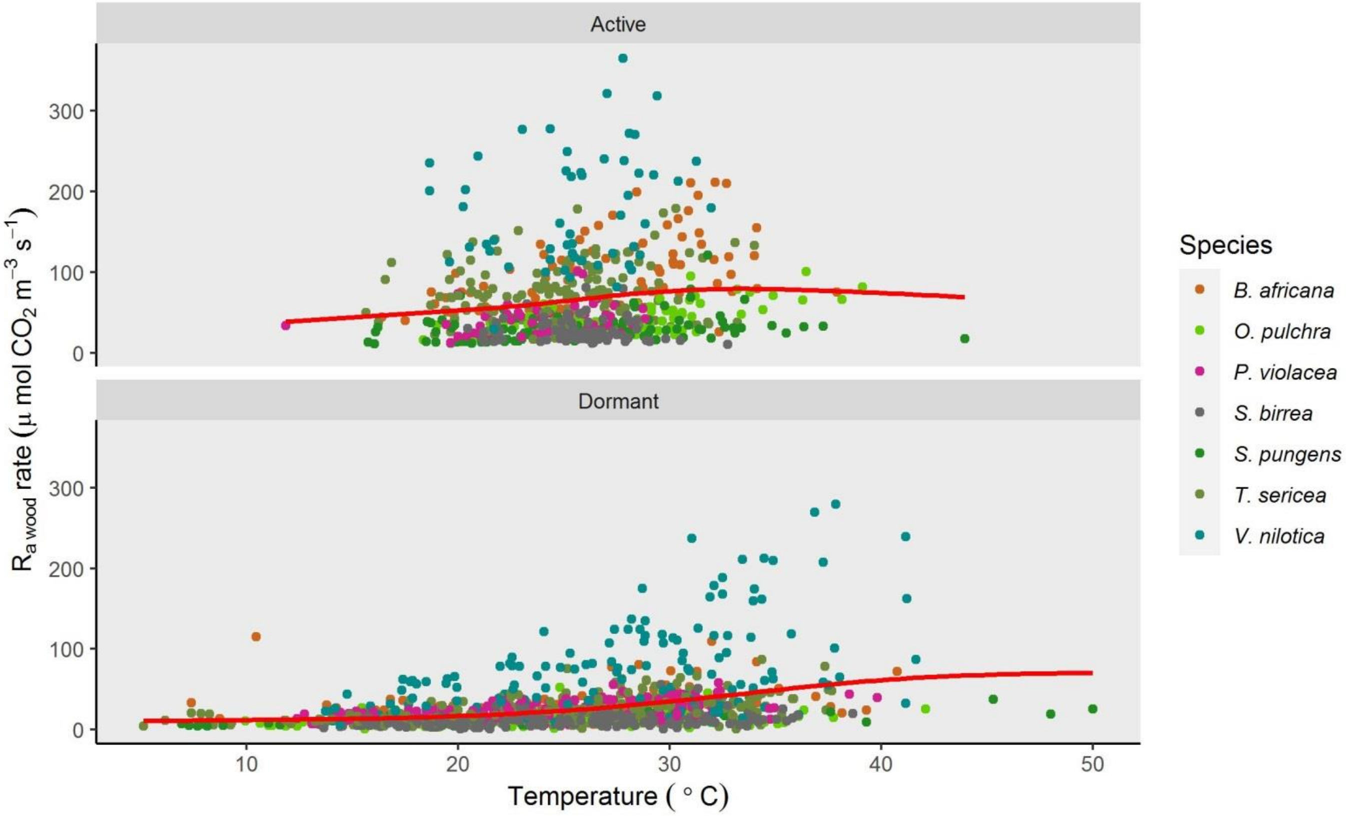


Figure 2.9: *Relationship between temperature and wood respiration rates per sapwood volume where a hump-shaped function best fits data from the physiologically active season and a logistic function best fits data from the physiologically dormant season.*

The effects of season of the year

Soil moisture

Additional to air temperature (Figure 2.7), other environmental variables could potentially be useful in explaining wood respiration around the Skukuza EC tower (KNP), such as soil moisture. For the years 2016 to 2019, there is enough data to show that soil moisture in the 0-30 cm layer in this site ranges on average from 4.9% volumetric mid-winter to 12.8% mid-summer (Figure 2.10). This shows that this savanna is mainly physiologically '*active*' from November to April (during the rainy season) and physiologically '*dormant*' from May to October (Figure 2.10) (when there is not enough water on the ground).

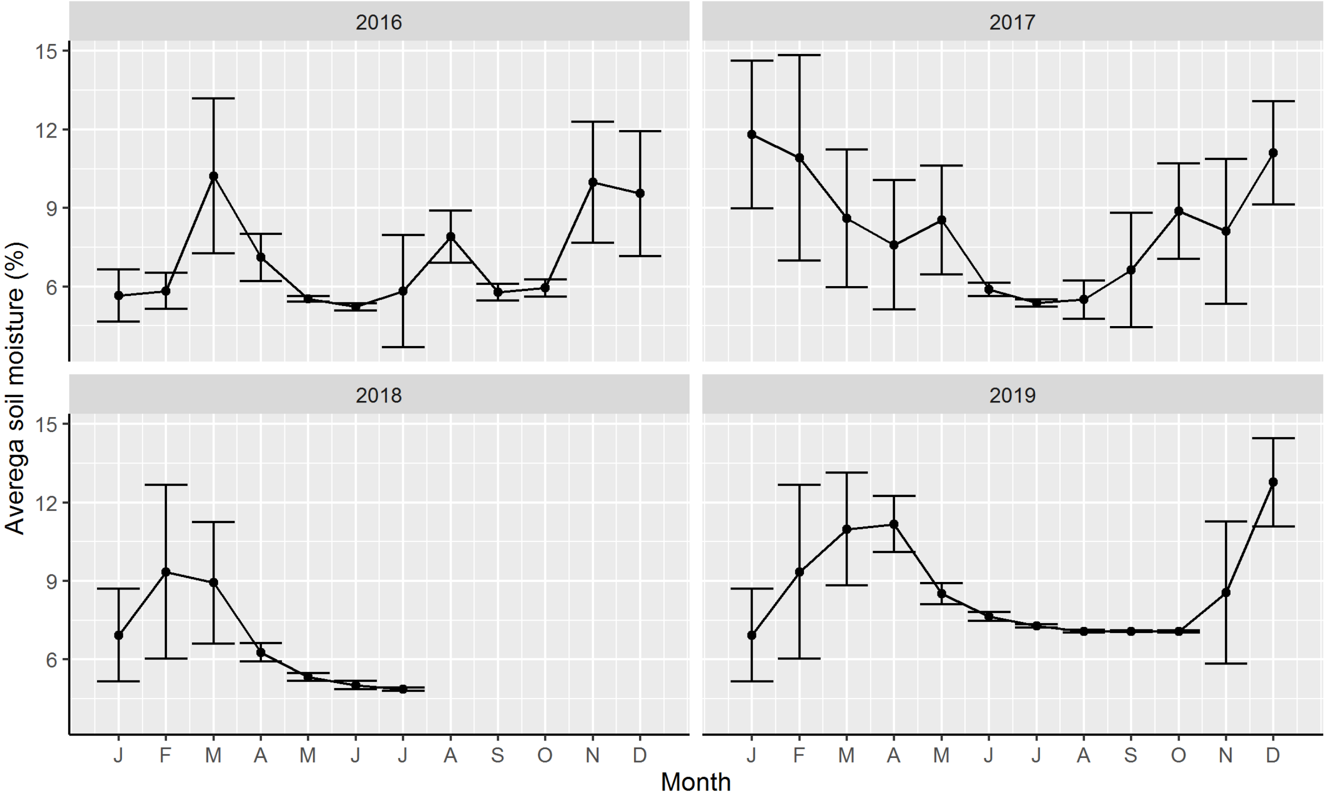


Figure 2.10: *Monthly average soil moisture from 2016 to 2019 around the Skukuza EC tower, showing the general seasonal trend. This data may be requested from (https://www.csir.co.za/smart-places).*

The effect of season on wood respiration

The respiration f sapwood volume model shows that season of the year is significantly associated with wood respiration rate ($p < 0.001$, β = 0.58), even when temperature and time of day are controlled for (i.e. temperature kept at mean bark temperature of 25 °C and time of day kept at 11H40) (Figure 2.11). Respiration in the middle of the dry season (-1) is about 24 μmol $CO_2/m^3/s$ and increases threefold to about 79 μmol $CO_2/m^3/s$ during the middle of the wet season (Figure 2.11).

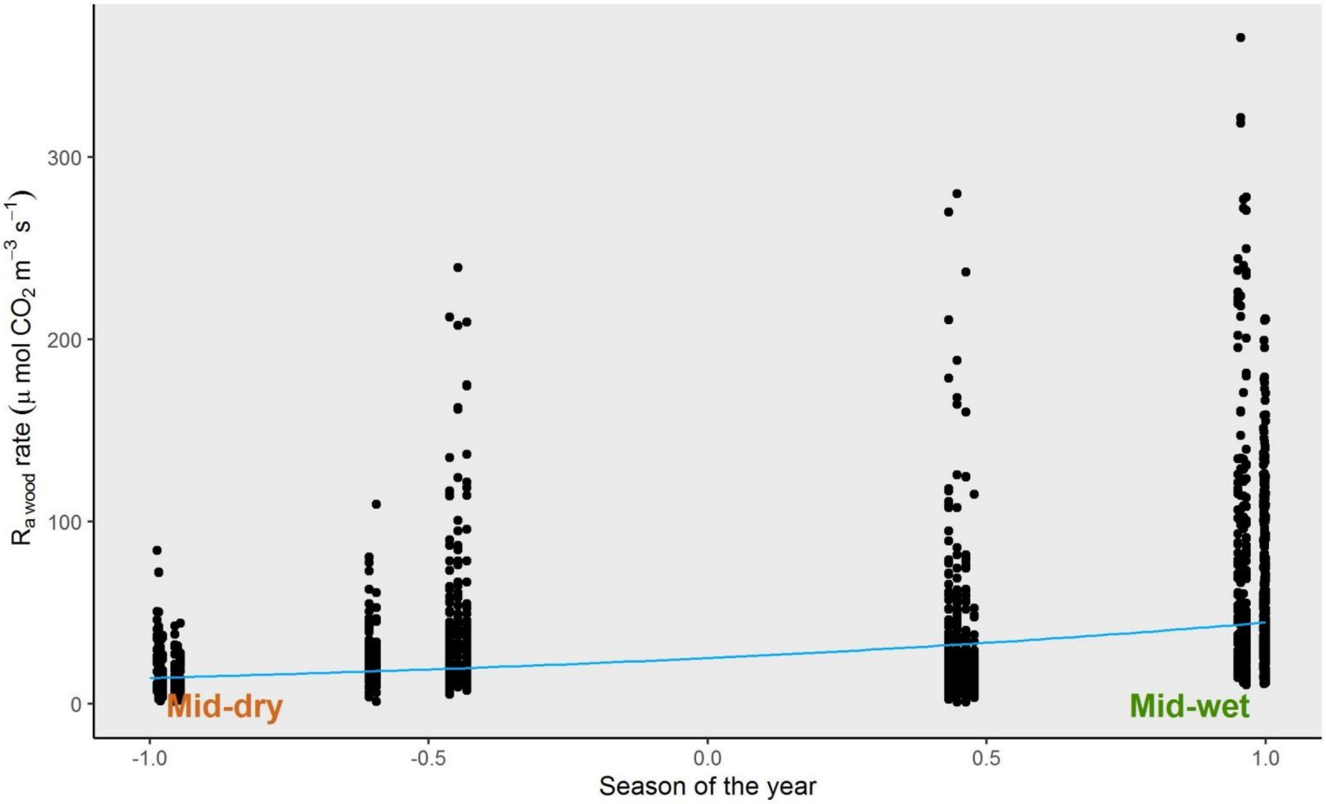


Figure 2.11: *The predicted relationship between season of the year and $R_{a,\ wood}$ rates per sapwood volume when temperature and time of day are kept constant (25 °C and 11H40).*

Results from polynomial regression analyses of seasonal effect on wood respiration

Using wood respiration rates normalised by species (i.e. values of respiration divided by the species mean), I fitted multiple functions (linear to exponential to polynomial) to account for the observed pattern over the season. A cubic polynomial function (similar to a trigonometric sine graph) was the best fitting function (NNR: $R^2 = 0.43$, $p < 0.001$ and WRF: $R^2 = 0.41$, $p < 0.001$) (Figure 2.12). These models confirm the results from the mixed-effects model, where the lowest respiration rates were recorded in the middle of the dry season for each site (NNR and WRF), while the highest rates were measured in the middle of the wet season (Figure 2.12).

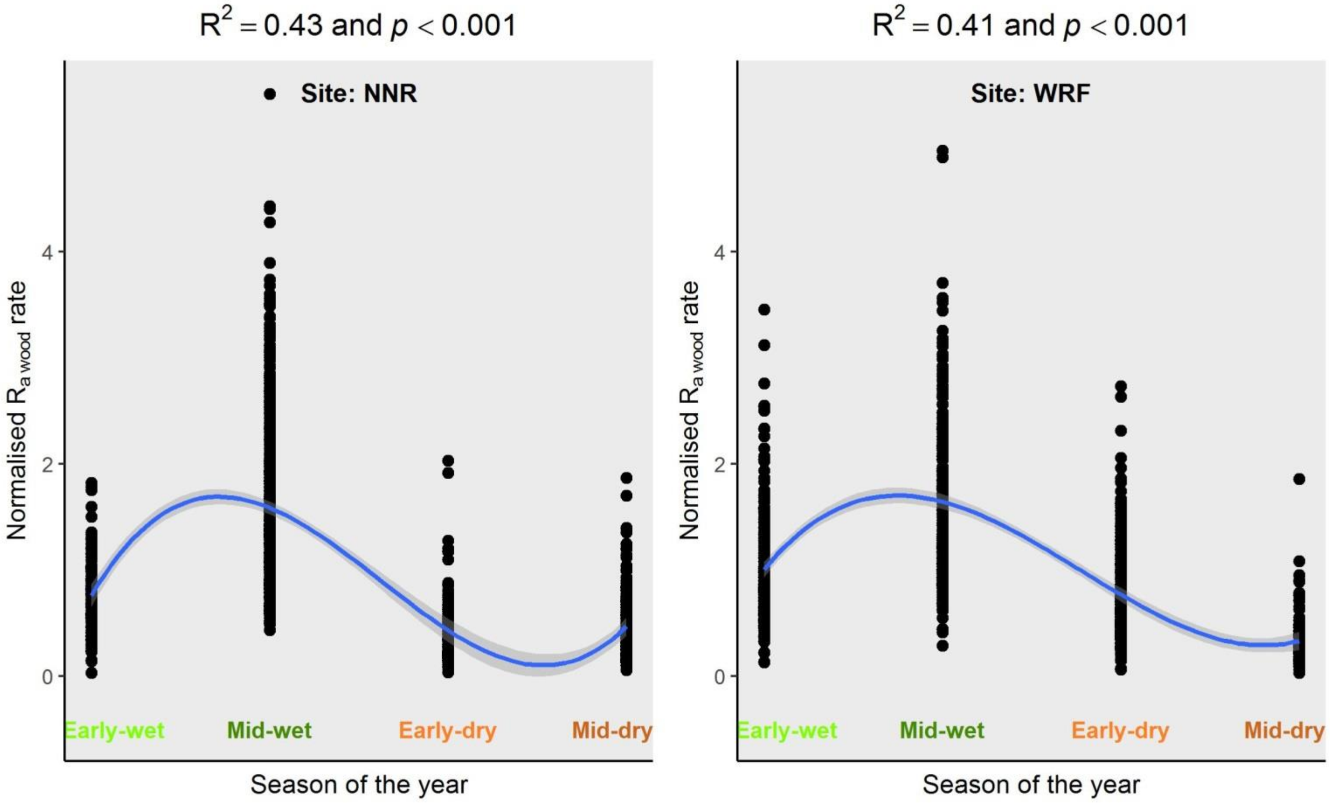


Figure 2.12: *The regression relationship between season of the year and normalised wood respiration rates / sapwood volume (i.e. respiration values divided by species mean).*

The effects of time of day

The effect of time of day on wood respiration

Time of day was another significant driver of wood respiration per sapwood volume ($p < 0.001$, $\beta = -0.0001$) but seems to have a minor effect compared to the other two factors. When temperature and season are controlled (i.e. temperature kept at mean bark temperature of 25 °C and season kept at mid-wet (+1)), respiration is predicted to slightly decrease from morning to afternoon (Figure 2.13). In the morning, respiration was about 79 µmol $CO_2/m^3/s$ and slightly decreased to about 64 µmol $CO_2/m^3/s$ in the afternoon, all else being equal (Figure 2.13).

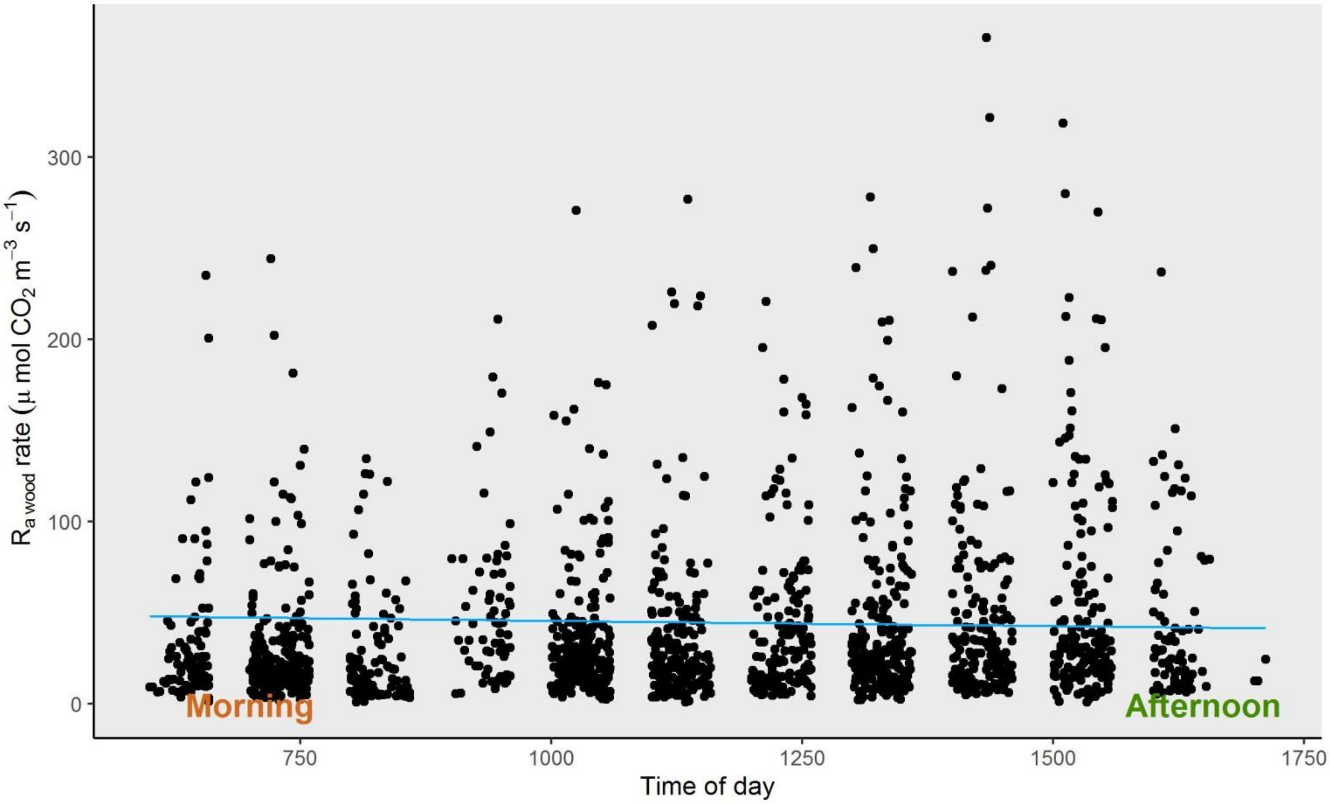


Figure 2.13: *The predicted relationship between time of day and $R_{a,\,wood}$ rates per sapwood volume, when temperature and season are kept constant (25 °C and mid-wet season).*

Why do species respire at different rates?

Savanna species differ from one another concerning many traits which could be associated with wood respiration. They exhibit different phenologies - some are deciduous, some semi-deciduous and some are evergreens (see Table 2.1 and 2.5). They also differ in nitrogen content and wood density in their bark, sapwood and total wood (Table 2.5).

Table 2.5: *Species-specific traits measured during this study that could be predictors of wood respiration.*

Species	Phenological functional type	Diameter (m)	Thickness (cm)			Density (g/cm^3)			Nitrogen %		
		Stem	Bark	Sapwood	Entire wood	Bark	Sapwood	Entire wood	Bark	Sapwood	Entire wood
		Mean ± SD	Mean	Mean	Mean	Mean	Mean	Mean	Mean	Mean	Mean
C. apiculatum	Deciduous	0.38 ± 0.21	0.39	3.18	3.57	0.56	1.07	1.01	0.49	0.23	0.72
S. birrea	Deciduous	0.94 ± 0.33	1.41	11.83	13.23	0.68	0.67	0.67	0.25	0.26	0.51
S. nigrescens	Deciduous	0.80 ± 0.50	0.85	3.22	4.10	0.56	0.84	0.78	1.61	0.36	1.96
S. africana	Semi-deciduous	0.36 ± 0.09	0.88	3.70	4.18	0.70	0.78	0.83	1.50	0.35	1.86
B. africana	Deciduous	0.42 ± 0.07	0.80	4.70	5.50	0.67	0.77	0.74	1.34	0.62	1.95
O. pulchra	Deciduous	0.23 ± 0.03	0.97	7.50	8.50	0.55	0.73	0.70	0.85	0.57	1.42
S. pungens	Evergreen	0.27 ± 0.04	0.57	10.92	11.48	0.57	0.76	0.76	0.92	0.67	1.56
T. sericea	Deciduous	0.40 ± 0.15	1.27	6.56	7.83	0.63	0.88	0.84	0.47	0.16	0.63
P. violacea	Semi-deciduous	0.85 ± 0.32	1.13	11.80	12.94	0.51	0.81	0.78	1.17	1.32	2.49
V. nilotica	Deciduous	0.36 ± 0.14	1.20	2.93	4.12	0.50	0.99	0.85	0.87	0.22	1.09

The mixed-effects model revealed that there are significant differences in intercepts of species (i.e. random effects) once all other variables have been accounted for (Figure 2.14). These were used as the response variable in predicting which of the above traits significantly drive wood respiration.

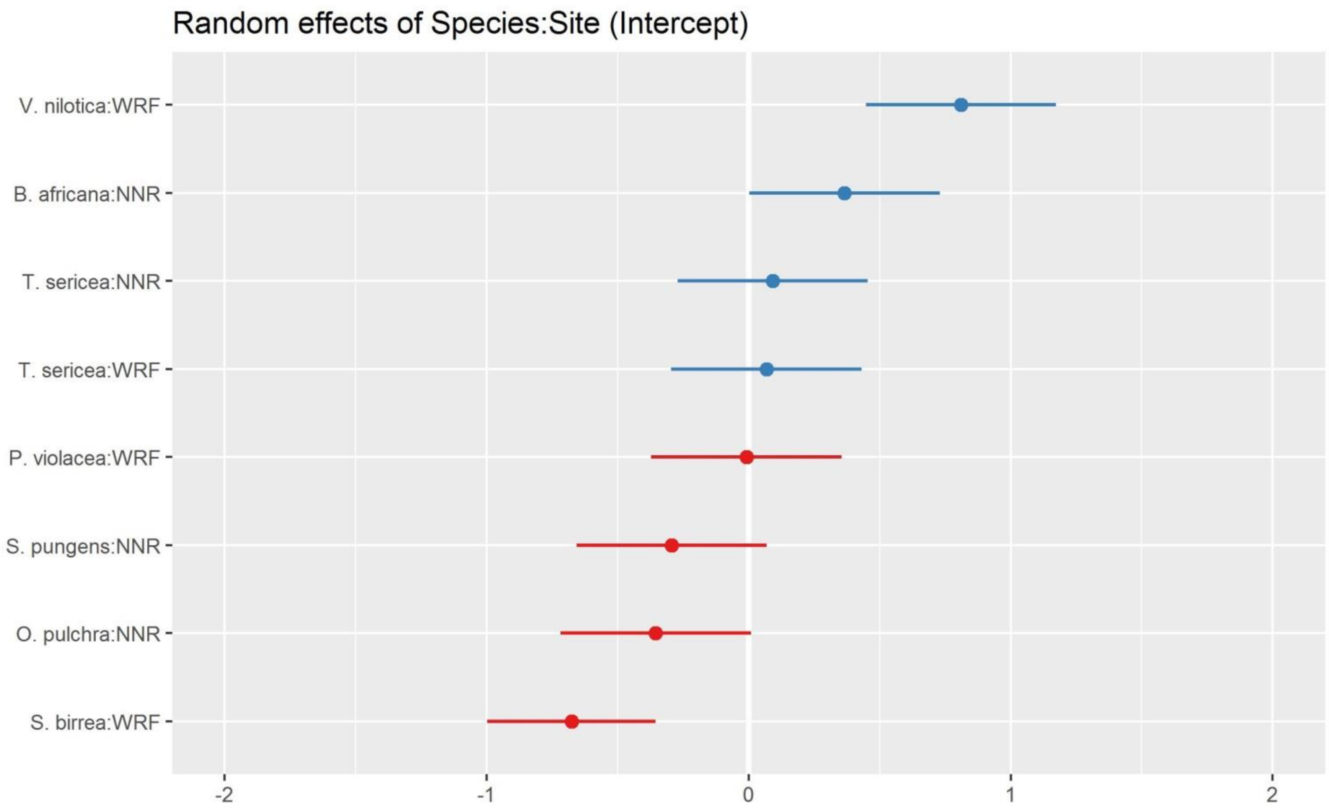


Figure 2.14: *Intercepts of species from the mixed-effects model, showing how species differ in response to the fixed effects presented.*

Sapwood density was the only significant factor associated with the observed differences in wood respiration among savanna species (p = 0.05, R^2 = 0.60) (Figure 2.15). Other non-significant traits-respiration results are presented in the *supplementary results* section of Appendix A.

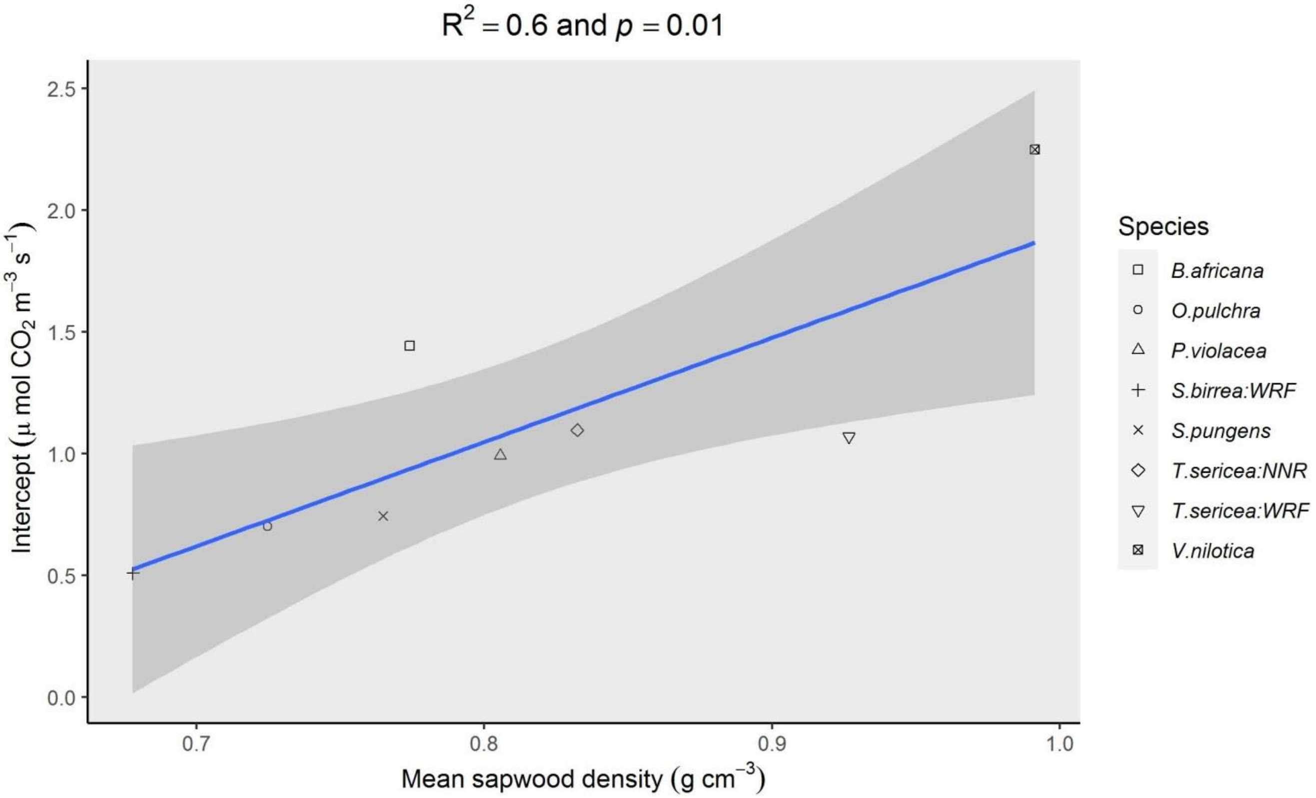


Figure 2.15: *The relationship between mean sapwood density for each species and the intercepts from LMM2.*

Discussion

This study is the first of its kind for African savannas. A greater fraction of the variance in wood respiration was accounted for when expressed as per unit sapwood volume than when expressed per unit bark surface area. I found temperature, season of the year and time of day as the major factors associated with of wood respiration rate (regardless of whether the latter were described per unit area, or per unit sapwood volume). Differences between savanna species remained after the effects of temperature, season and time of day were accounted for. This difference between species was only associated with sapwood density, accounting for 60% of the between-species variance. These findings are generally consistent with those from research in other biomes. With respect to temperature, the savanna biome seems different to the relationships found in cooler biomes.

Effects of temperature

Most studies report (or assume) an exponential increase in the wood respiration rate as temperature increases (Chan et al., 2018; Darenova et al., 2018). Some soil respiration research, especially from the hot and semi-arid African savannas, has found that respiration and temperature do not always have an exponential relationship (Makhado and Scholes, 2011). Instead, they suggest a sigmoid response function, or a 'hump-shaped' function, represented by a parabolic relationship or a generalised Poisson distribution (Archibald et al., 2009). I found an S-shaped relation between wood respiration rates and bark temperature up to maximum respiration between 35 - 45 °C, and a decrease afterwards. This function is more pronounced during the active season than in the dormant season. *V. nilotica* responds more strongly to temperature compared to other species in both the active and dormant seasons.

In savannas, temperatures can be extreme (air temperatures reaching over 48 °C occasionally during the day in summer, especially in the October pre-rainy season). These extremes correspond with the low soil moistures, as shown in Figure 2.10. With low moisture content in the soil and extremely high air temperatures, the physiological activity in living tissues may be constrained. Respiration does not decrease beyond high temperatures during the 'dormant' season partly because the tissues are largely physiologically inactive already, and the dry season temperatures never go as high. The decrease in $R_{a,\ wood}$ during the active season (or levelling off during the dormant season) beyond maximum temperatures between 35 - 45 °C could be associated with the denaturing of the critical enzyme(s) (Selinioti et al., 1986). Temperature damages the plasmalemma and membranes of cells, which makes them leaky and disturbs vital cellular activities like metabolism (Ahrens and Ingram, 1988; Chaisompongpan et al., 1990), which could also be the result of reduced respiration at higher temperatures. High respiration is associated with high water loss by plants (even that from woody tissues, diffusing through lenticels in the bark), so this reduction in wood respiration beyond certain high temperatures might also relate to hydration rather than temperature directly (Bazzaz and Sombroek, 1996).

Additional to the commonly reported Q_{10} temperature relationship, some studies (e.g. Zhao et al., 2018) have found that the moisture content of the air also has a significant exponential relationship with $R_{a,\ wood}$. I did not evaluate the possible humidity effect in this study as it is strongly temperature-dependent and also confounded with rainfall seasonality.

Effects of season of the year

African savannas show marked and characteristic seasonality. Generally, there are two distinct seasons, a wet growing or active season and a dry dormant season. The wet season falls within the hotter months (November to April in the southern hemisphere) while the dry season falls within relatively cooler months (May to October), but never gets cold enough for the low temperature to result in complete physiological shut-down. In the middle of the wet season is when the majority of plant metabolic activities (i.e. photosynthesis or growth or productivity) occur in these ecosystems, while there is not much activity during the dry season. Season of the year was uncorrelated with bark temperature but they both simultaneously are associated with variations in $R_{a,\ wood}$.

I measured a three-fold increase in wood respiration rates between the middle of the dry ‘dormant’ season and the middle of the wet growing season. This is consistent with other studies (Wieser and Bahn, 2004; Zha et al., 2004). There is research in non-savanna ecosystems teasing respiration apart into that associated with the growth of new tissues (dominant in the wet season) and that resulting from tissue maintenance (occurs in both the wet and dry season) (Amthor, 1984; Lavigne and Ryan, 1997; Ryan, 1990). Such research still needs to be done for savannas. Our study design did not allow us to estimate this split, but a dataset of savanna tree growth could be used to distinguish construction respiration from maintenance (see e.g. Chan et al., 2018). If I assume that there is zero growth during the dry season, then the respiration rates I observed during this season are a measure of maintenance of wood tissues. The respiration rates I measured during the wet season were from both construction and maintenance of wood tissue. Therefore, construction respiration would be the difference between wet season respiration and the dry season respiration, adjusted for temperature. In rough terms, based on my data and these assumptions, maintenance respiration would be about a quarter of the total.

Effects of time of day

Time of day when measurements were taken was another significant but weak predictor of wood respiration for savannas. Wood respiration is higher early in the day and decreases towards the late afternoon. There is high productivity by savanna trees during the day (especially early in the morning to mid-morning), where photosynthesis and transpiration reach their highest around this time due to optimal temperatures (Kgope and Musil, 2004; Linder and Troeng, 1980).

Effects of species

I found that savanna species respire at different intrinsic rates, but the ranking depends on whether you express the rates on a surface area or volume basis. In both cases, legumes (*P. violacea* and *V. nilotica*) recorded the highest rates. They are both also relatively fast-growing species. Sapwood density was the only significant predictor of the differences between species wood respiration per sapwood volume. Species with high sapwood density (e.g. *T. sericea and V. nilotica*) respire more per unit sapwood volume than those with low wood density (e.g. *S. birrea* and *O. pulchra*). High density means a greater mass of tissue participating in respiration, but it also means less space between cells for gaseous diffusion. Even though less dense wood enables high gas diffusion, if the quantity being diffused is relatively low, then there is low overall respiration. This is especially true for sapwood density since sapwood contains the majority of the woody respiring tissue (Ryan, 1989). Studies in other biomes have found that species respire at different rates due to physiological and structural differences (Asao et al., 2015; Rodríguez-Calcerrada et al., 2015; J. Y. Yang et al., 2012; Q. Yang et al., 2012).

None of the other factors investigated (i.e. nitrogen content, phenology and tree diameter) could significantly explain the difference in wood respiration I observed among savanna species. There is not that much nitrogen content in wood (Table 2.5), which was not much of a surprise, but it was surprising that even though some species have more N in their tissues than others, nitrogen does is not significantly associated with differences in wood respiration. Tree diameter is significantly linked to wood respiration, but accounting for sapwood volume technically included tree diameter into the analysis, since sapwood thickness is closely related to stem diameter. A study specifically looking at more than one species per phenological type would help support this study in trying to account for phenology in $R_{a,\ wood}$ differences among species.

Conclusion

This study has shown that there are two over-riding predictors of wood respiration in savannas: temperature and season of the year; and a minor effect from the time of day. I have also shown that different species respire at different rates even once the effects of temperature, season and time of day are accounted for. I found that during the active season respiration increases to its peak between 35 - 45 °C and then start decreasing at higher temperatures, while during the dormant season it levels off rather than decreases at higher temperatures.

Acknowledgements

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Chapter 3: Respiration fluxes in a South African savanna ecosystem

This chapter is written as a stand-alone paper, intended for submission to Global Change Biology.

Mpilo Z. Khumalo[1, 2]

[1]School of Animal, Plants and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

[2]Global Change Institute, University of the Witwatersrand

Correspondence

Mpilo Z. Khumalo, School of Animal, Plants and Environmental Sciences,

University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

Email: mpilozenzele0@gmail.com

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1.1 Abstract

Carbon dioxide returns to the atmosphere from terrestrial ecosystems through a range of respiratory fluxes, which together add up to ecosystem respiration (R_{eco}). R_{eco} can be estimated in a ‘top-down’ way using eddy covariance flux towers, with some limitations, but this does not provide information regarding the contributions by the various component fluxes. This research collates and upscales the main respiratory flux estimates from an eddy covariance equipped savanna site near Skukuza in the Kruger National park, for the period 2016 to 2019, to provide a ‘bottom-up’ to Total Ecosystem Respiration (TER). The respiratory fluxes include those from soil, leaf, wood, herbivores and fire. For the period 2016 - 2019 R_{eco} averaged 2 239 g $CO_2/m^2/y$, with an inter-annual standard deviation (SD) of 1 534 g $CO_2/m^2/y$, and an estimated uncertainty ($\underline{+}$ 1SD) in any given year of around 29% of the mean. Over the full flux tower record (2000 – 2019), R_{eco} ranged 1 041 to 19 584 g $CO_2/m^2/y$, with a mean of 6 597 g $CO_2/m^2/y$ and SD of 4 702 g $CO_2/m^2/y$. Over this same period (2000 - 2019), TER averaged 3 907 g $CO_2/m^2/y$, with an uncertainty of around 30%. NPP was estimated at 2 333 ± 1 516 g $CO_2/m^2/y$. The contributions of the various component fluxes were: soil and litter respiration 84%, live leaf respiration 10%, fires 3%, live wood 2% and herbivores 1%.

KEYWORDS

Soil, wood, fire, leaf, root, heterotrophic, autotrophic, herbivory

Introduction

Savannas, defined as ecosystems where trees and grasses co-dominate the primary production (Cole, 1987; Huntley and Walker, 2012; Scholes and Archer, 1997), are one of the most geographically extensive terrestrial ecosystems, occupying more than an eighth of the Earth's land surface on six continents (Scholes et al., 2015; Scholes and Walker, 1993). In Africa, savannas are the largest biome, covering more than half of the land surface (Biggs, 2003). Savannas are characterised by alternating wet and dry seasons (Scholes and Walker, 1993). Savannas, because of both their extent and the relatively large magnitude of key exchange processes such as carbon assimilation and respiration, are an important but poorly quantified part of the global carbon cycle (Archibald et al., 2009; Makhado and Scholes, 2011; Scholes et al., 2015). Under current conditions, savannas (along with other largely undisturbed terrestrial ecosystems) are overall carbon sinks, especially during the wet growing season and in years of above-average rainfall (Archibald et al., 2009; Chen et al., 2003; Räsänen et al., 2017).

What determines whether savannas are carbon sinks or sources is the resultant of two major fluxes (Figure 3.1): (1) the incoming gross primary production (GPP); and (2) the outgoing ecosystem respiration (R_{eco}). The sum of GPP and R_{eco} (noting the sign convention that GPP is negative and R_{eco} is positive) is the Net Ecosystem Exchange (NEE). NEE can be measured at the landscape scale using eddy covariance (EC) techniques (Archibald et al., 2009; Moffat et al., 2007). An estimate of R_{eco} can be derived from diurnally-resolved EC measurements after some assumptions have been made regarding the relationship between nigh-time and daytime R_{eco}. It is usually assumed that positive EC fluxes during the night represent respiration (Archibald et al., 2009; Lavigne et al., 2012; A. Nickless et al., 2011), and these can be rescaled, with or without temperature adjustment, to cover the daytime period as well. This widely-applied procedure is fraught with questionable assumptions and potential errors (Moffat et al., 2007). By itself, this approach cannot distinguish between the different fluxes that make up R_{eco}.

The principal sources of R_{eco} in a typical savanna ecosystem are illustrated in Figure 3.1. Lateral carbon transfers by erosion, leachates, migration of animals or harvest by humans must be corrected for if it is quantitatively meaningful (Kirschbaum et al., 2001). Given that the larger respiration terms can only be estimated within about 10% relative error (Reichstein et al., 2005), the small terms are very hard to resolve using budget closure approaches (Duvert et al., 2020; Kirschbaum et al., 2019).

The 'bottom-up' sum of the individual respiratory fluxes is called the total ecosystem respiration (TER) to distinguish it from the integrated 'top-down' measurement of R_{eco} (Figure 3.1). Soil, leaf and wood respiration are typically measured using chambers equipped with gas analysers (Khumalo and Scholes, 2020 [submitted][d]) (Kgope and Musil, 2004; Makhado and Scholes, 2011).

Litter respiration can be directly estimated, and thus separated from soil respiration, using known litterfall rates and measured litter decomposition rates (Scholes and Walker, 1993), or by removing litter from a subset of soil respiration measurement chambers. Fire emissions are usually estimated by a calculation involving fuel load, fraction combustion, fuel carbon content and frequency of burning (Cachier et al., 1995; Hao et al., 2012). Respiration by animals is estimated from animal biomass, using known relationships between metabolic rate and body size (Darveau et al., 2002; Heusner, 1985).

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[d] Chapter 2 of this dissertation

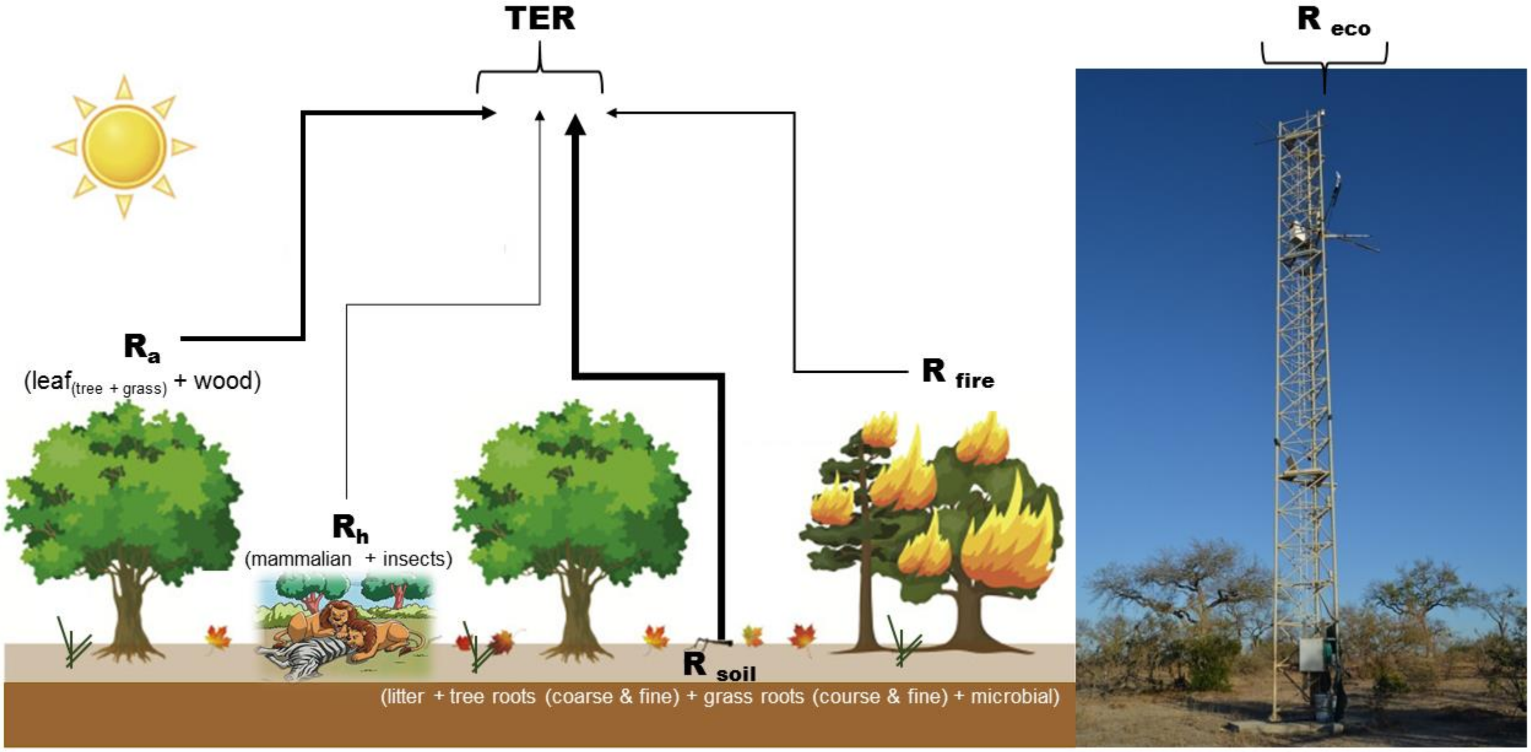

Figure 3.1: *An overview of the respiration fluxes in a typical savanna. Soil and litter layer respiration ($\mathbf{R}_{soil}$), is mostly microbial but includes the belowground part of autotropic respiration (fine and coarse root respiration). The other components are leaf respiration, including tree and herbaceous leaves and fruiting bodies ($\mathbf{R}_{a, leaf}$); wood respiration including stems, branches and twigs but excluding roots ($\mathbf{R}_{a, wood}$); fire emissions ($\mathbf{R}_{fire}$); and (5) respiration by herbivores, which can be subdivided into that by insects ($\mathbf{R}_{h, insect}$) and that from large mammal herbivores ($\mathbf{R}_{h, mammalian}$). There are other relatively minor terms, such as respiration by carnivores and by microbes associated with aboveground biomass. Together, they sum to Total Ecosystem Respiration (TER). The photo on the right is of the eddy covariance flux tower at the Skukuza site in South Africa, which estimates ecosystem respiration (R_{eco}) by extrapolation of night-time NEE to the entire day plus night period. TER plus net lateral fluxes should equal R_{eco}. Adapted from: (Xiao et al., 2019) and www.csir.co.za/sites/default/files/DSC_1415_RESIZED.jpg*

The respiratory flux components of respiration are measured at small scales relative to EC flux measurements. They, therefore, need to be scaled up to ‘ecosystem’ or ‘landscape’ level before comparing TER with R_{eco}.

Scaling is a widespread challenge in both basic and applied research (Wu, 1999). Ecological measurements are often made at small scales and over short periods, and need to be brought to a common, larger-area, longer-duration scale for inter-comparison (Cheng et al., 2010; Meir and Grace, 2002; Wu, 1999). When scaling, the biased propagation of errors is the main problem to be avoided.

Spatial upscaling

Spatial upscaling of a mass-conserved property such as carbon flux requires knowledge of the spatial heterogeneity of the fluxes (Griebel et al., 2020), which can then be summed appropriately (Wu, 1999). Savannas are famously patchy, at a range of scales. Some of the key sources of inhomogeneity are within and between grass tufts; beneath and between tree canopies; between disturbance patches; and between the soil types of a catena (Biggs, 2003; Scholes and Archer, 1997; Scholes and Walker, 1993). The spatial decorrelation as a result of these heterogeneities can be thought of as a ‘semivariogram’ (Figure 3.2), showing coherence as a function of the linear distance between locations (Curran, 1988). The semivariogram never really saturates until the spatial scale of the whole world is reached, but shows clear jumps at certain scales (Wang et al., 2009). Selecting a scale of about 1000 m, to representing the savanna landscape, works well in most cases. The Skukuza EC system samples the atmosphere at a height of 17 m above ground level (about 1.6 times the mean tree height), which results in a spatial footprint of about 500 m upwind of the tower.

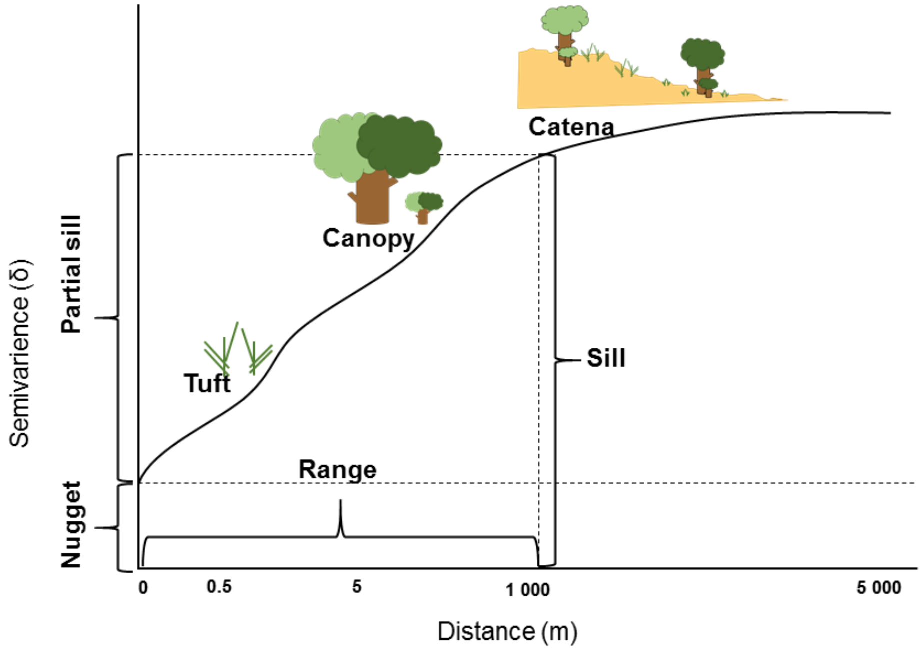

Figure 3.2: *A conceptual sketch of the increasing decorrelation of processes in savannas with the spatial distance between locations, expressed here as a semivariance. Total variance (the*

> ***sill**) can be separated into two parts: the **nugget** (spatially unresolved variance) and **partial sill** (spatially-linked variance). Jumps in spatial structure occur at the scale of **tufts,** the **tree canopy** and the different parts of the **catena**. All of these scales of variation are encompassed by observations with a nominal scale of about 1000 m (i.e. 1 ha), called the **range**.*

Temporal upscaling

Patterns over time are also inhomogeneous, but the structure is often cyclic (Wu, 1999). For instance, there is a strong daily solar radiation cycle thanks to the rotation of the Earth (reflected, for instance, in the daily cycle of air temperature) and a strong annual cycle due to the tilt of the Earth's axis, reflected in the progression of seasons (Falge et al., 2002). You can then use a covariate, such as air temperature, for which you have time-continuous measurements, to interpolate the unevenly distributed and brief measurements of the fluxes you are interested into daily or annual scales. The key temporal driver in savannas is soil moisture, which has both an overall cyclic structure (the wet and dry season) (Chen et al., 2002), and a quasi-stochastic structure at the day-to-week scale, resulting from individual rain events (Williams et al., 2009; Williams and Albertson, 2004). Integration to an annual timescale makes logical sense for ecosystem inter-comparisons.

There are assumptions associates with each flux estimate, including regarding the capabilities of the measurement instruments, correlations between the flux and environmental variables, and "predictable" and "random" sources of (WU and LI, 2006). After the measurement, the values are converted to convenient formats and analysed. If there are missing data, there are algorithms that are applied to fill the gaps. Throughout the various assumptions and steps of data collection and processing, systematic errors can be introduced (Wu, 1999). These errors, which may initially be relatively small, propagate in the integrated or accumulated flux. This propagation of uncertainty in flux estimates is a problem that can be reduced in many ways, through an understanding of the fluxes, statistics, modelling, and optimal study design. This study uses various techniques to estimate and report these uncertainties (Malhi et al., 2004; Pérez-Priego et al., 2015).

The carbon budget is incomplete without knowing all the major fluxes. In the case of African savannas, wood respiration is one of the potentially major fluxes from plants (autotrophs) that are typically not well quantified. Chapter 2 of this dissertation reported new measurements of wood respiration, which allow the budgets to be closed and the importance of the various components of respiration to be evaluated.

Aims, objectives and key questions

The aims of this chapter are: (1) to calculate the total amount of wood respiration ($R_{a, wood}$) at a landscape scale for a full year for the savanna at Skukuza; (2) compare $R_{a, wood}$ to the various other upscaled respiratory fluxes in this savanna; and (3) compare total respiration as estimated from the sum of fluxes (TER) to an integrated measurement of respiration (R_{eco}).

Objective 1: Upscale measurements of wood respiration to the annual, one-hectare ('landscape') scale. The spatial upscaling uses surveys of tree species, heights and stem diameters and allometric relations between tree size and sapwood volume. The temporal upscaling uses the relationship between wood respiration, the season of the year and bark temperature (driven by air temperature, which measured at hourly intervals throughout the year.)

Objective 2: Upscale other savanna CO_2 fluxes (soil respiration, leaf respiration, fire emissions, insect and large mammalian respiration) in time and space to the same level as wood respiration, using techniques appropriate to each flux.

Objective 3: Sum the respiratory fluxes to provide an estimate of TER, and compare it to R_{eco} derived from EC measurements.

Methods

Study site description

This study builds on wood respiration measurements reported in Chapter 2 of this dissertation. Those measurements were made at three study sites: (1) Skukuza flux tower site in the Kruger National Park (KNP); (2) Sandfields and Forests, immediately north of Nylsvley Nature Reserve (NNR); and (3) Wits Rural Facility (WRF), 100 km northwest of the Skukuza sits, in a similar environment. All three sites are semi-arid savannas located in the Mpumalanga and Limpopo provinces of South Africa. I chose to do the upscaling of respiration fluxes for the Skukuza flux tower site (25.0167° E, 31.4833° S, and 365 m.a.s.l.) (Figure 3.3) because it has a long-term EC measurement record (see Archibald et al., 2009), an existing study of soil respiration, allometric models for the biomass of all the major tree species (Chave et al., 2014; Muzite, 2017; Alecia Nickless et al., 2011; Poungoué, 2003) and a full tree survey (Colgan et al., 2014; Kirton et al., 2009; Scholes et al., 2001).

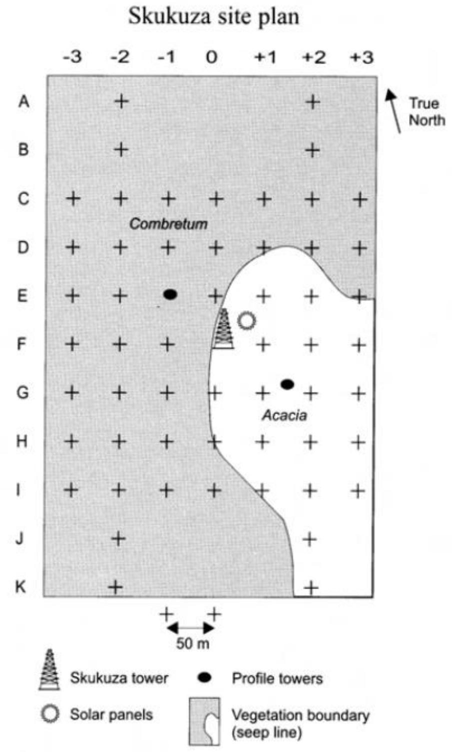

Figure 3.3: *Skukuza flux tower site in the Kruger National Park, South Africa. The tower is located at the ecotone between two savanna types (broadleaved Combretum savanna and fine-leaved Senegalia (formerly Acacia) savanna). Source: (Scholes et al., 2001).*

The Skukuza flux site is located astride the mid-slope position of a gently undulating landscape that forms a distinctive catena. The flux tower is located on an ecotone, marked by a seasonal seep-line (Scholes et al., 2001) (Figure 3.3). This seep-line separates the upslope broadleaved savanna, dominated by *Combretum apiculatum* trees, from downslope fine-leaved savanna dominated by *Senegalia nigrescens* trees (Archibald et al., 2009; Makhado and Scholes, 2011; Scholes et al., 2001). Like all climatically mono-modal savannas, this site experiences two distinct seasons; a dry season (here lasting from May to October) and a wet season (here from November to April) (Archibald et al., 2009; Scholes et al., 2001). Temperatures reach maximums in excess of 44 °C during the summer and can drop below 0 °C at night during the winter; but the daytime temperatures, even in winter, are warm. The mean annual rainfall at Skukuza, 20 km to the northeast, is 550 mm (SD=160mm, 100-year record) (Makhado and Scholes, 2011; Scholes et al., 2001).

The trees are typically 8 – 10 m tall, with aboveground biomass of about 20 t/ha (Archibald et al., 2009; Scholes et al., 2001). The grass can grow to a height of 1 m, but is typically grazed shorter than that, to about 30 cm. The grass aboveground biomass is extremely variable within and between years, but never exceeds about 5 t/ha. The grass layer comprises species like *Panicum maximum*, *Digitaria eriantha*, *Eragrostis rigidior*, *Urochloa mossambicensis, Bothriochloa radicans* and *Pogonarnthria squarrosa* (Scholes et al., 2001), along with a wide diversity of forbs.

I upscaled each flux for the years 2016 to 2019 since there was both adequate environmental data and R_{eco} for these years. The monthly average air temperature is highest in summer and lowest in winter, at 16 m as measured on the Skukuza EC tower between 2016 and 2019, ranged 13.6 °C to 32.8 °C with a mean of 22.6 °C (Figure 3.4).

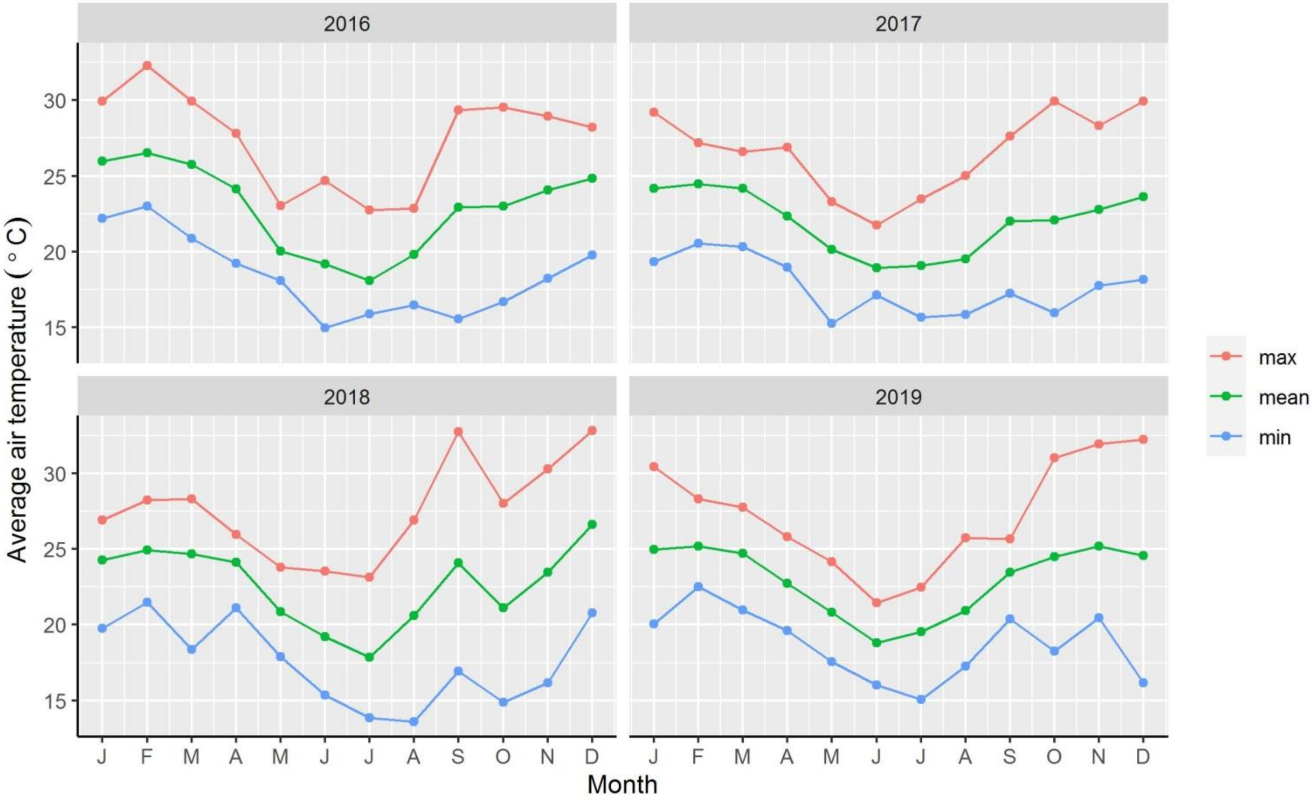

Figure 3.4: *Seasonal changes in air temperature (monthly minimum, mean and maximum) from 2016 to 2019.*

Soil moisture at this site also shows strong seasonality and is potentially a stronger controller of most respiratory fluxes than is temperature. For the year 2016 to 2019, the soil moisture in the 0-30 cm later at this site ranged from 4.9% volumetric (typically in mid-winter) to 12.8% in mid-summer (Figure 3.5).

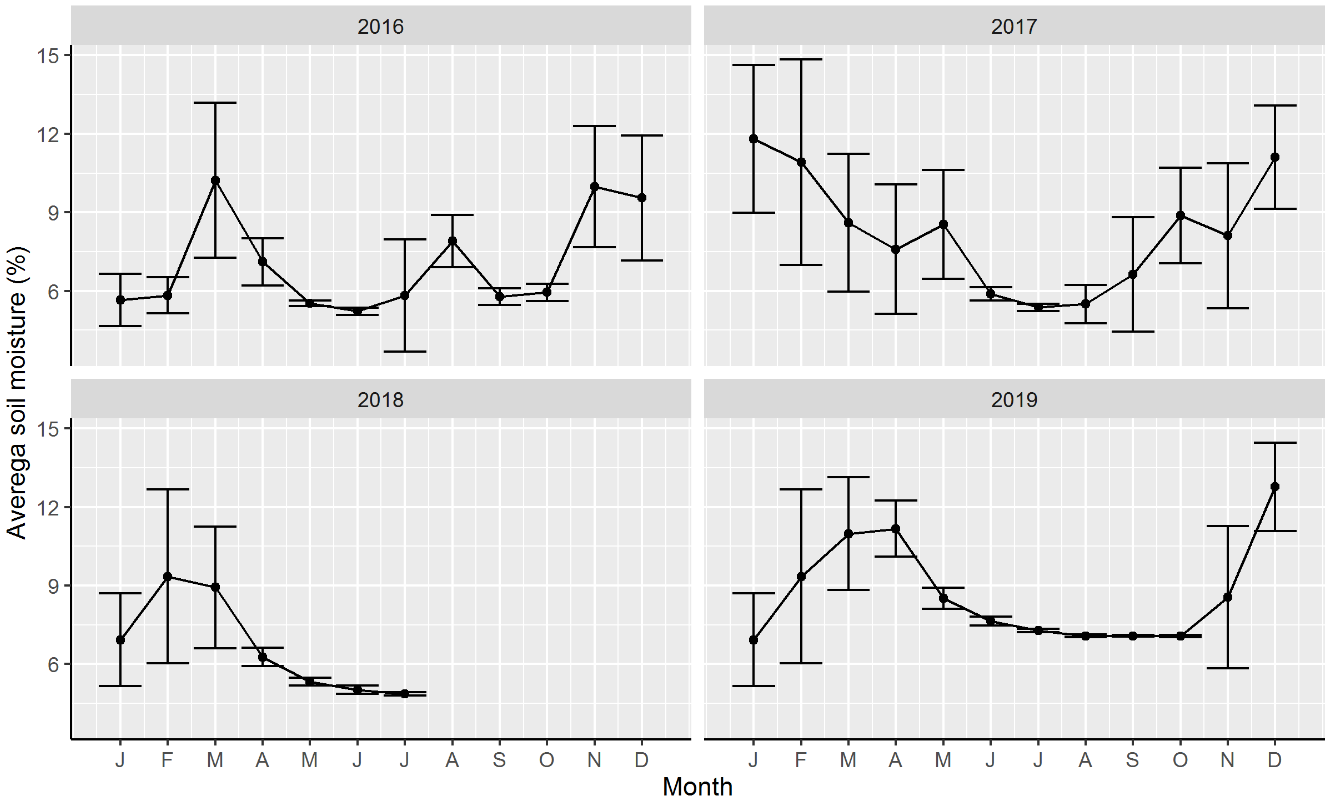

Figure 3.5: *Monthly average soil moisture in the period 2016 to 2019 in the vicinity of the Skukuza EC tower, showing the general seasonal trend.*

Upscaling wood respiration

Wood respiration rates differed between species and were better predicted by sapwood volume than by the surface area of the trees (Chapter 2). Wood respiration rates were predicted by bark temperature and season of the year, and minimally by time of day. For upscaling wood respiration rates I focussed on three tree species, which together contribute 80% of the biomass and basal area in the study site: *C. apiculatum*, *S. nigrescens*, and *Sclerocarya birrea,* (Colgan et al., 2014; Alecia Nickless et al., 2011; Scholes et al., 2001). The remaining 20%, including 21 species (*Grewia hexamita, Carissa edulis, Terminalia sericea, Ziziphus mucronata, Grewia bicolor, Vachellia nilotica, Combretum zeyheri, Combretum imberbe, Dalbergia melanoxylon, Dichrostachys cinerea, Grewia flava, Pterocarpus angolensis, Lannea schweinfurthii, Grewia flavescens, Euclea divinorum, Peltophorum africanum, Schotia brachypetala, Lonchocarpus capassa, Piliostigma thoningii, Vachellia* *tortilis,* and *Cissus cornifolia*) was predicted using a generalised model based on pooled data for all ten species measured in chapter 2.

First I calculated total tree wood volume (including bark) per individual stem using allometric equations from Colgan et al., 2014; Alecia Nickless et al., 2011; Poungoué, 2003. Since in the chapter 2 study I recorded bark and sapwood thicknesses for all the species of interest (Table 2.5) I was able to fit a regression model between sapwood thickness and stem diameter, and another between bark thickness and stem diameter for each species (Appendix B). This enabled me to solve for sapwood volume alone (see Appendix B for more information). For each tree stem within the site sapwood volume was given by

$$\text{Sapwood volume} = \text{Tree volume} - (\text{heartwood volume} + \text{bark volume})$$

Trees with a circumference of less than 10 cm (the lower threshold of the allometric equations) were assumed to have volume fractions of 98% sapwood, 1% bark and 1% heartwood, and their volume was predicted as a linear function of circumference, passing through zero and the 10 cm-predicted volume. The most recent tree density and species composition survey at the flux site was done in 2009 when four hectares (40 000 m^2) were sampled around the tower. In that campaign, 155 *C.apiculatum* trees were counted, ranging from 0.013 m to 0.379 m in diameter, 33 *S. nigrescens* trees with tree diameters ranging between 0.038 m and 0.499 m, and 52 *S. birrea* trees ranging from 0.079 m to 0.805 m in diameter. Table 3.1 summarises the key variables derived from this dataset.

Table 3.1: *Dimensions of the three major tree species around the Skukuza flux site based on a sample of 240 trees in a 4 ha area centred on the tower. The circumference and height of individual stems were used to estimate the total mass, volume and sapwood volume of each species at the site.*

Species	Diameter (m)	Bark thickness (m)	Sapwood thickness (m)	Heartwood thickness (m)	Tree mass (kg)	Tree volume (m^3)	Tree sapwood volume (m^3)
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
C. apiculatum	0.18 ± 0.07	0.05 ± 0.01	0.01 ± 0.00	0.04 ± 0.03	167.08 ± 163.42	0.18 ± 0.18	0.15 ± 0.15
S. nigrescens	0.22 ± 0.11	0.04 ± 0.002	0.01 ± 0.00	0.07 ± 0.06	675.10 ± 1001.85	0.23 ± 0.23	0.16 ± 0.13
S. birrea	0.41 ± 0.13	0.10 ± 0.01	0.01 ± 0.00	0.10 ± 0.06	715.62 ± 599.15	1.73 ± 1.18	1.54 ± 0.99
Other woody species	0.06 ± 0.07	0.001 ± 0.001	0.03 ± 0.03	0.0003 ± 0.0003	33.62 ± 102.89	0.04 ± 0.13	0.03 ± 0.07

A mixed-effects model of wood respiration per sapwood volume from chapter 2 was used to estimate wood respiration per tree, per hour, by species (Appendix B). Air temperature (measured half-hourly by a weather station mounted on the flux tower, at a height of 17 m) was positively linearly correlated with bark temperature. The weather station temperature record (Appendix B) was used to estimate hourly bark temperature (Figure 3.6). Season of the year was expressed as a continuous sine-wave variable ranging between -1 (for mid dry season) and +1 (for mid wet season).

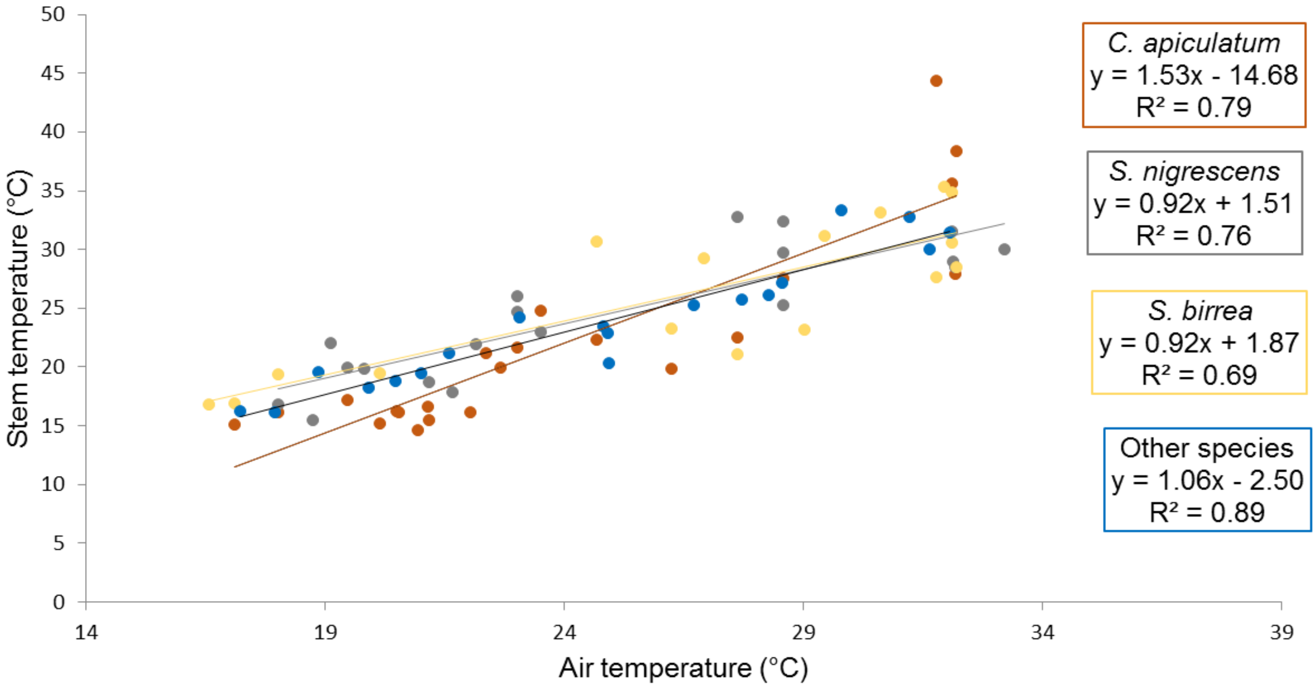

Figure 3.6: *Relationship between air temperature and stem temperature for each species.*

The estimated season- and temperature-adjusted wood respiration rates (µmol $CO_2/m^3_{sapwood}/s$) were multiplied by the sapwood volume per individual stem, and then by $3600*44.01/10^6$ to convert the moles to grams and seconds to an hour. For each stem of each species, these hourly rates were summed for the whole year to get g CO_2/y. The stem annual aggregate was summed across all individuals to get wood respiration for each species, for the year 2019. The sum over species of wood respiration gives the wood respiration rate for the four-hectare tree sample plot, which I divided by 40 000 to get g CO_2/m^2/y.

The uncertainty associated with this estimate was calculated as follows. The respiration per tree stem is the product of an estimated sapwood volume and an estimated respiration rate per unit sapwood volume. The standard deviation (square root of the variance) associated with the first term was estimated from the uncertainty associated with the allometric equations, reported to be 10% of the mean (Alecia Nickless et al., 2011). The standard deviation associated with the second term can be estimated from the error terms in the respiration rate model presented in chapter 2 of this dissertation, to be 20.3% of the mean (Table 2.4).

Wood respiration estimation:

$$\ln R_{a,\ wood} = 1.11 + 0.12 * \text{stem temperature} - 0.0013 * \text{stem temperature squared} + 0.58 * \text{season} - 0.00013 * \text{Time of day}$$

Propagation of uncertainty:

$$\sigma_{wood}^{2} = [(\bar{x}_{wood\ respiration})^{2} * (\sigma_{sapwood\ volume})^{2}] + [(\bar{x}_{sapwood\ volume})^{2} * (\sigma_{wood\ respiration})^{2}] + [(\sigma_{wood\ respiration})^{2} * (\sigma_{sapwood\ volume})^{2}]$$

I then assumed the two variance terms to be independent, resulting in an overall uncertainty of 19%. Since the stem census was a total count, there is no uncertainty term accruing from this source, and the errors made measuring stem circumference and the air temperature are assumed to be a negligible contribution to the total variance.

Upscaling the other respiratory fluxes

Soil and litter respiration (R_{soil})

(Makhado and Scholes 2011) reported soil respiration in the vicinity of the flux tower as a function of soil type, soil moisture content and soil temperature. A simple water balance model, driven by daily rainfall measured at the tower for the same year as wood respiration was estimated, and daily potential evapotranspiration calculated from radiation, temperature, humidity and wind speed recorded the tower, was used to generate daily soil moisture content in the topsoil (0 – 300 mm). A simple daily average topsoil temperature model was based on time-lagged air temperature data (Appendix B). These inputs were used to drive a soil respiration model for the hillcrest sandy soils, and another for the valley-bottom clayey soils, based on the equations in (Makhado and Scholes, 2011). The average of the rates on the two soils provided the respiration rate for the site as a whole since the site straddles the two soil types more-or-less equally. The uncertainty associated with this estimate was estimated from the parameter uncertainties given by Makhado and Scholes, 2011 to be 24% of the mean.

Soil respiration estimation for Combretum savanna:
$f(\text{T°C}) = -0.0062 * \text{soil temperature}^2 + 0.3483 * \text{soil temperature} - 3.8058$
$f(H_2O) = 0.125 * (\text{soil moisture}) - 0.125$
mean monthly soil respiration = Makhado and Scholes, 2011
$R_{\text{soil}} = \text{mean monthly soil respiration} * f(\text{T°C}) * f(H_2O)$

Soil respiration estimation Senegalia savanna:
$f(\text{T°C}) = -0.0045 * \text{soil temperature}^2 + 0.2707 * \text{soil temperature} - 3.0833$
$f(H_2O) = 0.1111 * (\text{soil moisture}) - 0.1111$
mean monthly soil respiration (Makhado and Scholes, 2011)
$R_{\text{soil}} = \text{mean monthly soil respiration} * f(\text{T°C}) * f(H_2O)$

Propagation of uncertainty:

$$\sigma_{\text{soil}}^2 = [(\bar{x}_{\text{soil respiration}})^2 * (\sigma_{\text{soil temperature}})^2 * (\sigma_{\text{soil moisture}})^2] + [(\bar{x}_{\text{soil temperature}})^2 * (\sigma_{\text{soil respiration}})^2 * (\sigma_{\text{soil moisture}})^2] + [(\bar{x}_{\text{soil moisture}})^2 * (\sigma_{\text{soil respiration}})^2 * (\sigma_{\text{soil temperature}})^2]$$

The mean dry season litter mass on the soil surface is relatively small in savannas, compared to forests, partly because they are frequently burned (Scholes and Walker, 2004). Litter respiration is included in the soil respiration measurements (since litter was not removed from the chambers before soil respiration was measured) and was not separately estimated.

Leaf respiration ($R_{a,\ leaf}$)

Several studies of leaf-level photosynthesis have been conducted on the tree and grass species that occur at the Skukuza site. Typically these collect an assimilation rate versus light intensity curve, whose intercept (i.e. when the leaf is in darkness) is the leaf respiration rate (Kgope and Musil, 2004) (Appendix B). The leaf respiration rate expressed at a reference temperature of 25 °C, was assumed to have the same temperature dependence as the photosynthetic processes, for which the average $Q_{10} = 2.0$. This temperature function was used to scale leaf respiration through the year (by assuming leaf temperature was equal to air temperature, on diurnal average). The maximum leaf area per species was known from allometry, and its seasonal progression was modelled from satellite-derived Leaf Area Index (LAI), allowing $R_{a,\ leaf}$ to be calculated at hectare scale for the entire year (Appendix B). Grass leaf respiration rates were modelled using a standard respiration rate per gram live grass leaf for all species, using a reference leaf temperature of 30 °C and assuming an average Q_{10} of 2.5, since these are C4 grasses (Scholes and Walker, 1993) (Appendix B).

Leaf respiration estimation:

$$R_{a,\ \text{leaf (broad-leaf)}} = 0.04066 * 2.0^{(\text{temperature}/10)} * \text{LAI}$$

$$R_{a,\ \text{leaf (fine-leaf)}} = 0.19622 * 2.0^{(\text{temperature}/10)} * \text{LAI}$$

$$R_{a,\ \text{leaf (grass-leaf)}} = 0.0864 * 2.5^{(\text{temperature}/10)} * \text{LAI}$$

$\text{LAI}_{\text{trees}}$ = 0.5 mid-summer and 0.1 mid-winter (Appendix B)

$\text{LAI}_{\text{grass}}$ = 0.4 - 0.5 mid-summer and 0.05 mid-winter (Appendix B)

Propagation of uncertainty:

$$\sigma_{\text{leaf}}^{2} = [(\bar{x}_{\text{leaf respiration}})^{2} * (\sigma_{\text{LAI}})^{2}] + [(\bar{x}_{\text{LAI}})^{2} * (\sigma_{\text{leaf respiration}})^{2}] + [(\sigma_{\text{leaf respiration}})^{2} * (\sigma_{\text{LAI}})^{2}]$$

Uncertainty was estimated to amount to about 20% of the mean, consisting of the standard deviation of the dark respiration rates (27% of the mean) and uncertainty of leaf area (more or less 17%, based on multiple leaf area index measurements at the site) (Kgope and Musil, 2004; Midgley et al., 2004; Scholes et al., 2004).

CO_2 fluxes from fires (R_{fire})

The long term fire history of the site is known (mean fire return of ~4.2 years, measured over 30 years) (Govender et al., 2006; Van Der Werf et al., 2003). The main fuel load for the fires, which occur in the dry season, is grass and litter. Using data from measurements conducted during the SAFARI-2000 experiment in the same landscape, a few kilometres away (Shea et al., 1996; Trollope and Potgieter, 1985) I quantified the mean grass fuel load as 161 ± 23 g DM/m^2 and litter fuel load as 171 ± 21 g DM/m^2. The fraction combusted was 99 and 92% respectively. I assumed a CO_2 emission factor of 1699 g CO_2 /kg DM (Hao et al., 2012; Ward et al., 2012), which is based on a measured mean fuel carbon content of 41%.

Fire CO_2 estimation:
For dry grass, litter and dead wood =
Biomass burnt (kg DM/ha) from Shea et al., 1996; Trollope and Potgieter, 1985
Emission factor (gCO_2/kg DM) = 1699 from Hao et al., 2012; Ward et al., 2012
CO_2 emitted (gCO_2/kg DM) = biomass burnt * emission factor
CO_2 emitted (gCO_2/m2/y) = CO_2 emitted / 10 000

The various other carbon-containing emissions, such as carbon monoxide, methane, and non-methane hydrocarbons amount to the equivalent of a further 11 g $CO_2/m^2/y$. These gases eventually turn into CO_2, so they were added to the sum. The long-term average R_{fire} can thus be calculated as

$$\frac{1}{\text{return time}} \times (\text{grass fuel load} \times \text{grass combustion completeness} + \text{litter fuel load} \times \text{litter combustion completeness}) \times 1702\ \frac{\text{g CO2}}{\text{kg}}\text{DM}$$

The standard deviation was estimated as 41%, based almost entirely on the standard error of the fuel loads and combustion completeness (Trollope and Potgieter, 1985).

Respiration by large mammal herbivores ($R_{h,\ mammalian}$)

The long-term large mammal herbivore biomass for the landscape in which the site is located is known, by species, as a result of wildlife census conducted annually in the park. Large mammal herbivores are defined as having a body mass greater than 5 kg LW. The dominant mammalian herbivores at the Skukuza site comprise 14 species, mostly mid-sized ruminants in the family Bovidae. Their total live biomass comes to 3 155 kg/km^2 (Biggs, 2003) (with a standard deviation of around 600 kg/km^2). Using the mean mature female live weight per species to represent the herd-averaged mean body mass for the species (M), and the equation $Basal\ Metabolic\ Rate\ = aM^b$ (Archibald and Hempson, 2016; Darveau et al., 2002; Heusner, 1985) (where the mass coefficient a = 70 kcal/M$^{3/4}$ (mass in kg), M = body mass (kg), and the exponent b= 3/4), the annualised respiratory flux could be calculated per species, and then summed over the species. The uncertainty term was assumed to be dominated by the uncertainty in the biomass, about 20% (Archibald et al., 2009).

Respiration by herbivorous insects ($R_{h,\ insect}$)

The insect biomass in savannas is highly variable season to season and site to site and is poorly known (Biggs, 2003; Scholes and Walker, 1993). The general observation from insect exclusion studies is that insect herbivory removes about 15% of aboveground NPP (Scholes and Walker, 1993), a somewhat higher fraction than mammalian herbivory, despite the obvious abundance of large mammal herbivores. Belowground insect herbivory is also likely significant but is already captured in R_{soil}. By weight, the biomass of herbivorous insects is about 1.5 – 2 times more than the biomass of large mammalian herbivores (Scholes and Walker, 1993). I assumed the insect herbivory to equal 15% of the aboveground grass NPP and equated the insect respiration flux to this number after converting to CO_2 equivalents, with an uncertainty of ± 50%.

Calculating TER, R_{eco} and ANPP

The sum of all the main CO_2 respiratory fluxes results in Total Ecosystem Respiration (TER). TER was calculated for four years (2016 - 2019), with variability in each flux driven mainly by changes in climatic and environmental variables (e.g. air temperature, soil moisture and soil temperature, and LAI). The overall uncertainty in TER was estimated as the sum of uncertainties arising from each contributing flux, expressed in absolute terms (i.e. $gCO_2/m^2/y$ rather that %, absolute uncertainty = relative uncertainty/100* mean). This is a conservative approach since the terms are probably largely uncorrelated, and so to some degree cancel each other out.

Total Ecosystem Respiration estimation:

$$TER = R_{soil} + R_{a,\ wood} + R_{a,\ tree\ leaf} + R_{a,\ grass\ leaf} + R_{fire} + R_{h,\ insect} + R_{h,\ mammalian}$$

Propagation of uncertainty:

$$\sigma_{TER} = \sqrt{[(\sigma_{soil}^2 + \sigma_{wood}^2 + \sigma_{leaf}^2 + \sigma_{fire}^2 + \sigma_{insect}^2 + \sigma_{mammalian}^2) / n]}$$

TER was thus estimated to have an uncertainty (expressed as standard deviation (σ)) amounting to not more than 30% of the mean.

NEE at the Skukuza flux tower has been collected (with gaps, which were pre-patched using the Fluxnet procedures) since 2000. R_{eco} is calculated half-hourly, based on temperature-extrapolated night-time NEE (Moffat et al., 2007). These were converted from µmol $CO_2/m^2/s$ to g $CO_2/m^2/y$. See Appendix B for a link to the data source and description of how I analysed the data. The estimated uncertainty of R_{eco} has a random error component (the error of measurement of the fluxes, thought to be around 15% for eddy covariance) (Archibald et al., 2009; Goldstein et al., 2000), and a systematic error component, based on the assumptions made (such as that that night-time NEE can be rescaled using temperature to give daytime R_{eco}). The latter is not easily estimated, but is thought to amount to not more than 35% (Baldocchi et al., 2015; Berger et al., 2001; Goldstein et al., 2000; Kutsch et al., 2008; Lasslop et al., 2012; Loescher et al., 2006, 2003; Reichstein et al., 2005). Thus the overall R_{eco} uncertainty is in the order of 29%.

I did not have the access to the full dataset for the fluxes, so some major fluxes such as GPP and NPP were unavailable for me to use. Therefore, I used knowledge of the relationships between variables to first estimate GPP using R_{eco} from FLUXNET 2000 to 2013 data on NEE and R_{eco} (APPENDIX B). I then assumed that autotrophic respiration (R_a) comprises $R_{a,\ leaf} + R_{a,\ wood} + {\sim}50\%R_{soil}$, to estimate NPP

$$\mathrm{NPP} = \mathrm{GPP} - \mathrm{Ra}\ (\text{though conventionally GPP is assigned a negative sign})$$

Results

Wood respiration rates

The total amount of CO_2 emitted by sapwood of woody species around the Skukuza flux tower for the year 2019 was 54.8 g ± 8.9 g $CO_2/m^2/y$ (Table 3.2). Although the density of mature *S. birrea* trees amounted only to 12.5 per ha, this species had a higher sapwood volume (1.54 ± 0.99 m^3) than the other species, which lead to it contributing the largest amount (45.3%) to the wood respiration (Table 3.1 and 3.2). The 39.5 *C. apiculatum* trees and 2.8 *S. nigrescens* trees per ha contribute about 36.2% to the annual CO_2 emitted by wood respiration (Table 3.2). Other woody species contributed 112.5 trees per ha, but their stem diameters were small (Table 2.5 and 3.1), which lead them to contribute only about 18.5% to the annual CO_2 emitted by wood respiration. The wood respiration shows a wet season peak (October to March), as expected.

Table 3.2: *Monthly wood respiration around the Skukuza EC tower for the year 2019.*

Month	*C. apiculatum*		*S. nigrescens*		*S. birrea*		*Other species*	
	Sapwood volume (Mean ± SD) 0.15 ± 0.15 m^3		Sapwood volume (Mean ± SD) 0.16 ± 0.13m^3		Sapwood volume (Mean ± SD) 1.54 ± 0.99 m^3		Sapwood volume (Mean ± SD) 0.3 ± 0.07 m^3	
	Stem temp (°C)	$R_{a,\ wood}$ (g $CO_2/m^3_{sapwood}$/month)	Stem temp (°C)	$R_{a,\ wood}$ (g $CO_2/m^3_{sapwood}$/month)	Stem temp (°C)	$R_{a,\ wood}$ (g $CO_2/m^3_{sapwood}$/month)	Stem temp (°C)	$R_{a,\ wood}$ (g $CO_2/m^3_{sapwood}$/month)
	Mean ± SD	Sum	Mean ± SD	Sum	Mean ± SD	Sum	Mean ± SD	Sum
Jan [0.27]	23.51 ± 5.93	1.67	24.57 ± 3.58	0.37	24.45 ± 3.89	2.49	24.18 ± 4.47	1.04
Feb [0.70]	23.84 ± 5.07	1.95	24.77 ± 3.06	0.43	24.66 ± 3.33	2.90	24.42 ± 3.82	1.22
Mar [0.95]	23.15 ± 5.01	2.41	24.35 ± 3.02	0.54	24.21 ± 3.29	3.63	23.9 ± 3.77	1.52
Apr [0.96]	20.10 ± 5.26	2.02	22.51 ± 3.18	0.48	22.21 ± 3.46	3.19	21.61 ± 3.97	1.29
May [0.71]	17.17 ± 6.94	1.61	20.74 ± 4.19	0.40	20.29 ± 4.56	2.63	19.4 ± 5.23	1.04
Jun [0.28]	14.09 ± 7.14	1.03	18.88 ± 4.31	0.27	18.27 ± 4.69	1.78	17.08 ± 5.38	0.67
Jul [-0.24]	15.20 ± 8.51	0.86	19.55 ± 5.14	0.22	19.00 ± 5.59	1.43	17.92 ± 6.41	0.56
Aug [-0.69]	17.37 ± 8.14	0.73	20.86 ± 4.92	0.18	20.42 ± 5.34	1.18	19.55 ± 6.13	0.47
Sept [-0.95]	21.22 ± 8.13	0.73	23.18 ± 4.93	0.17	22.95 ± 5.34	1.11	22.45 ± 6.13	0.45
Oct [-0.96]	22.80 ± 8.53	0.84	24.14 ± 5.15	0.18	23.98 ± 5.60	1.21	23.64 ± 6.43	0.51
Nov [-0.71]	23.85 ± 7.56	0.97	24.77 ± 4.57	0.21	24.67 ± 4.96	1.40	24.43 ± 5.70	0.60
Dec [-0.27]	22.89 ± 8.65	1.28	24.20 ± 5.22	0.27	24.05 ± 5.68	1.84	23.71 ± 6.52	0.78
Species annual total (g $CO_2/m^3_{sapwood}$/y)	16.11		3.71		24.80		10.15	
Site annual total (g $CO_2/m^3_{sapwood}$/y)	54.76							
Site annual error	19%							

There is a clear difference in wood respiration among savanna species, but there is very little inter-annual variation in respiration within each species (Figure 3.7). The pattern is similar for each year; *S. birrea* respires more (~25 g CO_2/m^2/y) than other species, followed by *C. apiculatum* (~17 g CO_2/m^2/y) followed by *S. nigrescens* (~4 g CO_2/m^2/y) and 10 g CO_2/m^2/y for all other species combined (Figure 3.7).

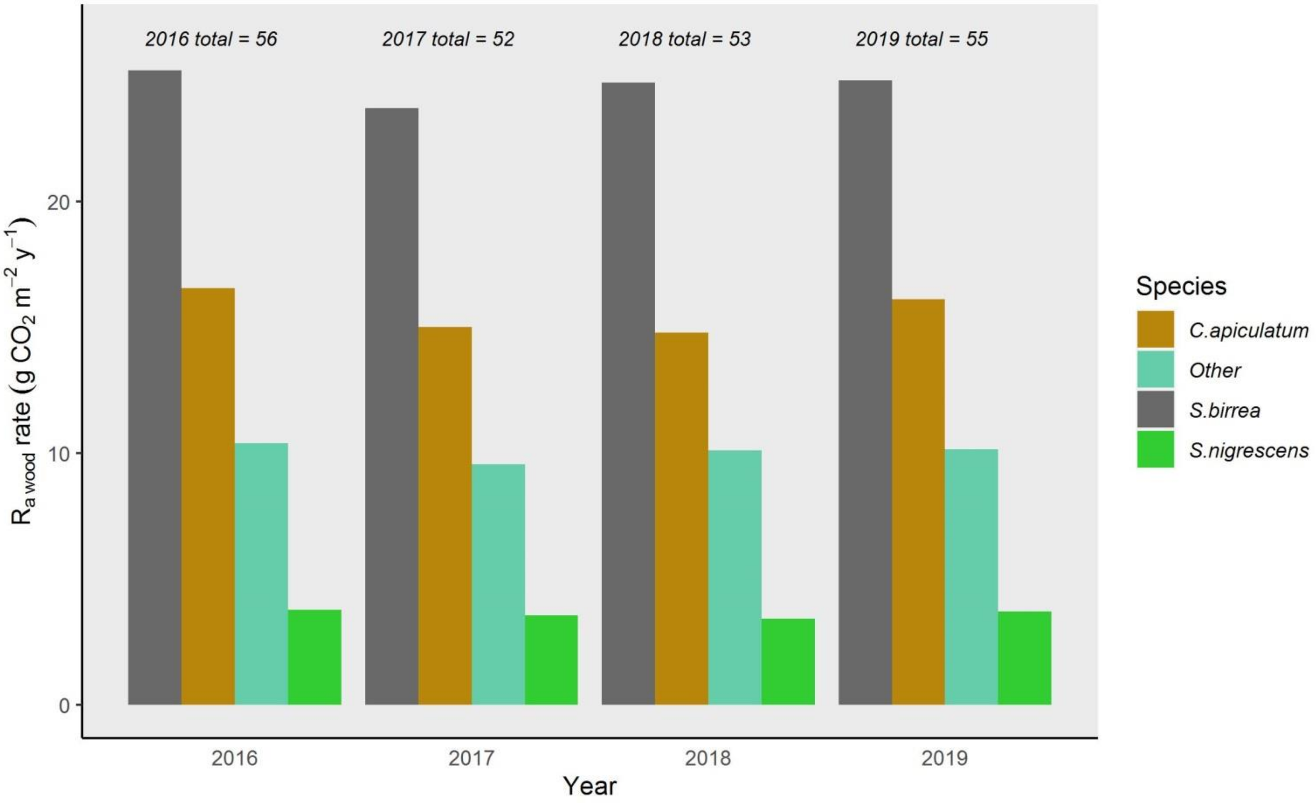

Figure 3.7: *Annual wood respiration among savanna species from 2016 to 2019 at the Skukuza EC tower.*

Soil respiration

The total annual soil respiration at the Skukuza flux tower site, averaging the sandy and clayey soil types, amounted to 3 439 ± 183 g $CO_2/m^2/y$ for the year 2019 (Table 3.3). The decomposition of dung from large mammals added an estimated18 g $CO_2/m^2/y$ (Table 3.3). The soil respiration flux is strongly seasonal, with most of the CO_2 released between October and March (the rainy warm season) (Makhado and Scholes, 2011).

Table 3.3: *Soil respiration from the two soil types (clay and sand) surrounding the Skukuza EC tower for the year 2019.*

Month	Soil moisture (%)		Soil temperature (°C)		Soil respiration (g CO_2/m^2/month)	
	Sandy soil	Clayey soil	Sandy soil	Clayey soil	Sandy soil	Clayey soil
	Mean + SD	Mean + SD	Mean + SD	Mean + SD	Sum	Sum
Jan [0.27]	7.29 ± 1.13	7.29 ± 1.13	27.56 ± 2.49	27.56 ± 2.49	201.03	162.08
Feb [0.70]	9.92 ± 3.91	9.92 ± 3.91	27.44 ± 2.05	27.44 ± 2.05	312.02	265.85
Mar [0.95]	11.38 ± 1.68	11.38 ± 1.68	26.56 ± 2.34	26.56 ± 2.34	518.85	486.13
Apr [0.96]	11.17 ± 1.06	11.17 ± 1.06	25.20 ± 2.08	25.20 ± 2.08	393.95	379.28
May [0.71]	8.51 ± 0.40	8.51 ± 0.40	22.63 ± 1.22	22.63 ± 1.22	308.17	258.65
Jun [0.28]	7.65 ± 0.17	7.65 ± 0.17	20.51 ± 1.08	20.51 ± 1.08	131.99	113.90
Jul [-0.24]	7.28 ± 0.07	7.28 ± 0.07	21.35 ± 1.35	21.35 ± 1.35	101.83	73.66
Aug [-0.69]	7.08 ± 0.06	7.08 ± 0.06	23.62 ± 1.56	23.62 ± 1.56	95.70	64.27
Sept [-0.95]	7.08 ± 0.04	7.08 ± 0.04	23.86 ± 2.32	23.86 ± 2.32	39.25	34.18
Oct [-0.96]	7.07 ± 0.05	7.07 ± 0.05	27.15 ± 2.57	27.15 ± 2.57	385.46	384.97
Nov [-0.71]	8.56 ± 2.70	8.56 ± 2.70	26.83 ± 1.84	26.83 ± 1.84	485.51	528.67
Dec [-0.27]	12.77 ± 1.70	12.77 ± 1.70	25.64 ± 2.43	25.64 ± 2.43	599.90	552.56
			Soil type annual total: (g CO_2/m^2/y)		3573.65	3304.21
			Large mammalian dung decomposition: (g CO_2/m^2/y)		18.33	
			Site annual total: (g CO_2/m^2/y)		3 438.93	
			Site annual error:		24%	

Combretum savanna (i.e. sandy soils) is estimated to emits slightly more CO_2 per year (~3 574 g CO_2/m^2/y) from 2016 to 2019 compared to the *Senegalia* savanna (i.e. clayey soil) which emits about 3 304 g CO_2/m^2/y (Figure 3.8). There is no big difference between the years (Figure 3.8).

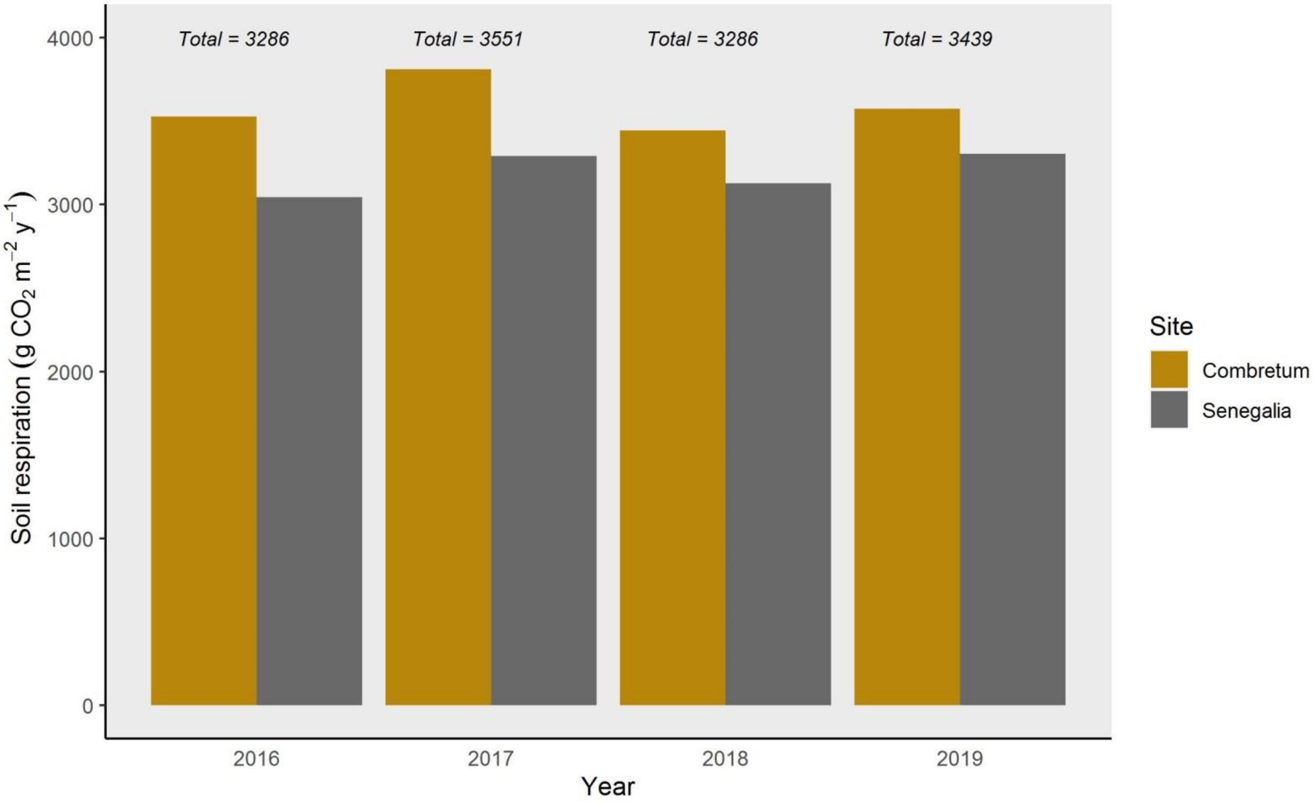

Figure 3.8: *Annual soil respiration from the two savanna types around the Skukuza EC tower.*

Leaf respiration

Leaf respiration at the Skukuza flux tower sites was 409 ± 21 g CO_2/m^2/y for the year 2019 (Table 3.4). About 70% of this CO_2 comes from the leaves of trees and shrubs (combining fine-leafed and broad-leafed vegetation types) and about 30% comes from grasses (Table 3.4). This imbalance is because the green leaf duration (LAI) of grasses is shorter than trees, despite their similar peak leaf area (Table 3.4). The leaf respiration flux is concentrated during the growing season, from November to March.

Table 3.4: *Leaf respiration from trees and grasses around the Skukuza flux tower site for 2019.*

Month	Air temperature (°C)	Tree LAI m^2/m^2	Tree leaf respiration ($g\ CO_2/m^2$/month)		Grass LAI m^2/m^2	Grass leaf respiration ($g\ CO_2/m^2$/month)
			Broad leafed	Fine leafed		
	Mean ± SD	Mean	Sum	Sum	Mean	Sum
Jan [0.27]	24.96 ± 3.88	0.5	14.03	67.72	0.50	29.82
Feb [0.70]	25.17 ± 3.32	0.5	12.74	61.47	0.40	21.65
Mar [0.95]	24.72 ± 3.28	0.5	13.66	65.91	0.20	11.61
Apr [0.96]	22.73 ± 3.45	0.4	9.25	44.62	0.10	4.91
May [0.71]	20.82 ± 4.55	0.3	6.40	30.90	0.05	2.27
Jun [0.28]	18.8 ± 4.68	0.1	1.80	8.70	0.05	1.91
Jul [-0.24]	19.53 ± 5.58	0.1	2.00	9.67	0.05	2.13
Aug [-0.69]	20.95 ± 5.34	0.1	2.20	10.62	0.05	2.34
Sept [-0.95]	23.46 ± 5.34	0.1	2.52	12.16	0.05	2.68
Oct [-0.96]	24.49 ± 5.59	0.3	8.51	41.09	0.10	6.03
Nov [-0.71]	25.18 ± 4.95	0.4	11.33	54.70	0.20	12.04
Dec [-0.27]	24.56 ± 5.66	0.5	14.26	68.81	0.40	24.24
Annual subtotal ($g\ CO_2/m^2/y$)			98.71	476.36		121.63
Site annual total: ($g\ CO_2/m^2/y$)			409.16			
Site annual error:			20%			

Fine leaved savanna trees emit more CO_2 per year (476 g $CO_2/m^2/y$) compared to broad-leafed trees (99 g $CO_2/m^2/y$) and grasses (122 g $CO_2/m^2/y$) (Figure 3.9). Although the differences among species are wide, there is no inter-annual variability in leaf respiration (Figure 3.9). There is no significant interannual variation in leaf respiration (Figure 3.9).

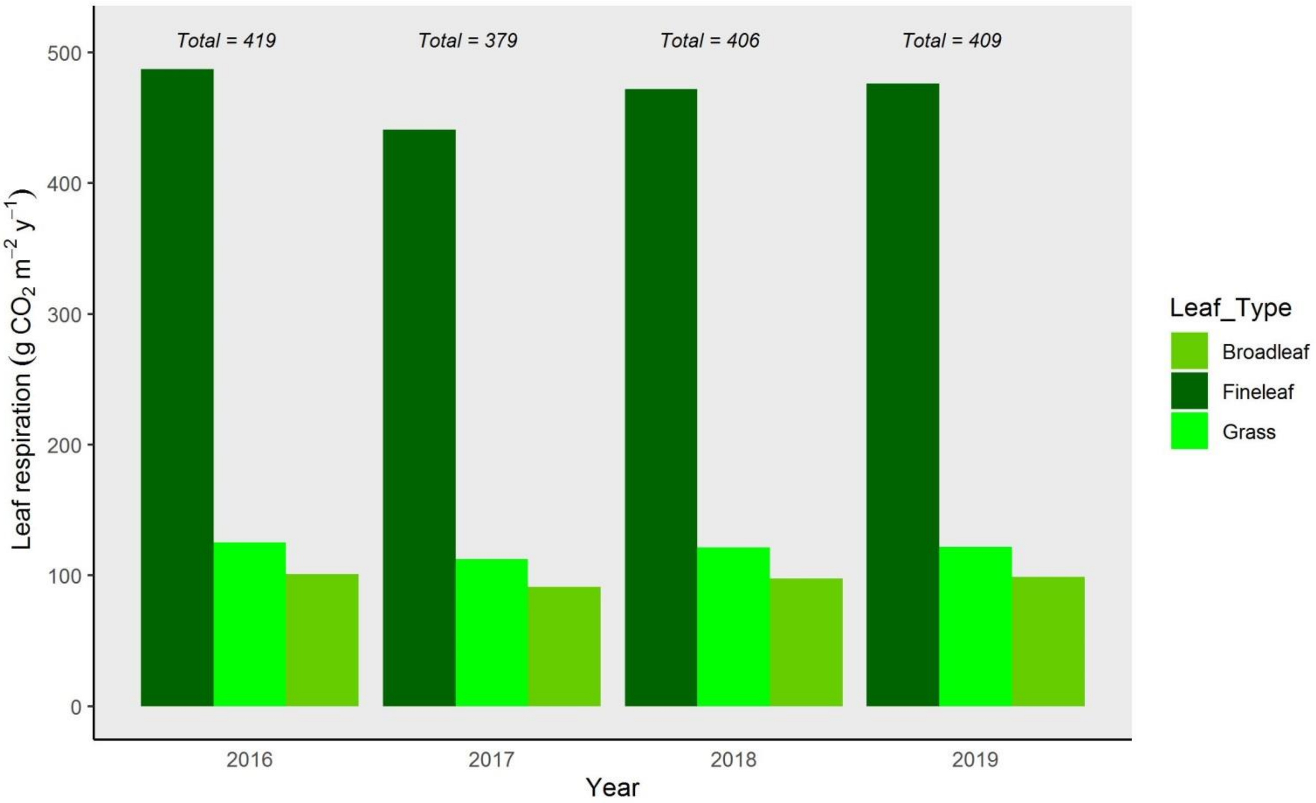

Figure 3.9: *Annual leaf respiration by fine-leafed trees, broad-leafed trees and grasses around the Skukuza EC tower from 2016 to 2019.*

CO_2 emissions from fires

Although occurring briefly and sporadically, emissions of CO_2 from savanna fires amount on average to 149 ± 27 g $CO_2/m^2/y$ (Table 3.5). This flux occurs almost entirely in the dry season, and lasts for a few hours per episode, on average once every four years (Trollope and Potgieter, 1985). In principle, this should be measured by the EC tower, but is almost certainly not well estimated, since the equipment often malfunctions during a fire and the turbulence assumptions are violated. It is therefore not part of the R_{eco} estimation.

Table 3.5: *Fire CO_2 emissions around the Skukuza flux tower.*

Component	Fuel load	Biomass burnt	Combustion completeness	Emission factor	Emitted CO_2
	kg DM/ha	kg DM/ha	%	g CO_2/kg DM	g $CO_2/m^2/y$
	Mean + SD	Mean + SD	Mean	Constant	Total
Grass	1615 ± 228	1597 ± 224	99	1699	65
Litter	1712 ± 215	1572 ± 183	92	1699	64
Dead wood	1028 ± 356	249 ± 42	24	1699	10
Emissions from other carbon campounds (e.g. CO and CH_4)					11
Site annual total	4355 ± 795	3418 ± 450	3121 ± 1805	1699	149 ± 27
Site annual error	18%				

Herbivore respiration

The combined large mammals and insects herbivory at Skukuza amount to 41.3 ±13.2g $CO_2/m^2/y$ in an average year (Table 3.6). This flux occurs throughout the year.

Table 3.6: *Respiration by herbivores from around the Skukuza flux tower for 2019.*

Component	Respiration rate
	(g $CO_2/m^2/y$)
Large mammalian respiration	16.50
Insect respiration	24.75
Total herbivory respiration:	41.25
Estimated error:	32%

TER versus R_{eco} versus NPP

The mean (for the period 2016 to 2019) of the bottom-up sum of all major respiration fluxes, TER, was 4 046 ± 114 g $CO_2/m^2/y$ including fire, and 3 907 ± 114 g $CO_2/m^2/y$ without fire (Table 3.7). The top-down R_{eco} for the same period was estimated to be 2 239 ± 1 534 g $CO_2/m^2/y$ (Table 3.7). Both of these estimates have high associated uncertainty and it is impossible to say which of them is more ‘right’. They are both likely to be wrong, and by similar relative amounts. The estimation of R_{eco} from EC data has many potential errors, including factors like the EC footprint, invalid micrometeorological assumptions relating to turbulence and drainage, and the crude algorithms used to extrapolate night-time NEE to daytime R_{eco}. All the likely TER errors are mentioned above. Also, there has been substantial tree turn-over since 2009 when the tree census was performed, and many of the large *S. nigrescens* have died, which might explain why the TER estimated values are higher than the recent R_{eco} measurements There is a strong inter-annual variation in both TER and R_{eco} at this site. R_{eco} ranged from 1 041 g $CO_2/m^2/y$ to 19 584 g $CO_2/m^2/y$ over nineteen years (Table 3.7) and had an inter-annual standard deviation over the period 2016 to 2019 for which TER was estimated of 1 534 g $CO_2/m^2/y$. The main reason for the high inter-annual variability is differences between years in the amount and timing of precipitation, that then results in differences in leaf area duration and soil moisture from year-to-year (Archibald et al., 2009; Kutsch et al., 2008; Merbold et al., 2009). Precipitation in semi-arid savannas is famously variable between years (with a coefficient of variation of around 30%), which has led them to be considered ‘non-equilibrium’ systems (Ellis and Swift, 1988).

Because of the temperature, rainfall and phenological sensitivity of soil, leaf and wood respiration, and the sporadic nature of fires, there is also a high inter-annual variability in TER (Archibald et al., 2009; Kutsch et al., 2008; Räsänen et al., 2017). Since R_{eco} measured by eddy covariance does not adequately capture fire emissions, the more valid comparison is between TER excluding fire and R_{eco}. After this correction, mean TER was about 42% larger than mean R_{eco}. A few possible reasons for this include: (1) there may be a general underestimation of R_{eco}, resulting from either the application of gap-filling methods to bridge over the missing intra-annual data or from the R_{eco} algorithm applied (or from both sources), (2) The algorithms applied here to calculate the components of TER may have overestimated one or more of the larger terms (in particular, many of the large trees that were alive in 2009 have since died) and (3) there may be systemic biases involved in the fundamental measurements that go into either EC measurements (thus propagating into R_{eco}) or in the drivers of TER elements.

Table 3.7: *Comparison of TER and* R_{eco} *at the Skukuza flux tower site*

Period	Total ecosystem respiration (TER)		Ecosystem respiration (R_{eco})	
	TER$_{\text{(with fire)}}$ (g CO_2/m^2/y)	TER$_{\text{(without fire)}}$ (g CO_2/m^2/y)		R_{eco} (g CO_2/m^2/y)
2016	3 958.48	3 820.19		2 433.19
2017	4 179.69	4 041.40		4 335.38
2018	3 943.31	3 805.02		1 146.85
2019	4 100.72	3 962.44		1 041.00
Mean$_{(2016-2019)}$:	4 045.55	3 907.26	Mean$_{(2016-2019)}$:	2 239.10
			Mean$_{(2000-2019)}$:	6 597.09
Standard deviation$_{(2016-2019)}$:	114.12	114.12	Standard deviation$_{(2016-2019)}$:	1 534.11
			Standard deviation$_{(2000-2019)}$:	4 701.63
Minimum$_{(2016-2019)}$:	3 943.31	3 805.02	Minimum$_{(2016-2019)}$:	1 041.00
			Minimum$_{(2000-2019)}$:	1 041.00
Maximum$_{(2016-2019)}$:	4 179.69	4 041.40	Maximum$_{(2016-2019)}$:	4 335.38
			Maximum$_{(2000-2019)}$:	19 584.40
Estimated error:	30%		29%	

There is a strong inter-annual variability in ecosystem carbon exchange (Figure 3.10). From 2016 to 2019, the Skukuza EC tower shift between sink and source of carbon (Figure 3.10).

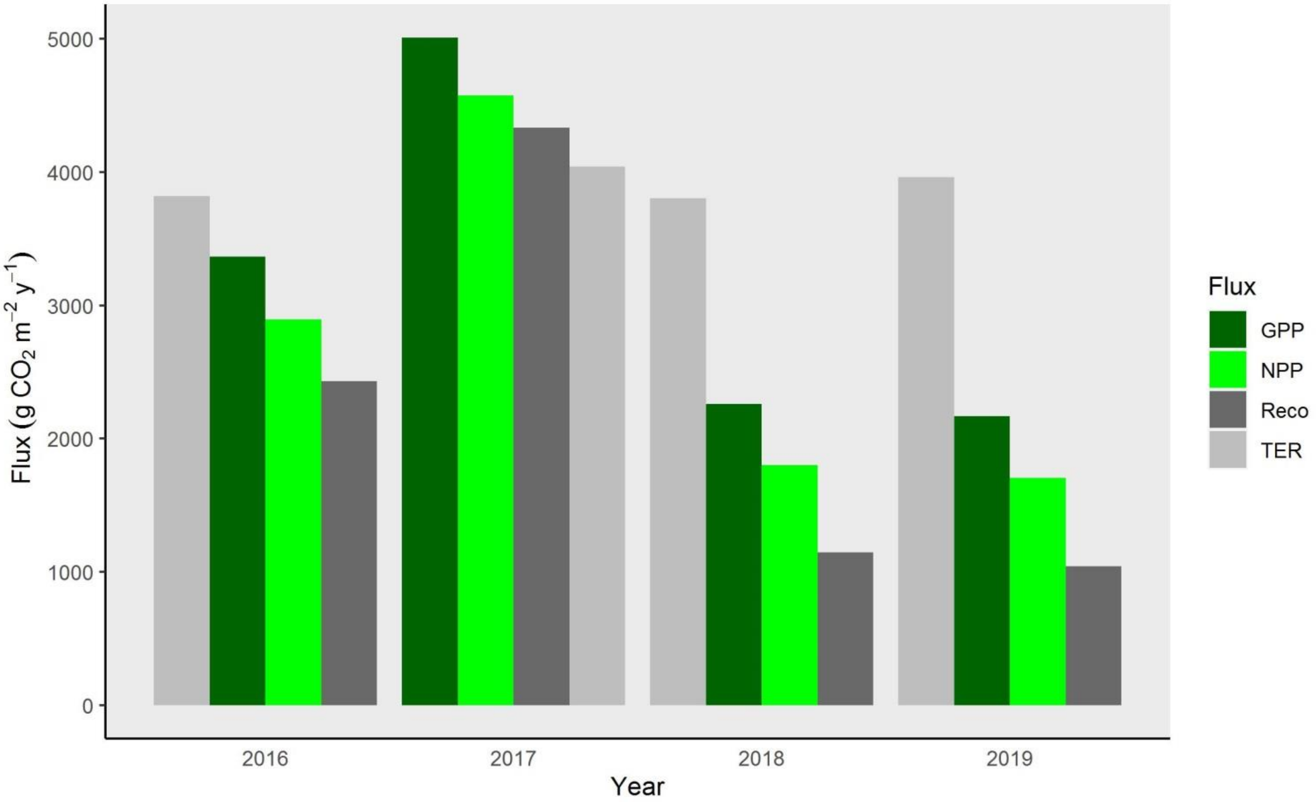

Figure 3.10: *Annual and inter-annual major carbon fluxes around the Skukuza flux tower from 2016 to 2019.*

Discussion

Wood respiration

Wood respiration contributes around 55 ± 9 g $CO_2/m^2/y$, or 1 to 2%, to the estimated total ecosystem respiration in the African savanna at Skukuza. This is substantially less than the 7.1% reported for a tropical Australian savanna (Chen et al., 2003). This may be because the Australian savanna has higher tree biomass. Wood respiration from a boreal forest site was estimated at 326 g $CO_2/m^2/y$, and from temperate and tropical forests at 909 g $CO_2/m^2/y$ and 1 855 g $CO_2/m^2/y$ respectively (Yang et al., 2016). The wide range between woody ecosystems underscores the variability, which is largely driven by differences in wood biomass (or perhaps sapwood volume) and productivity.

The other respiratory fluxes

Soil respiration is usually found to be the largest source of CO_2 from terrestrial ecosystems (Fan et al., 2015; Lloyd and Taylor, 1994; Makhado and Scholes, 2011; Reichstein et al., 2003). Our findings at Skukuza are consistent with this view. Soil respiration is the sum of three major ecosystem processes: (1) heterotrophic respiration from soil-dwelling organisms, mostly microbes but also including invertebrates, (2) autotrophic respiration by roots (grass and tree roots, including both the more metabolically-active fine roots, with greater length, and the coarse roots, which have greater mass), and (3) decomposition of litter at the soil surface – also principally microbial, but potentially including photo-oxidation and respiration by litter-consuming invertebrates (Scholes and Walker, 1993). More than 84% of CO_2 respired from the Skukuza savanna is contributed by soil respiration, which coincidentally is the same proportion estimated for the Australian savanna (Chen et al., 2003). The high contribution by soil respiration (even if corrected for surface litter respiration), underscores the very large fraction of savanna NPP which is allocated belowground (Scholes and Walker, 1993). This fraction is frequently underestimated. Many models assume a belowground allocation in woody ecosystems of 20%. The belowground biomass in savannas nearby to Skukuza is around 33% of the total biomass (Colgan et al., 2013). The discrepancy between the fraction of biomass (33%) and the fractional contribution to respiration (84%) is likely to be due to the fine roots, which are seldom adequately measured, and are much more metabolically active than coarse roots(Hanson et al., 2000; Vose and Ryan, 2002). Fine roots are metabolically analogous to leaves, just as coarse roots are analogous to aboveground stems. Part of the difference could be due to root exudates – either mucous exuded at the root tips to allow penetration into the soil, or sugars exuded as subsidies to soil symbionts (Walker et al., 2003).

Leaf respiration was the second-largest respiratory component in this savanna, contributing about 10% to the TER. In Australian savannas, leaf respiration was estimated to be 9% of TER (Chen et al., 2003). These are surprisingly similar, even though there are important differences in structure and physiologies between African and Australian savannas (Lehmann et al., 2014). The particular Australian savanna reported has a low fraction of grass biomass, and the grasses are annual. The trees are dominated by the Myrtaceae, with a low leaf nitrogen content and high sclerophylly. The leaf respiration in the Australia case (Chen et al., 2003) was estimated using a general leaf equation from (Ryan, 1991b) while for Skukuza savanna I used a locally generated and parameterised model, based on measurements by (Kgope and Musil, 2004; Midgley et al., 2004).

There have been many studies of savanna fire ecology that quantify fuel load (Shea et al., 1996; Trollope and Potgieter, 1985; Ward et al., 2012) and fire return period (Govender et al., 2006). Though fires do not occur every year, averaged over time they contribute 3% to the TER at this site (Beringer et al., 2007).

The release of CO_2 by herbivores, by contrast, contributes only about 1% to the TER, despite this site being one of the great wildlife sanctuaries of Africa. Respiration by herbivores is of a similar order of magnitude to $R_{a,\ wood}$, and is thought to be slightly dominated by insects rather than large mammals (Scholes and Walker, 1993).

Ecosystem respiration in comparison with Net Primary Production

At the steady-state and in the absence of measurement error, TER = R_{eco} = NPP. This site is under primary vegetation and has been throughout the past 120 years of recorded history. That does not mean that it is undisturbed – apart from the droughts and fires every half-decade or so, the wildlife population is also variable in space, time and activity. In particular, the number of elephants has been increasing, particularly in this region, and as a result, the wood biomass has declined markedly at this site throughout observation (Archibald et al., 2009; Sankaran et al., 2005; Whyte, 2001). There are also numerous micro-disturbances resulting from burrowing animals (Moncrieff et al., 2008; Smit et al., 2010). Like other ecosystems, the Skukuza savanna is subject to climate change – temperatures have risen by nearly 2 °C for the record (since 1904), and CO_2 concentrations by about 60% since the pre-industrial period (Scholes et al., 2015). The long term NPP at this site (2016 – 2019) is estimated to be 2 333 ± 1 516 g $CO_2/m^2/y$. Long-term NEE measurements suggest that it is on average a small net source of CO_2 to the atmosphere (Archibald et al., 2009; A. Nickless et al., 2011). My findings rank the terms TER > NPP > R_{eco}, but with uncertainties such that the possibility that TER=NPP=R_{eco} cannot be excluded.

Conclusion

This study estimated the main respiration fluxes from an example of a semiarid African savanna, represented by the Skukuza flux site. The bottom-up estimates were on average about 42% larger than the top-down estimates for the chosen comparison period (2016-2019), but R_{eco} was in reasonable agreement with NPP estimates for this site. There is an element of circularity in that finding since their estimation is not independent. Approximately 84% of the respiratory flux comes from the soil, 10% from leaves, and 3% from fire. About 2% of Total Ecosystem Respiration at this site comes from woody tissues, and 1% comes from herbivores. The respiratory fluxes peak in the wet season between October and March. The site has been assessed to be a net carbon source, based on long-term NEE measurements (Archibald et al 2009). Based on the temperature sensitivity of most of the large respiratory fluxes, I predict that the landscape may become a larger source in future, as temperatures rise.

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Chapter 4: Overarching discussion and conclusions

This dissertation has successfully addressed both the aims laid out in chapter one. As a result, our understanding of respiration fluxes in savannas, and wood respiration, in particular, has been substantially improved, albeit from a low base.

The first aim, which was to quantify wood respiration from African savanna trees and relate it to species, size of tree, season and temperature, was addressed in chapter 2. This is the first known systematic measurement of wood respiration in African savannas, and only the second measurement in savannas worldwide, as far as I am aware. Using non-destructive methods, wood respiration was measured along with several factors that could be influencing it. It was expected that the wood respiration rate would increase with increasing temperatures, as it has been observed in other ecosystems, but it was not known exactly what form the relationship between respiration and temperature would take. I found evidence for an S-shaped relationship between wood respiration and temperature during the active season, declining somewhat at the highest temperatures, which is fundamentally different to the usual modelling assumption of an exponentially-increasing relationship (Davidson et al., 2006, p. 10). Wood respiration peaked at bark temperatures between 28 °C and 37 °C. During the dry, dormant season there was also an S-shaped curve, but with no apparent decline at very high temperatures. There are several plausible eco-physiological explanations for the observation of a plateau (and even a decline) in respiration at high temperatures, including denaturation of enzymes and failure of membranes. Alternatively, it could simply reflect a covariance between temperature and dehydration of the stem at high temperatures. The wood hydrature was not measured.

I also expected that species with a high proportion of sapwood, with a high nitrogen content and low wood density, to respire at greater rates than species with dense wood, low nitrogen contents and thin sapwood. The only clear relationship that emerged was with sapwood density, and the relationship was positive. Wood respiration was better predicted by sapwood volume than by bark surface area. I suggest this could be because sapwood contains xylem (the highly functional wood tissue) linked to maintenance respiration (Ryan, 1989). The other important finding was that wood respiration varies by season of the year, even after the effects of bark temperature were accounted for. The highest wood respiration rates, corrected for temperature, were observed during the middle of the growing season. A plausible explanation is that the tree is actively growing at that time, and this reflects growth respiration.

The fundamental and novel measurements of wood respiration reported in Chapter 2 were then contextualised in chapter 3, where the wood respiration model was used to upscale wood respiration to the whole landscape, for an entire year. This was done for the Skukuza flux site for the years 2016-2019. I also scaled up all other major respiratory CO_2 fluxes (R_{soil}, $R_{a, leaf}$, R_{fire}, $R_{h, insect}$, $R_{h, mammalian}$) to the landscape and year basis. The sum of all these fluxes (including $R_{a, wood}$) is the Total Ecosystem Respiration. R_{soil} contributed 84% (all the estimates are approximate and vary year to year), $R_{a, leaf}$ 10%, R_{fire} 3%, $R_{a, wood}$ 2%, and $R_{herbivores}$ 1% to the TER. The TER was compared to the R_{eco} as measured by EC for the period 2016-2019 and was found to be about 42% larger than R_{eco}. This suggests that I did not miss any major fluxes, but I might have overestimated some. Alternatively, and just as plausibly, R_{eco} has been underestimated. TER and R_{eco} are both within the 95% confidence interval of one another and have similar uncertainties, so it is not possible to say, based on the available data, which estimate is more correct.

The limitations and challenges faced while doing this research are as follows.

(1) Many assumptions have to be made regarding the carbon cycle, because of a general lack of research or measurements. For example; (1) ecosystem respiration is thought to have an exponential relationship with temperature (because many studies are conducted in cool to warm climates e.g. Edwards and Hanson, 1996; Lavigne and Ryan, 1997; Patterson et al., 2018), and this relation is used to extrapolate R_{eco} from nigh-time measurements to full-day measurements (2) Wood respiration is assumed to be the same for stems and branches, and that the base of the stem respires as much as the top, and leaf respiration is the same for different parts of the canopies (Araki et al., 2010; Asao et al., 2015).

(2) The number of observations, and their distribution through the year and across locations was adequate for an exploratory study, but leaves room for

further measurements – particularly of different species, and perhaps in relation to stem hydrature.

Some of the questions raised by this study include:

- Are undisturbed savannas carbon sinks, as is often assumed, helping to reduce the steadily-rising atmospheric CO_2, and if they are, will they continue to be?
- What is the more sensitive process contributing to productivity in savannas, respiration or photosynthesis?
- Is a bottom-up summation of fluxes more or less accurate than a top-down estimate, and how could the uncertainties in both be reduced?

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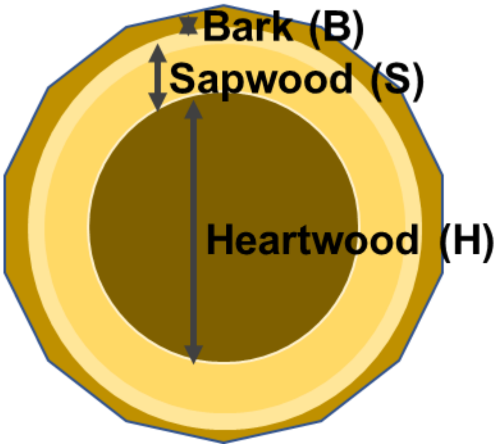
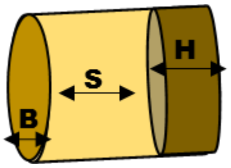
APPENDIX A

Sapwood volume under the chamber

Typical dimensions of a savanna tree

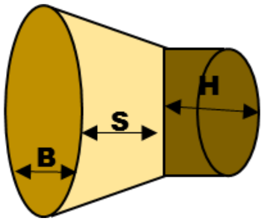


Method 1: Cylinder



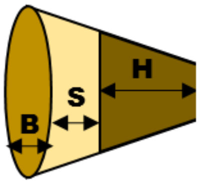
$$\boldsymbol{Sapwood\ volume} = Chamber\ surface\ Area \times Sapwood\ thickness$$

Method 2: Frustrum of a Nieloid



$$\begin{aligned}\boldsymbol{Sapwood\ volume} &\\ = \frac{sapwood\ thickness}{4} &\times (Chamber\ surface\ area \\ &+ \sqrt[3]{(Chamber\ surface\ area)^2 \times (final\ surface\ area)} \\ &+ \sqrt[3]{(Chamber\ surface\ area) \times (final\ surface\ area)^2} + final\ surface\ area)\end{aligned}$$

Method 3: Frustrum of a cone



$$\boldsymbol{Sapwood\ volume} = \frac{sapwood\ thickness}{3} \times \left(Chamber\ surface\ area + \sqrt{(Chamber\ surface\ area) \times (final\ surface\ area)} + final\ surface\ area\right)$$

Note:
Chamber surface area = Outer circular area under the chamber.
Final surface area = chamber surface area x (1 - sapwood thickness/tree radius)… the circular area before the start of heartwood

Management of errors, bias and outliers

There were some errors observed from field data collection which produced NANs and unexplainably high/low measurements. These were linked to factors such as; (1) bad weather (windy, rainy or scorching hot); (2) occasional equipment failure/shutdown (due to gas analyser overheating, high chamber humidity, batteries running out of energy, etc.); and (3) human error (exhaustion due to long field working hours, accidental/unintentional exhaling into the chamber before it completely closed, failure to ensure that the chamber is completely closed). All the missing data (i.e. NAs produced from these errors) could be interpolated using simple methods and R base functions and packages (e.g. kNN), but I chose to just delete the missing values (which were relatively few) and work with the raw data. This data was enough to produce sufficient degrees of freedom, but the dataset was also no perfectly longer balanced. This was taken care of by normalising and mixed-effects models.

Descriptive statistics

Year period: 2017 – 2019

Study sites (N=3): Kruger National Park (KNP), Nylsvley Nature Reserve (NNR) and Wits Rural Facility (WRF).

Seasons (N=4): Early dry, Late dry, Early wet, and Late wet.

Site	Species	Growth strategy	Diameter (m) Mean ± SD	Number of trees
KNP	*Combretum apiculatum*	Deciduous	0.38 ± 0.21	11
	Sclerocarya birrea	Deciduous	0.74 ± 0.40	14
	Senegalia nigrescens	Deciduous	0.80 ± 0.50	7
	Spirostachys africana	Semi-deciduous	0.36 ± 0.09	4
NNR	*Burkea africana*	Deciduous	0.42 ± 0.07	3
	Ochna pulchra	Deciduous	0.23 ± 0.03	3
	Strychnos pungens	Evergreen	0.27 ± 0.04	3
	Terminalia sericea	Deciduous	0.25 ± 0.12	3
WRF	*S. birrea*	Deciduous	1.13 ± 0.25	4
	T. sericea	Deciduous	0.54 ± 0.18	3
	Philenoptera violacea	Semi-deciduous	0.85 ± 0.32	3
	Vachelia nilotica	Deciduous	0.36 ± 0.14	3
				Total: 61

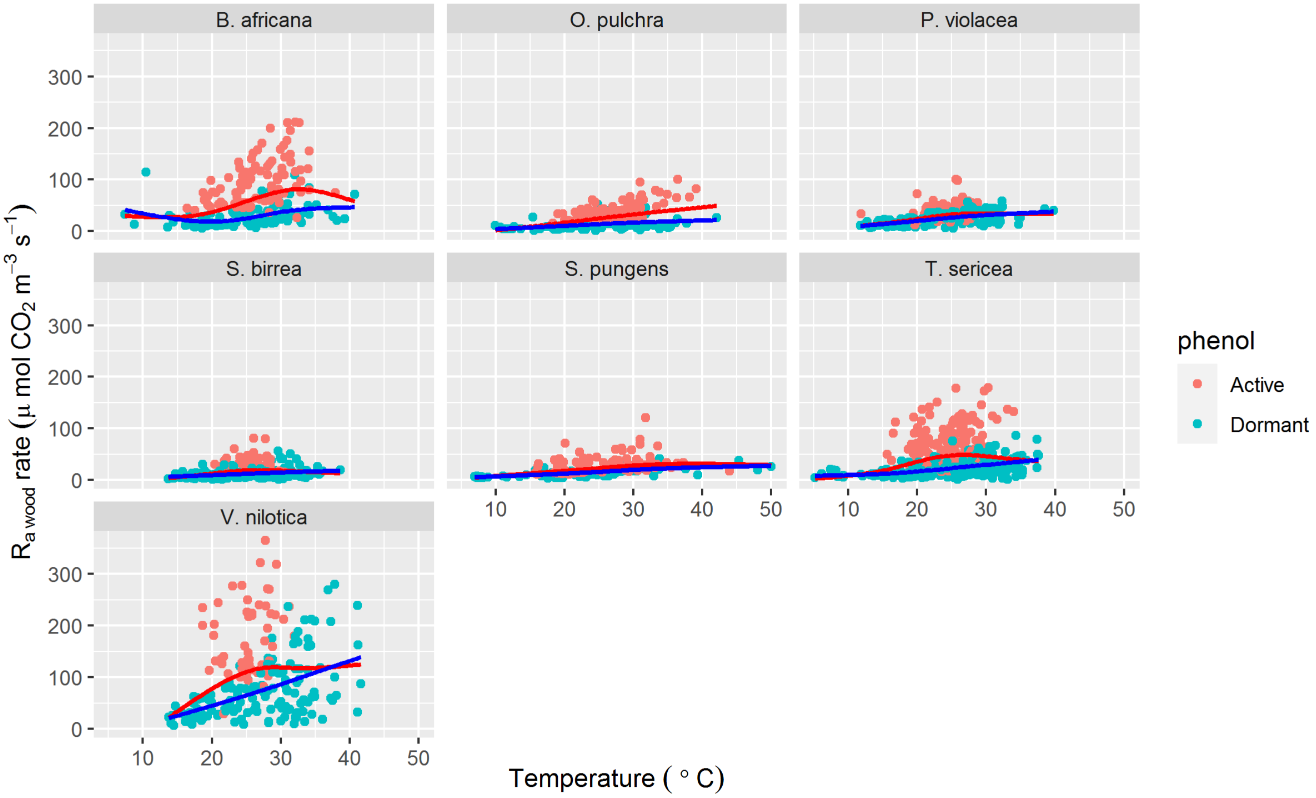
NOTE:
These species were chosen specifically because (1) are the dominant woody species in each study area (an important issue for upscaling measurements at a later stage; (2) they vary in wood densities and wood nitrogen contents; and (3) have different growth strategies (fast growers and slow growers). Diameter = mean ± standard deviation.

Species	Bark: Thickness (cm); Density (g/cm^3); Nitrogen (%)	Sapwood: Thickness (cm); Density (g/cm^3); Nitrogen (%)	Wood: Thickness (cm); Density (g/cm^3); Nitrogen (%)	Respiration (µmol CO_2/m^2/s)	Respiration (µmol CO_2/m^3/s)
	Means	Means	Means	Mean	Mean
C. apiculatum	0.39;0.56;0.49	3.18;1.07;0.23	3.57;1.01;0.72	1.34	57.75
S. birrea	1.41;0.68;0.25	11.83;0.67;0.26	13.23;0.67;0.51	1.69	17.19
S. nigrescens	0.85;0.56;1.61	3.22;0.84;0.36	4.10;0.78;1.96	1.54	48.21
S. africana	0.88;0.70;1.50	3.70;0.78;0.35	4.18;0.83;1.86	0.74	22.49
B. africana	0.80;0.67;1.34	4.70;0.77;0.62	5.50;0.74;1.95	2.57	60.14
O. pulchra	0.97;0.55;0.85	7.5;0.73;0.57	8.5;0.7;1.42	1.70	25.80
S. pungens	0.57;0.57;0.92	10.92;0.76;0.67	11.48;0.76;1.56	2.30	22.12
T. sericea	1.27,0.63;0.47	6.56;0.88;0.16	7.83;0.84;0.63	2.57	40.47
P. violacea	1.13;0.51;1.17	11.80;0.81;1.32	12.94;0.78;2.49	3.40	28.48
V. nilotica	1.20;0.50;0.87	2.93;0.99;0.22	4.12;0.85;1.09	2.98	102.45

Season	Species	Temperature (°C)	Respiration (µmol $CO_2/m^2/s$)	Respiration (µmol $CO_2/m^3/s$)
		Mean	Mean	Mean
Early dry	*C. apiculatum*	24.83	1.34	57.75
	S. birrea	25.54	1.18	15.39
	S. nigrescens	26.13	1.54	48.21
	S. africana	26.15	0.74	22.49
	B. africana	19.62	0.95	23.10
	O. pulchra	20.11	0.76	11.11
	S. pungens	17.97	1.28	11.48
	T. sericea	22.41	1.61	22.80
	P. violacea	23.81	3.34	28.09
	V. nilotica	26.38	2.48	88.68
Mean for the season:		24.27	1.57	31.60
Late dry	*S. birrea*	21.74	0.85	7.27
	B. africana	25.79	1.06	26.26
	O. pulchra	25.71	0.59	9.26
	S. pungens	24.78	1.48	14.48
	T. sericea	22.91	0.78	13.34
	P. violacea	19.77	1.35	11.46
	V. nilotica	22.84	0.61	21.94
Mean for the season:		23.45	0.94	14.52
Early wet	*S. birrea*	29.70	2.09	18.36
	B. africana	28.87	1.63	39.78
	O. pulchra	27.56	1.37	21.13
	S. pungens	28.81	2.13	19.66
	T. sericea	28.82	2.26	33.16
	P. violacea	27.76	3.53	29.53
	V. nilotica	30.59	2.55	91.37
Mean for the season:		28.88	2.30	36.36
Late wet	*S. birrea*	25.63	3.22	27.65
	B. africana	26.82	4.18	96.32
	O. pulchra	26.92	2.66	40.27
	S. pungens	25.78	3.09	30.22
	T. sericea	24.84	4.43	72.24
	P. violacea	24.18	4.73	39.36
	V. nilotica	25.45	5.05	177.46
Mean for the season:		25.69	3.85	65.59

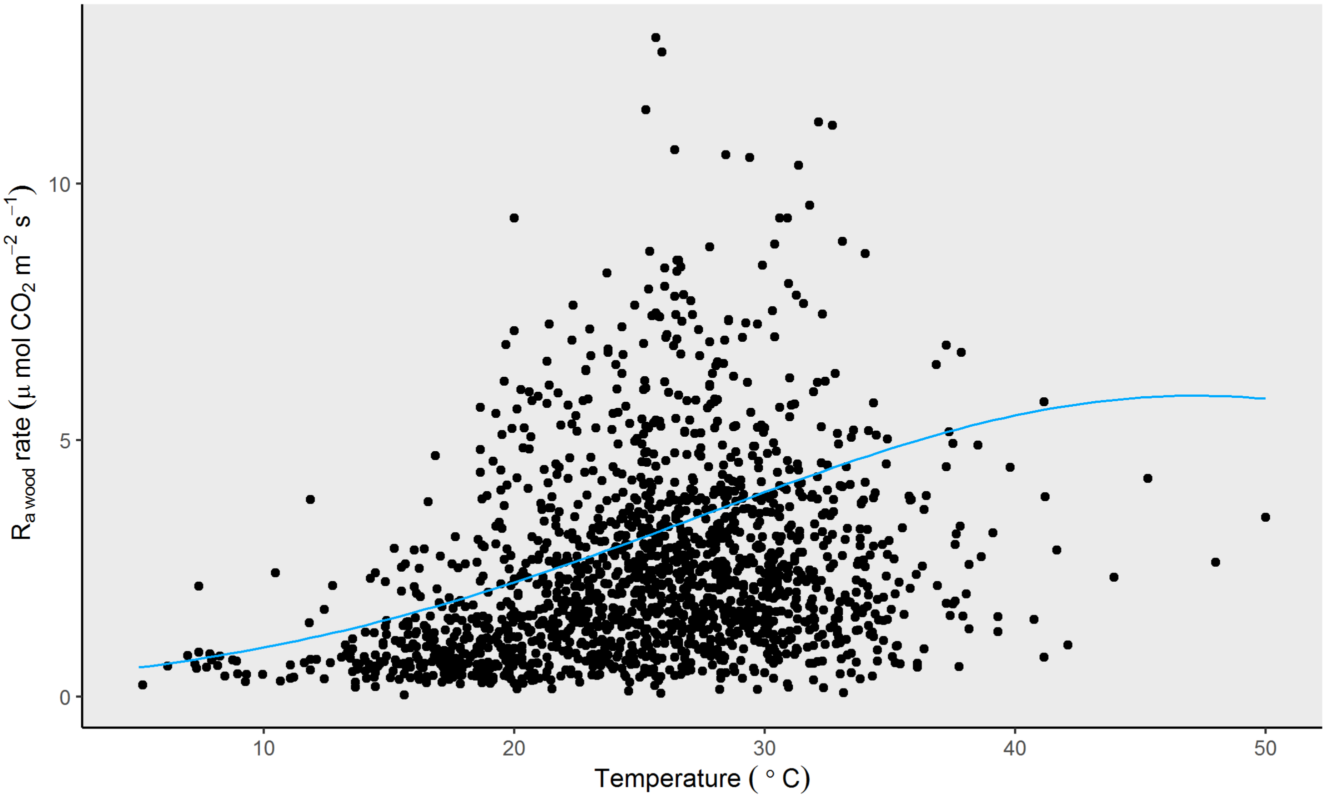
Supplementary materials

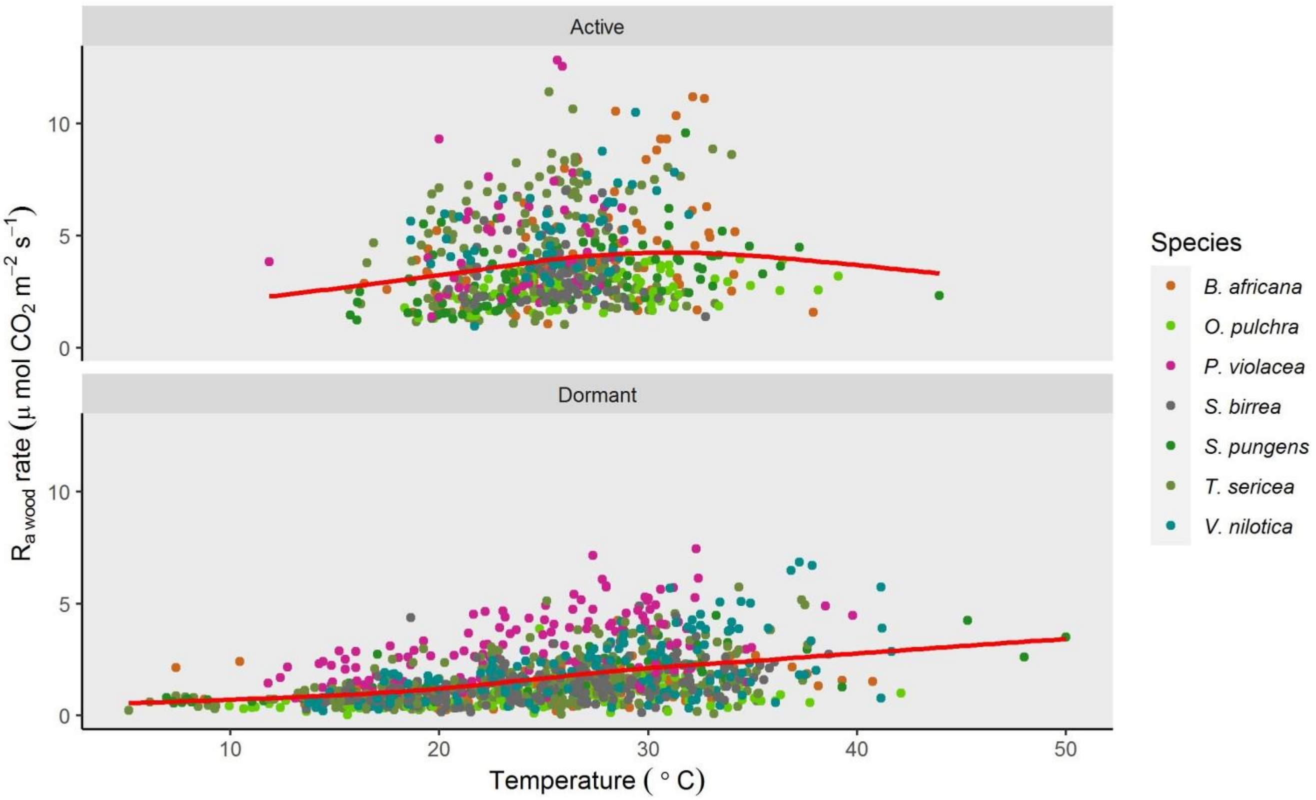
Results from the model of $R_{a,\ wood} = f$ sapwood volume

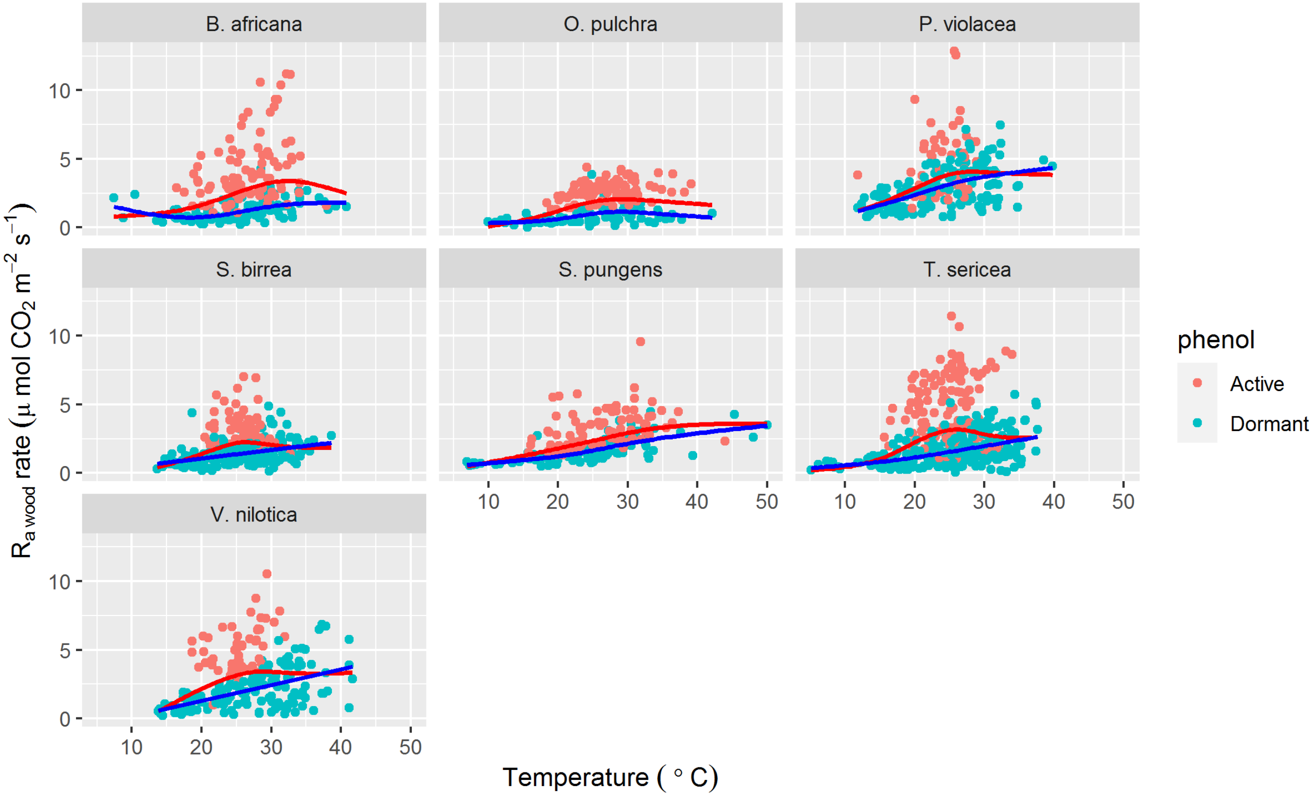


Results from the model of $R_{a,\ wood}$ = f surface area

The effect of temperature

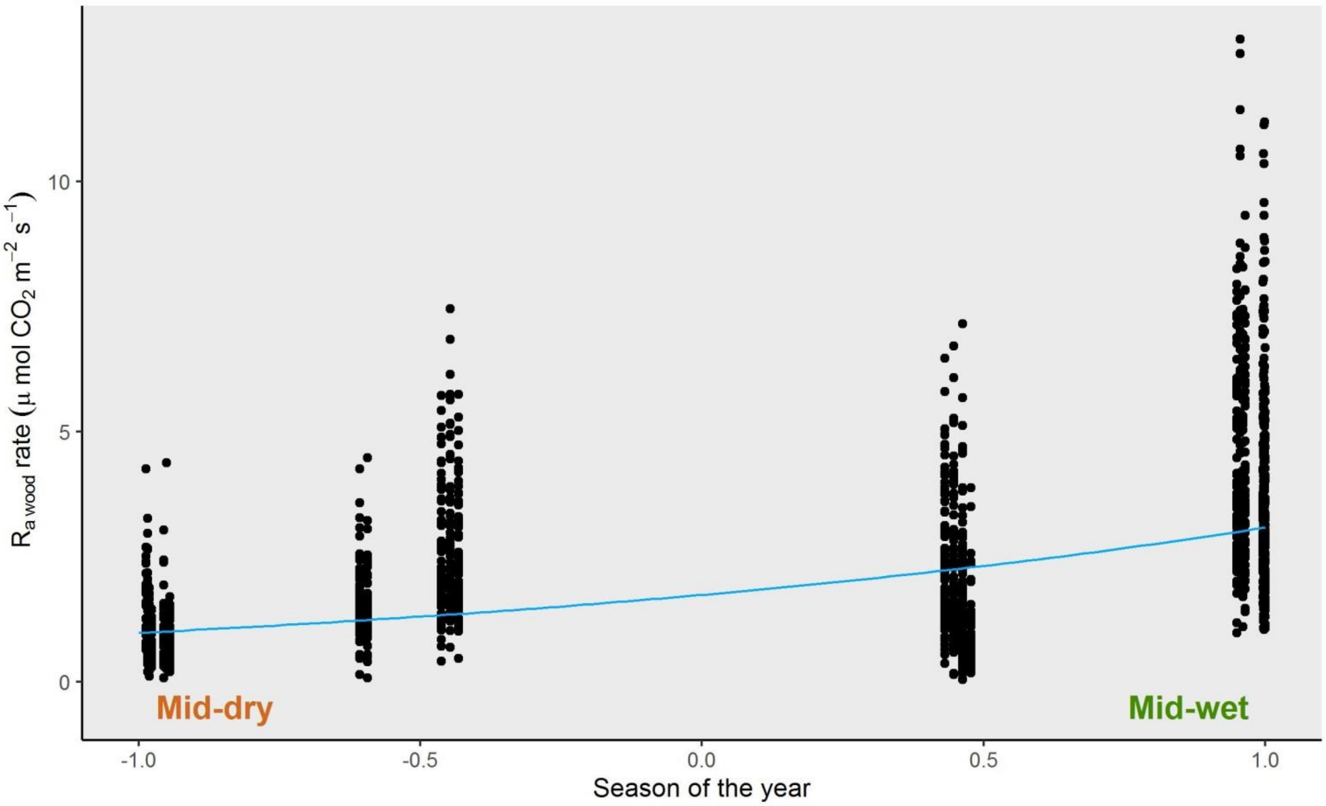


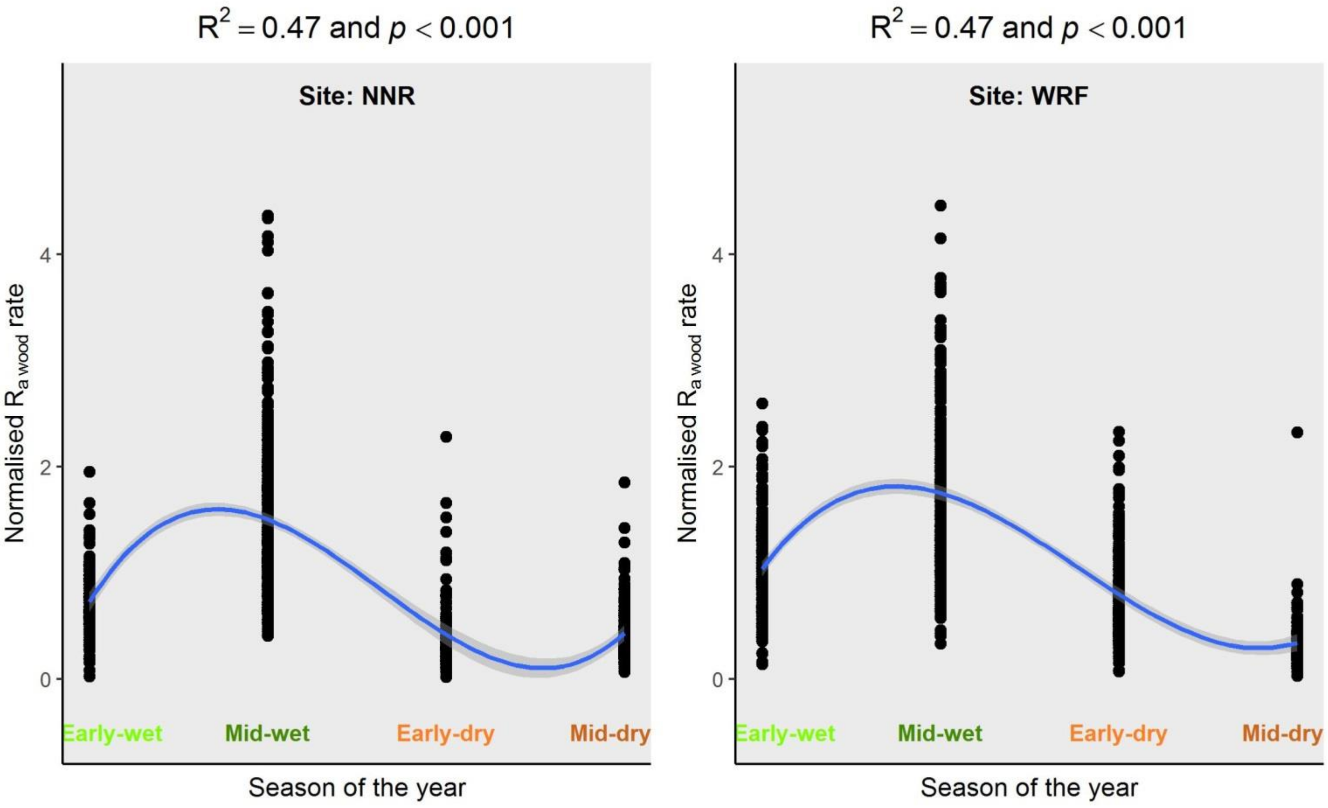

Active
Dormant
$R_{a\,wood}$ rate (μ mol CO$_2$ m^{-2} s^{-1})
0
5
10
0
5
10
10
20
30
40
50
Temperature (° C)
Species
B. africana
O. pulchra
P. violacea
S. birrea
S. pungens
T. sericea
V. nilotica


B. africana
O. pulchra
P. violacea
S. birrea
S. pungens
T. sericea
V. nilotica
10
5
0
10
20
30
40
50
$R_{a\,wood}$ rate (μ mol CO_2 m^{-2} s^{-1})
Temperature ($^\circ$ C)
phenol
Active
Dormant

The effects of season of the year

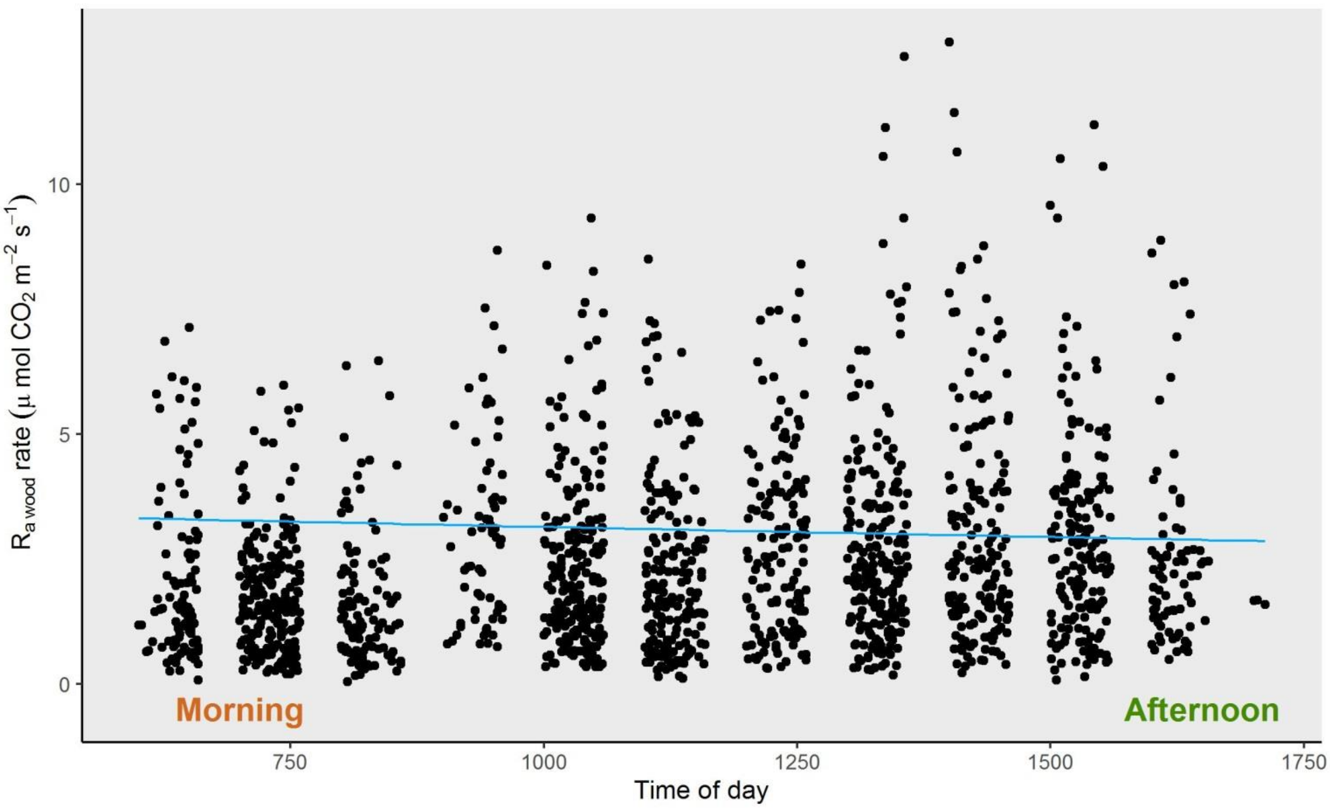
The effect of season of the year

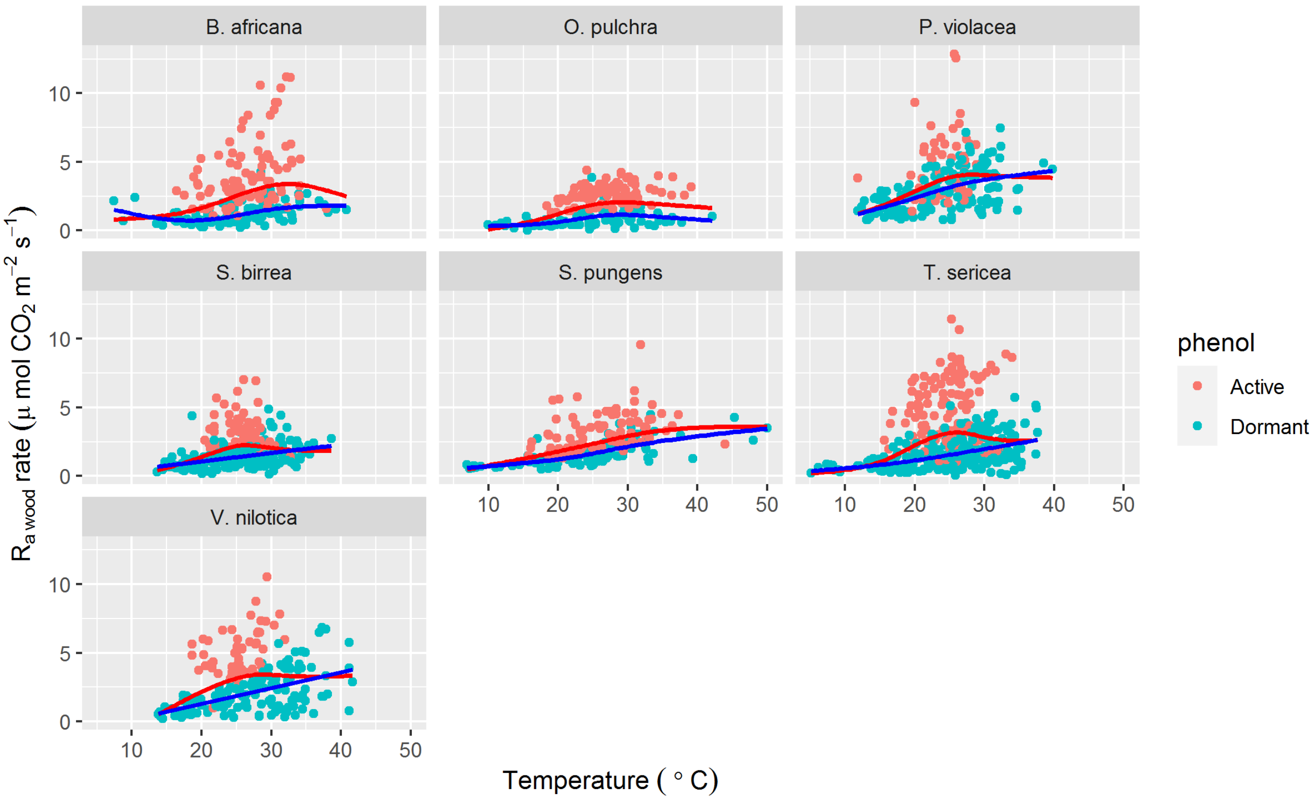


$R^2 = 0.47$ and $p < 0.001$
Site: NNR
$R^2 = 0.47$ and $p < 0.001$
Site: WRF
Normalised $R_{a\,wood}$ rate
0
2
4
Early-wet
Mid-wet
Early-dry
Mid-dry
Season of the year

The effects of time of day

The effect of time of day





Documentation of methods: R-markdown with code and notes

[Wood respiration analysis: Github]

[MSc Data]

APPENDIX B

Tree, bark, sapwood and heartwood volume

Thickness

1. *Combretum apiculatum*:

$$\text{Sapwood thickness}(\text{m}) = 0.0789 \times \text{Tree Diameter}(\text{m})^2 - 0.1314 \times \text{ Tree Diameter (m) } + 0.0694$$

$$\text{Bark thickness}(\text{cm}) = -1.7860 \times \text{Tree Diameter}(\text{m})^2 + 0.7781 \times \text{Tree Diameter}(\text{m}) + 0.4249$$

2. *Senegalia nigrescens*:

$$\text{Sapwood thickness}(\text{m}) = 0.00697 \times \text{Tree Diameter}(\text{m})^2 - 0.0217 \times \text{Tree Diameter}(\text{m}) + 0.0419$$

$$\text{Bark thickness}(\text{cm}) = 0.1674 \times \text{Tree Diameter}(\text{m})^2 + 0.9401 \times \text{Tree Diameter}(\text{m}) + 0.3159$$

3. *Sclerocarya birrea*:

$$\text{Sapwood thickness}(\text{m}) = -0.0860 * \text{Tree Diameter}(\text{m})^2 + 0.1201 * \text{Tree Diameter}(\text{m}) + 0.0658$$

$$\text{Bark thickness}(\text{cm}) = 0.0734 * \text{Tree Diameter}(\text{m})^2 + 0.4560 * \text{Tree Diameter}(\text{m}) + 0.6368$$

Mass and density

Species	Tree mass	Density
C. apiculatum	= -3.27 + 2.8 * ln(diameter(cm))	0.93
S. nigrescens	= -3.55 + 3.06 * ln(diameter(cm))	0.91
S. birrea	= -3.35+ 2.62 * ln(diameter(cm))	0.5

Mixed-effects model

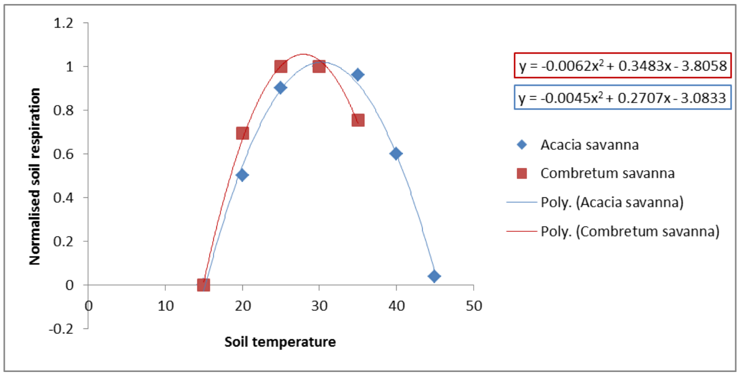
Species	Respiration
C. apiculatum	=exp(1.7595+0.12*stem temperature+0.5833*season-0.00013*time of day)
S. nigrescens	=exp(1.7303+0.12*stem temperature+0.5833*season-0.00013*time of day)
S. birrea	=exp(0.9171 +0.12*stem temperature+0.5833*season-0.00013*time of day)
Other species	=exp(1.11391+0.12*stem temperature+0.5833*season-0.00013*time of day)

Season: range from -1 (mid dry season) to + 1 (mid wet season), Time of day ranger from 0 to 2330.

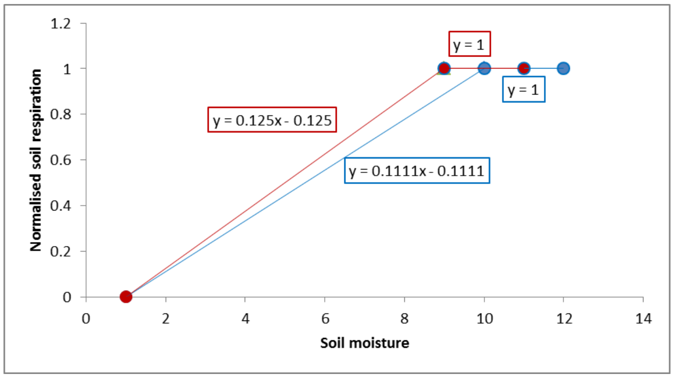
Stem temperature, soil temperature, soil moisture

Species	Stem temperature
C. apiculatum	=1.5301*air temperature-14.6792 (R^2 = 0.79)
S. nigrescens	=0.9238* air temperature +1.5114 (R^2 = 0.76)
S. birrea	=1.0044* air temperature -0.6185 (R^2 = 0.69)

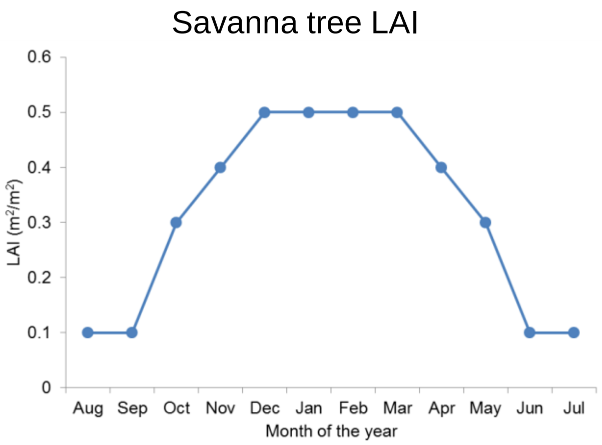
Soil temperature and normalised soil respiration

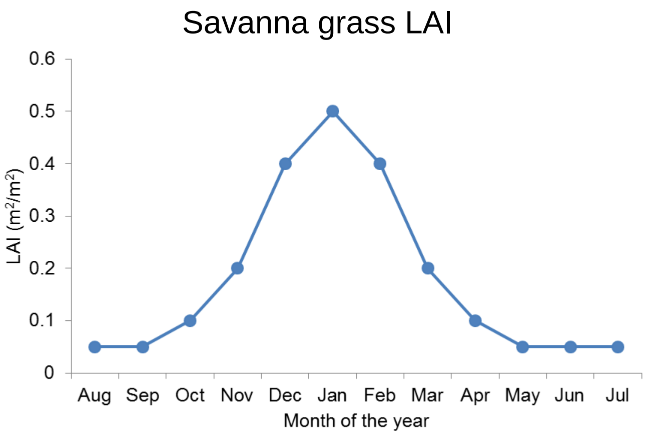


Soil moisture and normalised soil respiration



Leaf Area Index (LAI)





Leaf respiration

$$R_{leaf} = R_0 (Q_{10}{}^{\frac{T}{10}})$$

1. Fine-leafed savanna

$$R_{broad-leaf} = 0.19622213 \times (2^{(\frac{air\ temperature}{10})})$$

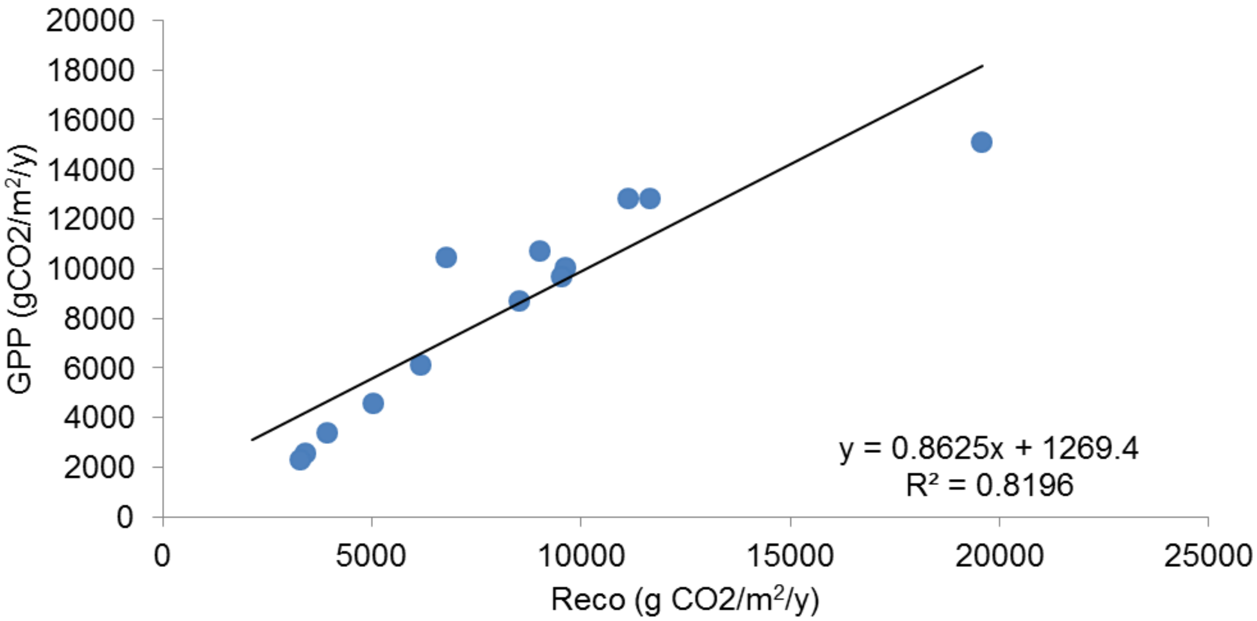
2. Broad-leafed savanna

$$R_{broad-leaf} = 0.040659 \times (2^{(\frac{air\ temperature}{10})})$$

3. Grass leaves

$$R_{broad-leaf} = 0.0864 \times (2.5^{(\frac{air\ temperature}{10})})$$

GPP



Link to all the data used in this research

MSc Data

Fluxnet data for the Skukuza tower