Differences in carbon sequestration and water use between a semi-arid native grassland and encroaching *Vachellia karroo* woodland

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Key words: Eddy covariance; woody plant encroachment; mass and energy fluxes; water use efficiency; drylands

Abstract

Tree and shrub encroachment and proliferation in global grasslands and savannas is widely considered to imply a trade-off between ecosystem C and H_2O regulating functions, based on the premise that increased C sequestration associated with higher woody biomass ostensibly drive declines in water production through concomitant increases in evapotranspiration (ET), but evidence for this across climatic and environmental gradients is equivocal. To evaluate these claims, we ran a paired eddy covariance experiment in a native semi-arid C4 grassland and adjacent encroaching *Vachellia karroo* woodland on the eastern seaboard of South Africa and compared ecosystem C and H_2O budgets over nearly a full year.

Near complete failure of spring/early summer rains resulted in reduced ecosystem physiological activity and C uptake in the early growing season in 2019, but systems recovered following above average rainfall over mid-summer/early autumn in 2020, with both the grassland and woodland achieving net negative C balances. The woodland was more productive than the grassland over the majority of the year, but these marginal C gains were offset by consistently higher respiration effluxes, resulting in the grassland sequestering significantly more C (197. 6 g C m^{-1}) than the woodland (114.5 g C m^{-1}). Differences in water use between the two systems were insignificant, and is likely explained by shallow soils and the absence of subsurface water at the site, which largely negated the competitive advantage in terms of access to water conferred by deeper rooting systems of *V. karroo*. Ecosystem water use efficiencies (WUE_E) were essentially identical across the year, but the grassland was more efficient at the peak of the growing season.

Our data suggest that encroachment by *V. karroo* in semi-arid grasslands may result in significant declines in C sequestration despite higher rates of productivity, but is unlikely to lead to substantial increases in water use where trees do not have access to water in deeper soil horizons on the other. These results support growing arguments to preserve semi-arid grassland ecosystems even when C sequestration is the primary objective of land management interventions.

Introduction

Large-scale reorganisation of terrestrial plant biota in the form of increasing dominance of trees and shrubs at the expense of grasses has been occurring throughout recent human history and has accelerated over the last circa 150 years in response to changing land management, biogeochemical, and climate drivers, which variously interact to shift competitive advantage between woody species and grasses over time (O'Connor et al., 2014). This process has been particularly rapid in drylands, defined as regions with an aridity index of < 0.65 and characterised by open ecosystems comprising a dynamic complex of woody C3 plant functional types and C4 grasses (Archer, 2002).

Woody encroachment and proliferation in these systems is widely considered to represent a potentially important global land C sink, but the data are equivocal, and suggest that the effects on C source/sink dynamics are mediated by a wide range of climatic and environmental variables, although the mechanisms are poorly understood and detailed accounting in many regions is lacking (Barger et al., 2011). Similarly, while extensive research has shown that increases in woody cover by exotic invasive plants and commercial forestry species may result in measurable declines in catchment water production through increases in water use linked to higher biomass, rooting depth, and phenology of trees (Le

Maitre et al., 2020), studies comparing the water use of indigenous woody species are sparse, and results at leaf to ecosystem scales often contradictory (Cavaleri & Sack, 2010).

In South Africa, approximately 10 % of the country's total land surface has experienced woody cover increases to varying degrees since the 1990s, with highest rates occurring in semi-arid and dry sub-humid grasslands and savannas with annual rainfall > 500 mm (Skowno, 2017). An estimated 75 % of the country's terrestrial C stocks reside in these systems, which combined account for just over 60 % of the land surface (National Terrestrial Carbon Sinks Assessment, 2020), and which are vulnerable to changes in vegetation structure that alter ecosystem C regulating functions. Similarly, woody cover increases in the country's strategic water producing upper catchments that displace original low biomass grassland and macchia-type Fynbos vegetation potentially imply important consequences for national water resources (Le Maitre et al., 2020). Identifying possible trade-offs in ecosystem C and water regulating functions accompanying woody encroachment in these systems is therefore of fundamental scientific and policy relevance.

Vachellia karroo Hayne (Fabaceae), a deep rooted nitrogen fixing legume, is one of the most prolific of approximately 40 identified encroaching species in South Africa, and is the dominant encroacher in the eastern and northern parts of the country (Skowno, 2017). We ran a paired eddy covariance experiment in a native semi-arid C4 grassland and adjacent encroaching *V. karroo* dominated woodland on the eastern seaboard of South Africa and compared ecosystem CO_2 and water budgets over a full year to evaluate potential trade-offs in C and water regulating functions linked to increases in woody cover in these systems.

Methods

The flux towers were installed on a commercial livestock ranch near the southern escarpment of the Amathole mountain range in the Eastern Cape province of South Africa (-32.742, 26.471; ~ 770 masl). The towers provide high frequency (10 Hz) measurements of mass (CO_2) and energy (sensible and latent heat) exchanges above vegetation canopies averaged over 30-minute intervals and integrated over footprint areas of several hectares. The flux sites are separated by a distance of 890 m on flat or gently undulating topography, with slopes over the footprint areas varying between 0 ° and 2.5 °. Soils are uniformly shallow (~ 1 m) and consist of a clay/loam complex above sandstones of the Beaufort Series. Mean annual precipitation is 730.4 (±158) mm, with cool dry winters (JJA) and hot summers (DJF). Rainfall is strongly seasonal, with ~70 % occurring over the austral spring and summer/early autumn months (October - March). Mean annual temperature is 17.7 (±3.2) ºC, with warmest temperatures in January (22.5 [±0.8] ºC) and coolest in July (13.2 [±1.5] ºC).

Vegetation at the grassland site is dominated by a variety of perennial C4 grass species with several dwarf shrub species in low abundances. *Vachellia karroo* canopy cover at the encroached site varies between ~ 20 - 40 % within the flux footprint with a mean canopy height of ~5 m. The herbaceous layer comprises largely continuous cover by a range of C4 grass and forb species. Historical aerial imagery indicates that most encroachment by *V. karroo* at this site has occurred since the 1990s.

Results and Discussion

Figure 1 shows the 7-day moving averages of daily C and H_2O fluxes over the study period. A full year of data was obtained at the grassland site from 1st September 2019 to 31st August 2020, although a power failure resulted in the loss of 44 days of data at the encroached site in the early growing season in 2019.

Near complete failure of spring/early summer rains in the early growing season in 2019 resulted in reduced physiological activity and C uptake at both sites over October to December, following initial upregulation of the systems in response to a series of rainfall events in late September/early October totalling 100 mm. GPP dominated the C flux at the grassland for several weeks following upregulation, resulting in a large amount of C uptake in late October/early November, but declined rapidly as declining soil moisture increasingly limited productivity from mid-November to the end of December. While the gap in the data precludes quantitative analysis for this period, available evidence suggests that the woodland functioned comparatively similarly in the early growing season.

Rainfall showed some recovery in January 2020, with 12 rain days totalling 160 mm. Respiration dominated ecosystem response to the onset of rainfall in this instance, with both sites switching to a large C source over this month. GPP showed a delayed response to rainfall, but dominated the C flux in both systems over the remainder of the growing season, with sustained net negative C balances in both systems until late June.

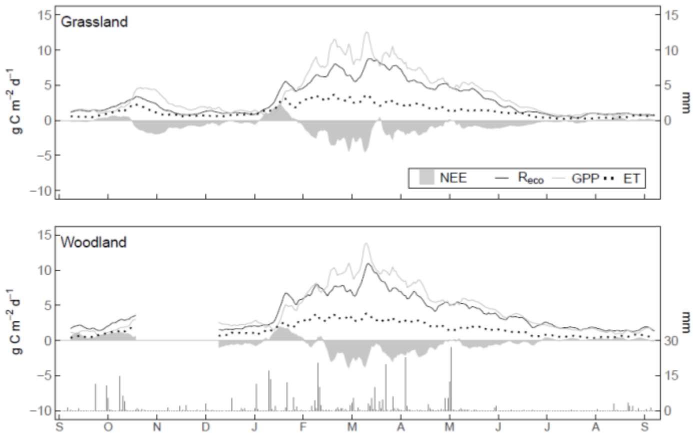

Figure 1: 7-day moving averages of daily C and H_2O fluxes relative to daily rainfall (bars).

The effects of relative differences between GPP and respiration fluxes on the net C balance are shown in Figure 2, where despite marginally higher total productivity at the encroached site, relatively larger total C losses in the latter resulted in significantly more C sequestered by the grassland over the 322 days of data availability at both sites (197.6 vs. 114.5 g C m^{-2} at the woodland); the complete annual C budget at the grassland by comparison was 248.1 g C m^{-2}.

Total water use over the 322 days was marginally higher at the encroached site (505.6 vs. 497.5 mm) and reflected differences in productivity (Figure 2). These marginal differences are likely explained by shallow soils and the lack of subsurface water at the site, which largely negates the competitive advantage of deeper rooting systems of *V. karroo* relative to grasses in terms of access to water. Ecosystem water use efficiency (WUE_E), expressed here as the ratio of daily GPP to ET, was almost identical over the 322 days, with the grassland assimilating 2.6 g C (kg H_2O)$^{-1}$ (R^2 = 0.75) relative to 2.7 g C (kg H_2O)$^{-1}$ (R^2 = 0.72) at the woodland (data not shown). Seasonal WUE_E values showed some variation however, with the grassland more efficient at the peak of the growing season (MAM), and the woodland more efficient in winter (JJA) (Figure 3).

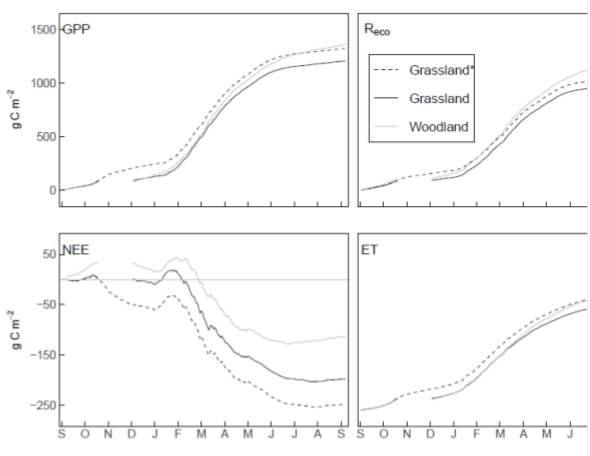

Figure 2: Cumulative totals of C and H_2O fluxes over 322 days at both sites (solid lines), and 366 days at the grassland site (dashed line, indicated by asterisk in legend).

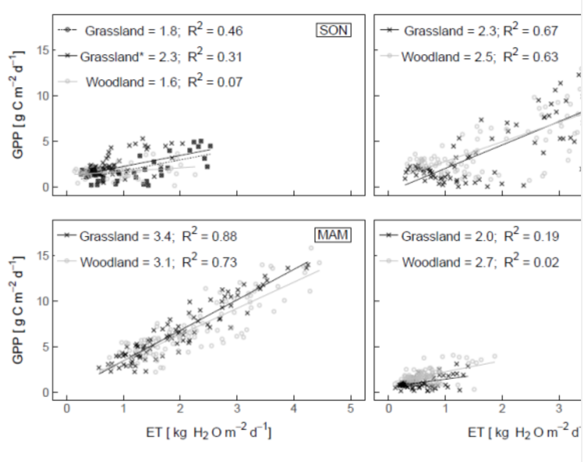

Figure 3: Scatterplots of seasonal WUEE; SON shows values for the full 91 days of data availability at the grassland in spring 2019 (indicated by asterisk in legend) as well as 47 days of data availability at both sites.

Conclusions and/or Implications

Our data suggest that encroachment by *V. karroo* in semi-arid grasslands may result in significant declines in C sequestration despite higher rates of productivity, but is unlikely to lead to substantial increases in water use where trees do not have access to water in deeper soil horizons on the other. Physiographic context and soil depth and physical properties, which largely determine runoff and drainage processes and the availability of subsurface water in tree/grass rooting zones, species functional traits, and tree-grass interactions that regulate subcanopy conditions likely play an important role in mediating these responses and may change under canopy cover thresholds that limit herbaceous understory growth. Efforts to partition C and evaporative fluxes to soil microbial and physical and plant physiological C3/C4 components would shed more light on these mechanisms.

Acknowledgements

Funding was provided by the National Research Foundation (NRF) through the Rated Scientist Incentive Programme, NRF SAEON, Rhodes University and Red Meat Research Development-SA.

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