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# C<sub>3</sub> perennial grass dominates mixed C<sub>3</sub>/C<sub>4</sub> grasslands after invasion by a C<sub>3</sub> woody sprouter

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**Key words:** *Prosopis*; *Nassella*; C<sub>3</sub> mid-grass; C<sub>4</sub> mid-grass; woody encroachment

## Abstract

Honey mesquite (*Prosopis glandulosa*) encroachment has resulted in decreased C<sub>4</sub> mid-grass production and increased C<sub>3</sub> mid-grass in the Southern Great Plains of the US. Woody legumes have had similar effects in Africa, Australia, and South America. *Prosopis* initially facilitates Texas wintergrass (*Nassella leucotricha*) growth under canopies, in part because N-fixation by this woody legume enriches subcanopy soils, favoring C<sub>3</sub> species. As stand density increases, *Nassella* extends into interspaces between trees as well. Here we report *Nassella* responses in several studies that either reduced *Prosopis* to indirectly impact *Nassella* or treated *Nassella* directly. In a 9-year study following mechanical top-kill of *Prosopis*, *Nassella* increased production for the first 3 years before slowly declining to pre-treatment levels. C<sub>4</sub> mid-grass production increased, but was limited to only a third of its potential by drought and *Prosopis* regrowth. Following a root-killing treatment of *Prosopis*, *Nassella* production and total herbaceous production were greater in treated than untreated intercanopy and subcanopy microsites 1-yr post-treatment. *Nassella* and perennial grass production declined in treated microsites 2-yrs post-treatment; however, total herbaceous production remained greater in treated than untreated microsites due to increased annual forb production. Targeted grazing reduced *Nassella* cover and reproduction, but increased bare ground. Multiple-stemmed *Prosopis* with low-hanging limbs protected *Nassella*, thus limiting targeted grazing success when trees were not removed. The *Prosopis*/*Nassella* state appears to be resistant to change and may permanently limit transition back to C<sub>4</sub> grassland unless *Prosopis* is root-killed, though our results indicate that even root-killing *Prosopis* does not guarantee an immediate increase in C<sub>4</sub> production. If so, managing *Prosopis* height and canopy cover, C:N ratios of the vegetative layer, and grazing *Nassella* during peak production and nutritional quality may allow profitable production until anthropogenic or natural processes result in large scale mortality of the *Prosopis* overstory.

## Introduction

Honey mesquite (*Prosopis glandulosa*; hereafter: *Prosopis*) is native to the Southern Great Plains (SGP), USA, but persisted in low densities prior to European settlement due to suppression by fire and competition from grasses (Van Auken 2000). *Prosopis* expansion throughout the SGP occurred through the exclusion of fire, overgrazing of grasses, and enhanced seed germination via cattle and wildlife endozoochory (Archer 1989, Ansley et al. 2017). Once *Prosopis* stand-level canopy cover exceeds 30%, C<sub>4</sub> mid-grass production severely declines (Ansley et al. 2004).

Texas wintergrass (*Nassella leucotricha*; hereafter: *Nassella*), a native C<sub>3</sub> perennial mid-grass, was thought to occur in small quantities in the C<sub>4</sub>-dominated grasslands characteristic of the region (Stubbendieck et al. 2017) but increased as *Prosopis* proliferated. *Nassella* responds more favourably to enhanced CO<sub>2</sub> levels and soil N than C<sub>4</sub> plants providing a competitive advantage under the canopies of leguminous trees today. It initially establishes under *Prosopis* canopies, then spreads to interspaces as *Prosopis* density increases (Simmons et al. 2008). It persists under woody canopies by maximizing photosynthesis and growth in early spring while *Prosopis* is leafless, and then enters dormancy during the summer when *Prosopis* is in full foliage (Teague et al. 2014). Therefore, it avoids competition with *Prosopis* for soil resources or light. In interspaces, C<sub>4</sub> mid-grasses have greater access to light but must compete with *Prosopis* lateral roots for soil moisture. There, N-fixation by the leguminous shrub may also favour C<sub>3</sub> plants (Ansley et al. 2014). C<sub>4</sub> short-grass roots primarily

occupy soil layers above where most *Prosopis* lateral roots reside. In dense stands of *Prosopis*, *Nassella* dominates the woody subcanopy and mixes with C<sub>4</sub>-grasses in the interspaces between trees.

We know very little about the stability of the *Prosopis/Nassella* association or the interactions of C<sub>3</sub> and C<sub>4</sub> grass species following *Prosopis* disturbance. Neither do we know much about *Nassella* responses to direct treatments designed to reduce its competitiveness with C<sub>4</sub> grass species. Disturbance-based state-and-transition models indicate that the *Prosopis/Nassella*-dominated state is reversible to a C<sub>4</sub>-dominated community after *Prosopis* elimination. Earlier studies supported this, but in some cases, possibly due to changes in C<sub>4</sub> grass propagule availability, increased *Prosopis* density, increased *Prosopis* and *Nassella* seedbanks, increased soil N availability, changes in depth of soil moisture penetration or seasonality of soil moisture availability, higher CO<sub>2</sub> levels, or a combination of these factors, the *Prosopis/Nassella* state seems more resilient and shifts to C<sub>4</sub>-dominated communities are more ephemeral when they occur. Such a phenomenon indicates that the *Prosopis/Nassella* association may now be a stable ecological state that is not reversible without significant changes in the processes and feedbacks driving the system. This paper provides information from a series of studies that, together, provide a systems-level examination of the biogeochemical relationships that determine the resilience of this state and may provide guidelines to manage these processes to facilitate transition to a more desirable community over time.

## Methods and Study Site

We examined the stability of the *Prosopis/Nassella* association in a series of three experiments in the SGP. Studies were conducted in north Texas, USA (34°01'52"N; 99°15'00"E; elevation 372 m). Mean annual precipitation is 710 mm and mean annual air temperature is 17.1°C. Soils are 1 to 2-m deep clay loams. The overstory is dominated by *Prosopis*. The herbaceous layer is comprised primarily of *Nassella* and the C<sub>4</sub> perennial short-grass, buffalograss (*Buchloe dactyloides*). C<sub>4</sub> perennial mid-grass species include sideoats grama (*Bouteloua curtipendula*), vine mesquite (*Hopia obtusa*), sand dropseed (*Sporobolus cryptandrus*), and Arizona cottontop (*Digitaria californica*).

The first experiment quantified perennial grass responses to a mechanical *Prosopis* top-killing treatment. Treatments, data collection procedures, and statistical analyses are outlined in Ansley et al. (2019). Briefly, grass production and basal cover were measured in top-killed and untreated *Prosopis* plots from 2007 – 2015. Since herbaceous species dynamics are related to *Prosopis* canopies, C<sub>3</sub> and C<sub>4</sub> grass responses were measured in intercanopy and subcanopy microsites.

The second experiment quantified grass and forb functional group productivity and soil N responses in subcanopy and intercanopy microsites for 2 years (2015 – 2016) after a root-killing aerial treatment with clopyralid-based herbicides (Ansley et al. in review). Four treated plots were paired with four adjacent untreated areas in a block design. Herbaceous clippings were collected in early summer (late May or June) and fall (late September or October), by functional group: C<sub>3</sub> mid-grasses, C<sub>3</sub> annual grasses, C<sub>4</sub> short-grasses, C<sub>4</sub> mid-grasses, perennial forbs, annual forbs, and litter. At those same times, subcanopy and intercanopy soil samples were collected at 0-15 and 15-30 cm depths for soil inorganic N and water-extractable organic N analyses via the Haney Soil Test procedure (Haney et al. 2010). A split block linear mixed-model was used to test effects of year, treatment, microsite, and their interactions on functional group production and soil N.

The third experiment examined *Nassella* responses to targeted grazing during peak cool-season growth (Hood 2019). Treatments included 1) ungrazed control, 2) one grazing period during February 2018, and 3) two grazing periods (February and late March 2018). All plots contained live, untreated *Prosopis*. Grazed treatments were stocked with cattle to approximately 33,600 kg live weight ha<sup>-1</sup> for 12 – 20 h to achieve a 5-cm grass stubble height in treated plots. We assessed herbaceous species coverage in January 2018 prior to treatment initiation, during *Nassella* reproduction (May) and dormancy (September), and again during the *Nassella* growing season (January 2019). In May 2018, *Nassella* reproductive tillers were separated from vegetative material to determine grazing effects on reproductive tiller density. For additional details about treatments, data collection procedures, and statistical analyses see Hood (2019).

## Results

### *Herbaceous Responses following Mechanical Top-kill of Prosopis*

*Nassella* production was 2 – 3 times greater in the top-kill than untreated intercanopy for three years after treatment (Ansley et al. 2019). Intercanopy C<sub>4</sub> mid-grass production increased in year 4 but severe drought stopped recovery in years 5 – 7. Recovery resumed in year 8, but by that time *Prosopis* regrowth was large enough to limit C<sub>4</sub> mid-grass production to a third of its potential. *Nassella* basal cover dominance remained

stable in untreated subcanopy microsites, even during drought. Following a brief decline in the top-kill subcanopy microsites, *Nassella* cover returned to pretreatment levels by year 8 as *Prosopis* regrowth increased to pretreatment levels. The *Prosopis/Nassella* association thus limited the window of C<sub>4</sub> mid-grass recovery to only a few years following *Prosopis* top-kill suppression.

#### ***Herbaceous and Soil Responses following Chemical Root-kill of Prosopis***

Perennial grass production and total herbaceous production were greater in treated than untreated subcanopy and intercanopy microsites 1-yr after *Prosopis* root-kill, due to increased *Nassella* production. *Nassella* and C<sub>4</sub> perennial grass production declined in treated microsites at 2-yrs post-treatment mainly because a spike in annual forb production replaced grass production. As a result, total herbaceous production remained greater in treated microsites than untreated microsites. Similar to the top-kill study, *Prosopis* treatment had no effect on C<sub>4</sub> short- or mid-grass production within the first few years post-treatment. Soil inorganic N increased from year 1 to year 2 in treated intercanopy and untreated and treated subcanopy. Correspondence analysis showed forb production was strongly linked to treated subcanopy, with weaker links to soil inorganic N and treated intercanopy in year 2.

#### ***Nassella Responses to Targeted Grazing***

Ungrazed *Nassella* cover was stable across all four measurement periods. In grazed-once and grazed-twice plots, *Nassella* cover was greatest in January 2018, prior to grazing initiation. By January 2019, *Nassella* cover decreased 65 and 62% in grazed-once and grazed-twice plots, respectively. From January 2018 to January 2019, bare ground increased 122 and 391% in the grazed-once and grazed-twice plots, respectively. *Nassella* in grazed-twice plots produced fewer reproductive tillers than the other treatments.

#### **Discussion and Conclusions**

Woody species facilitation of C<sub>3</sub> grass expansion in C<sub>4</sub>-dominated grasslands similar to the *Prosopis/Nassella* association discussed here, has been documented in other parts of Texas, the USA, and worldwide. Huisache (*Acacia farnesiana*) and Ashe juniper (*Juniperus ashei*) were associated with increased *Nassella* production in south and central Texas, respectively (Scifres et al. 1982, Fuhlendorf et al. 1997). In semi-arid rangelands of Argentina, Peruvian feathergrass (*Stipa ichu*) and Mexican feathergrass (*Nassella tenuissima*) were associated with *Prosopis* species in C<sub>3</sub>/C<sub>4</sub> mixed grasslands where C<sub>4</sub> grasses had previously been dominant (Rossi and Villagro 2003, Rauber et al. 2014). South African grass communities under sweet thorn (*Vachellia karroo*) became dominated by C<sub>3</sub> narrow-leaved turpentine grass (*Cymbopogon plurinodis*) to the exclusion of C<sub>4</sub> red grass (*Themeda triandra*) (Stuart-Hill and Tainton 1989). In Australia, Prober et al. (2005) reported that woodland understories became dominated with exotic C<sub>3</sub> annual grasses and the native C<sub>3</sub> perennial grass, snow tussock (*Poa sieberiana*).

Our first study demonstrated that a single top-killing event had little impact on the *Prosopis/Nassella* association to allow C<sub>4</sub> mid-grass recovery (Ansley et al. 2019). C<sub>4</sub> mid-grass production did not begin to replace *Nassella* until year 3 of the first study, and drought disrupted that trend. The second study suggests that root-killing *Prosopis* treatments need more than two years post-treatment for C<sub>4</sub> mid-grasses to respond. The combination of high rainfall in the fall of year 1, increased light to the soil surface following *Prosopis* root-kill, and increased soil inorganic N culminated in unexpected increased annual forb production in year 2. Results indicate that the *Prosopis/Nassella* association may even be resilient to root killing treatments if a flush of soil nitrogen and/or depleted seedbanks coincide with unusually wet seasonal rainfall immediately following treatment. The third study suggested that targeted grazing could be used to reduce *Nassella* dominance, but bare ground, rather than C<sub>4</sub> species, replaced *Nassella* in the single year of treatment.

Collectively, the three studies verify that pre-treatment spatial heterogeneity of herbaceous composition and soil N, caused by *Prosopis*, affect post-treatment herbaceous community dynamics and production. Study 2 revealed that even if there is an increase in *Nassella* production initially after treatment, under certain conditions the potential remains for forb production to replace C<sub>3</sub> grass production in subsequent years, although our study measured responses at only 1 and 2 years post-treatment. The longer-term study (study 1) found no difference in forb production between treated and untreated *Prosopis* sites during 9 post-treatment yrs. *Prosopis* suppression (i.e., top-kill) treatments that stimulate woody regrowth do not appear to be an effective means of reducing *Nassella* and restoring C<sub>4</sub> mid-grass dominance. Longer-term studies are needed to assess the merits of root-killing *Prosopis* treatments on this transition along with additional years of research on targeted grazing of *Nassella* following *Prosopis* root-killing treatments. Other management actions, such as augmenting the C<sub>4</sub> mid-grass seedbank and/or utilization of grass-specific, selective

herbicides may be needed to suppress *Nassella* production and enhance C<sub>4</sub> recruitment if the removal of *Prosopis* alone is not sufficient. The return to a C<sub>4</sub>-dominated community will be a long-term process, and persistent management that particularly favors C<sub>4</sub> mid-grasses or costly inputs will be needed to change the biological and ecological feedbacks that favored the *Prosopis/Nassella* state. Without putting the proper processes in place (e.g., seedbanks, improved C<sub>4</sub> reproduction and germination) to enable the response of C<sub>4</sub> grasses to *Prosopis* mortality, *Prosopis* root-kill alone may not guarantee a sustained shift back to C<sub>4</sub> grassland.

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