Hydraulic Responses of Shrubs and Grasses to Fire Frequency and Drought in a Tallgrass Prairie Experiencing Bush Encroachment

K. O'Keefe
University of Wyoming

R. Keen
Kansas State University

E. Tooley
Kansas State University

S. Bachle
Kansas State University

J. B. Nippert
Kansas State University

See next page for additional authors

This collection is currently under construction.

The XXIV International Grassland Congress / XI International Rangeland Congress (Sustainable Use of Grassland and Rangeland Resources for Improved Livelihoods) takes place virtually from October 25 through October 29, 2021.

Proceedings edited by the National Organizing Committee of 2021 IGC/IRC Congress
Published by the Kenya Agricultural and Livestock Research Organization

Presenter Information

K. O'Keefe, R. Keen, E. Tooley, S. Bachle, J. B. Nippert, and K. McCulloh

Hydraulic responses of shrubs and grasses to fire frequency and drought in a tallgrass prairie experiencing bush encroachment

O'Keefe, K[*‡]; Keen, R[†]; Tooley, E[†]; Bachle, S[†]; Nippert, JB[†]; McCulloh, K[‡]
* Department of Ecosystem Science & Management, University of Wyoming, Laramie, WY USA;
† Division of Biology, Kansas State University, Manhattan, KS USA
‡ Department of Botany, University of Wisconsin, Madison, WI USA

Key words: bush encroachment; drought; fire; tallgrass prairie; hydraulic traits

Abstract
The increase in abundance and density of woody plants in herbaceous ecosystems (i.e. bush encroachment) is occurring globally and is driven by reduced fire frequency, climate change, and the utilization of deeper, more reliable soil water by woody plants. Thus, a comprehensive understanding of the physiological processes through which woody and herbaceous plants use water will provide greater insight into the mechanisms of bush encroachment, as well as the trajectory of encroachment in a changing climate. Our objective was to assess how experimental changes in water availability and fire frequency impact belowground water-use traits in *Cornus drummondii*, the primary encroaching shrub within North American tallgrass prairies, and *Andropogon gerardii*, a dominant C_4 grass. Shelters that reduced precipitation by 50% (drought) and 0% (control) were built over mature shrubs growing in sites that were burned at 1-year and 4-year frequencies. We assessed the water transport capability of shrubs and grasses growing in each treatment by measuring the maximum hydraulic conductance (K_{max}) of entire root systems. We also assessed the vulnerability of shrub root segments to loss of hydraulic function by measuring the pressure at which 50% of the maximum hydraulic conductivity is lost (P_{50}). Grass and shrub roots had opposite responses to drought and these patterns varied with fire treatment. Grasses growing in drought plots had lower root K_{max} than control grasses. Conversely, root K_{max} did not differ significantly between treatments in shrubs. However, drought shrub roots were less vulnerable to water stress than control roots (P_{50}=-1.5 and -0.20 MPa, respectively). These results suggest that the ability of grass roots to use water declined with drought, while the ability of shrub roots to resist water stress increased with drought. Future work should investigate whether these drought responses are associated with altered root growth patterns.

Introduction
Bush encroachment, the increase in abundance and density of woody plants in herbaceous ecosystems, has occurred globally over the past century. This shift in land cover can have substantial impacts on the structure and functioning of grasslands and savannas, and previous work has shown that bush encroachment reduces vegetation diversity (Ratajczak et al. 2012), alters plant productivity (Knapp et al. 2008), reduces surface runoff and soil water recharge (Zou et al., 2018), and alters ecosystem-level water fluxes (Wang et al., 2010; Logan & Brunsell, 2015). Bush encroachment has been attributed to a variety of drivers including reduced fire frequency, increased grazing, and rising atmospheric CO_2 concentrations (Archer et al. 1995; Briggs et al. 2002). However, patterns and drivers of bush encroachment are often site-specific, which can complicate predictions of shifting grass-woody cover in different ecosystems. Predicting patterns and ecological consequences of bush encroachment is also complicated by an incomplete understanding of how woody and herbaceous species will function under future climate conditions. Improved predictions of future woody encroachment will therefore require a detailed understanding of the mechanisms facilitating the expansion of individual woody species in specific ecosystems, under both current and future climate conditions.

In the Great Plains region of North America, *Cornus drummondii* C.A. Mey. (roughleaf dogwood) is the primary shrub expanding across tallgrass prairie. *C. drummondii* is native to tallgrass prairie but has increased in abundance and distribution over the past several decades due to reduced fire frequency in the region (Briggs et al. 2002). When burned infrequently, this clonal shrub produces large "shrub islands" that limit herbaceous growth in their understory and consequently prevent fire from carrying through an individual (Ratajczak et al. 2011). Additionally, *C. drummondii* is deep-rooted and uses deep stored water throughout the growing season. Consistent use of deep water allows this shrub to maintain static physiological rates despite seasonal fluctuations in temperature and precipitation (Muench et al. 2016), and also results in substantially higher rates and amounts of water-use than for co-occurring shrubs and herbaceous species (O'Keefe et al. 2020). Thus, the reliance of *C. drummondii* on a stable water source that is inaccessible to many other neighbouring species may also contribute to its recent expansion across tallgrass prairie.

Water stored deep in the soil is typically recharged annually from winter precipitation (Ransom, 1998) and may become reduced over time as drought intensifies and/or utilisation by woody species increases with ongoing woody encroachment (Vero et al., 2017). If deep water stores do become reduced, *C. drummondii* may experience water-limitation that impacts its physiology, growth, and survival. Furthermore, if *C. drummondii* is more susceptible to drought than co-occurring C_4 grasses, the cover and expansion of this species may be more limited in a warmer, drier climate than current models predict. However, how *C. drummondii* will respond to drought is not yet characterized. Information regarding this species' susceptibility to drought will require a detailed investigation of the response of above- and below-ground hydraulic traits to experimental manipulations of precipitation

Our objective was to assess how experimental changes in water availability and fire frequency impact water-use traits in *C. drummondii* and *Andropogon gerardii* Vitman (big bluestem), a dominant C_4 grass. Specifically, we assessed the following questions: (1) How do fire frequency and drought impact belowground maximum hydraulic conductance (a metric of ease of water flow through a tissue)? (2) Does root maximum hydraulic conductance respond differently to fire frequency and drought between *C. drummondii* and *A. gerardii*? (3) Do fire frequency and drought impact the vulnerability of *C. drummondii* roots to loss of hydraulic function?

Methods and Study Site

Research was conducted during 2019 at the Konza Prairie Biological Station (KPBS), a Long Term Ecological Research (LTER) site located in the Flint Hills region of northeastern Kansas USA (39.1° N, 96.9° W). KPBS is a 3,487ha area of native tallgrass prairie that is divided into experimental watersheds, each of which receives various fire (burned every 1, 2, 4, or 20 years) and grazing (grazed by *Bison bison*, cattle, or ungrazed) treatment combinations. The landscape is generally dominated by a few C_4 grass species with many subdominant forb and shrub species (Smith and Knapp 2003). Frequent fire increases grass dominance, and infrequent fire promotes the expansion of native shrubs including *C. drummondii* (Ratajczak et al. 2011). This study was conducted in lowland locations of two ungrazed watersheds, one of which is burned every year and the other every 4 years. Rainout shelters were built in 2018 over mature *C. drummondii* growing with *A. gerardii* in each watershed. Seven shelters were built in each watershed, four of which reduced precipitation by 50% (drought) and three that did not reduce precipitation (control), resulting in 14 total shelters.

We measured maximum hydraulic conductance (K_{max}) in entire *C. drummondii* and *A. gerardii* root systems in August 2019. K_{max} is a metric of ease of water flow through a tissue with air bubbles that block water flow through water conducting cells (i.e. native embolisms) removed. Two clonal stems were measured on the same individual shrub per shelter and three individual grasses were measured per shelter. Each shrub stem or grass tiller was cut near the soil surface, attached to a high-pressure flow meter (HPFM), and root K_{max} was measured following Tyree et al. (1993) on a leaf area basis. We then analyzed differences in root conductance using a linear mixed effects model with species, fire treatment, and precipitation treatment as main effects, and shelter ID as a random effect.

We also assessed the vulnerability of individual *C. drummondii* roots to loss of function by measuring hydraulic vulnerability curves. *C. drummondii* roots were collected from each shelter and rehydrated in a 20 mmol KCl solution under a partial vacuum overnight. The following day, hydraulic conductivity was measured on fully hydrated samples using a hydrostatic pressure head. Hydraulic conductivity was then repeatedly measured as each sample was subjected to increasingly negative xylem pressures using the centrifuge method (Pockman et al. 1995). The pressure at which 50% of the maximum hydraulic conductivity was lost (P_{50}) was then calculated for all curves within each water treatment*fire treatment group.

Results

Maximum hydraulic conductance (K_{max}) varied among grass and shrub roots, as well as precipitation and fire treatments (Figure 1). *A. gerardii* had greater root K_{max} than *C. drummondii* ($p<0.05$), particularly in annually burned plots. Additionally, *A. gerardii* growing in the annually burned control plots had greater root K_{max} than annually burned grasses in the drought plots ($p<0.05$). Grasses growing in drought plots had lower root K_{max} than control grasses, particularly for 1-year burned plots. Conversely, root K_{max} was somewhat greater in drought shrubs compared to control shrubs for both burn treatments, but this trend was not significant ($p>0.05$). Shrub drought roots were also less vulnerable to water stress than control roots (P_{50}=-1.5 and -0.20 MPa, respectively). Shrub root vulnerability did not differ across fire treatments.

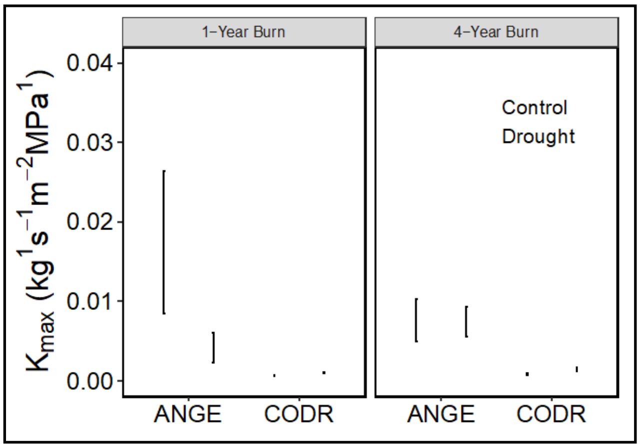

Figure 1. Maximum root conductance (K_{max}) measured in *A. gerardii* (ANGE) and *C. drummondii* (CODR) grown under control and drought conditions in 1-year and 4-year burned tallgrass prairie. Shown are the mean (± 1 SEM) for control (grey) and drought (black) treatments.

Discussion [Conclusions/Implications]

We show that *A. gerardii*, a dominant C_4 grass in tallgrass prairie, has greater root K_{max} than the encroaching shrub *C. drummondii* in an annually burned watershed. This result is unsurprising given that C_4 grasses have extensive, fibrous root systems in shallow soil that can efficiently utilize available water and outcompete co-occurring species (Kitchen et al. 2009; Ma et al. 2018; Xu et al. 2015). Additionally, frequent fire increases grass dominance (Hartnett et al. 1996; Collins and Calebrese 2012) and grass root biomass (Johnson and Matchett 2001), which may increase the overall efficiency of water uptake by grass root systems (i.e., promote the higher K_{max} that we observed in annually burned grassland). We also observed a significant decline in grass root K_{max} in our drought treatment, suggesting that the competitive ability of grasses to use water may decrease in a warmer, drier climate. If so, grass productivity may decline in the future with concomitant impacts on grassland biogeochemical cycling.

Conversely, *C. drummondii* root K_{max} did not differ between treatment contrasts. However, individual *C. drummondii* roots were less vulnerable to water stress when grown under drought compared to control conditions, which may be associated with shifts in root microanatomy in response to water limitation. Together, these results indicate that *C. drummondii* water use is not necessarily impacted by fire frequency but may be altered by future drought. Under future drought, *C. drummondii* will likely have root systems that will be more tolerant to low soil water availability.

These results are important because they suggest that the unique physiological responses of C_4 grasses and encroaching shrubs to drought may alter their functioning, competitive ability, and cover/distribution in a future climate. Grasses that exhibit lower root K_{max} under extended dry conditions may experience reduced aboveground growth and competition for belowground resources, which may ultimately reduce their presence in tallgrass prairie. Conversely, encroaching shrubs that exhibit reduced vulnerability to water stress may increase in cover and distribution in the future. Thus, *C. drummondii* physiology may facilitate its ongoing encroachment across tallgrass prairie in the Great Plains (O'Keefe et al. 2020). Future work should investigate whether these drought responses are associated with altered root growth patterns (e.g., root biomass and anatomical traits), and if these drought responses impact ecosystem processes in tallgrass prairie.

Acknowledgements

Funding was provided by the Department of Energy Terrestrial Ecosystem Science Award DESC0019037, the Division of Biology at Kansas State University, and the University of Wisconsin-Madison College of Letters and Science. The Konza Prairie Biological Station provided logistical support and the maintenance of the long-term fire and grazing treatments.

References

Archer, S., Schimel, D.S., and Holland, E.A. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? *Clim. change*, 29: 91-99.

Briggs, J.M., Knapp, A.K., and Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. *Am. Midl. Nat.,* 147: 287–294.

Collins, S.L., and Calabrese, L.B. 2012. Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *J. Veg. Sci.,* 23: 563-575.

Hartnett, D.C., Hickman, K.R., and Walter, L.E. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Rangel. Ecol. Manag.,* 49: 413-420.

Johnson, L.C., and Matchett, J.R. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology*, 82: 3377-3389.

Kitchen, D.J., Blair, J.M., and Callaham, M.A. 2009. Annual fire and mowing alter biomass, depth distribution, and C and N content of roots and soil in tallgrass prairie. *Plant Soil*, *32*: 235-247.

Knapp, A.K., Briggs, J.M., Collins, S.L., Archer, S.R., Bret-Harte, M.S., Ewers, B.E., et al. 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Glob. Chang. Biol.,* 14: 615–623.

Logan, K.E., and Brunsell, N.A. 2015. Influence of drought on growing season carbon and water cycling with changing land cover. *Agric. For. Meteorol.,* 213: 217-225.

Ma, Z., Guo, D., Xu, X., Lu, M., Bardgett, R.D., Eissenstat, D.M., McCormack, M.L. and Hedin, L.O. 2018. Evolutionary history resolves global organization of root functional traits. *Nature* 555.7694: 94-97.

Muench, A.T., O'Keefe, K., and Nippert, J.B. 2016. Comparative ecohydrology between *Cornus drummondii* and *Solidago canadensis* in upland tallgrass prairie. *Plant Ecol.,* 217: 267-276.

O'Keefe, K., Bell, D.M., McCulloh, K.A., and Nippert, J.B. 2020. Bridging the flux gap: Sap flow measurements reveal species-specific patterns of water use in a tallgrass prairie. *J. Geophys. Res. Biogeosci.*, 125: e2019JG005446.

Pockman WT, Sperry JS, O'Leary JW. 1995. Sustained and significant negative water pressure in xylem. *Nature* 378: 715–716.

Ransom, M.D., Rice, C.W., Todd, T.C., and Wehmueller, W.A. 1998. Soils and soil biota. In: Knapp, A.K., Briggs, J.M., Hartnett, D.C., and Collins, S.L., (eds.), *Grassland dynamics: long-term ecological research in tallgrass prairie* Oxford University Press, New York,. pp. 48-68.

Ratajczak, Z.R., Nippert, J.B., Hartman, J.C., and Ocheltree, T.W. 2011. Positive feedbacks amplify rates of woody encroaching in mesic tallgrass prairie. *Ecosphere,* 2: 121.

Ratajczak, Z.R., Nippert, J.B., and Collins, S.L. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, 93: 697-703.

Smith, M.D., and Knapp, A.K. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.,* 6: 509-517.

Tyree, M.T., Cochard, H., Cruiziat, P., Sinclair, B., and Ameglio, T. 1993. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant, Cell Environ*., 16: 879-882.

Vero, S.E., Macpherson, G.L., Sullivan, P.L., Brookfield, A.E., Nippert, J.B., Kirk, M.F., et al. 2017. Developing a conceptual framework of landscape and hydrology on tallgrass prairie: A critical zone approach. *Vadose Zone J.,* doi:10.2136/vzj2017.03.0069

Wang, L., Caylor, K.K., Villegas, J.C., Barron-Gafford, G.A., Breshears, D.D., and Huxman, T.E. 2010. Partitioning evapotranspiration across gradients of woody plant cover: assessment of a stable isotope technique. *Geophys. Res. Lett.,* 37: L09401.

Xu, X., David M., and Rodriguez-Iturbe, I. 2015. Relation between rainfall intensity and savanna tree abundance explained by water use strategies. *Proc. Natl. Acad. Sci*., 112.42: 12992-12996.

Zou, C.B., Twidwell, D., Bielski, C.H., Fogarty, D.T., Mittelstet, A.R., Starks, P.J., Will, R.E., Zhong, Y. and Acharya, B.S. 2018. Impact of Eastern Redcedar proliferation on water resources in the Great Plains USA – Current state of knowledge. *Water,* 10: 1768.