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RESEARCH PAPER

Photosynthetic performance of invasive *Pinus ponderosa* and *Juniperus virginiana* seedlings under gradual soil water depletion

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ABSTRACT

Changes in climate, land management and fire regime have contributed to woody species expansion into grasslands and savannas worldwide. In the USA, *Pinus ponderosa* P.&C. Lawson and *Juniperus virginiana* L. are expanding into semiarid grasslands of Nebraska and other regions of the Great Plains. We examined *P. ponderosa* and *J. virginiana* seedling response to soil water content, one of the most important limiting factors in semiarid grasslands, to provide insight into their success in the region. Photosynthesis, stomatal conductance, maximum photochemical efficiency of PSII, maximum carboxylation velocity, maximum rate of electron transport, stomatal limitation to photosynthesis, water potential, root-to-shoot ratio, and needle nitrogen content were followed under gradual soil water depletion for 40 days. *J. virginiana* maintained lower L_s, higher A, g_s, and initial F_v/F_m, and displayed a more gradual decline in V_{cmax} and J_{max} with increasing water deficit compared to *P. ponderosa*. *J. virginiana* also invested more in roots relative to shoots compared to *P. ponderosa*. F_v/F_m showed high PSII resistance to dehydration in both species. Photoinhibition was observed at ~30% of field capacity. Soil water content was a better predictor of A and g_s than Ψ, indicating that there are other growth factors controlling physiological processes under increased water stress. The two species followed different strategies to succeed in semiarid grasslands. *P. ponderosa* seedlings behaved like a drought-avoidant species with strong stomatal control, while *J. virginiana* was more of a drought-tolerant species, maintaining physiological activity at lower soil water content. Differences between the studied species and the ecological implications are discussed.

INTRODUCTION

The Nebraska Sandhills are the largest stabilized sand dune formation in the Western Hemisphere (50,000 km^2, Bleed & Flowerday 1998). Although the Sandhills are dominated by grasses and managed mainly as rangelands for livestock production, the area has been witnessing changes in vegetation cover, including a significant increase in woody species expansion (Fuhlendorf *et al.* 2008; McKinley & Blair 2008), especially eastern red cedar (*Juniperus virginiana* L.) and ponderosa pine (*Pinus ponderosa* P.&C. Lawson). *P. ponderosa* is a major forest type in the western USA (Sala *et al.* 2005), and has expanded into adjacent grasslands from historical grassland–woodland ecotones (Steinauer & Bragg 1987; Shinneman & Baker 1997). *J. virginiana* is the most widely distributed *Juniperus* species in the continental USA, and can be found in every state east of the 100th meridian (McKinley & Blair 2008). It is spreading and increasing in abundance and dominance throughout the Nebraska Sandhills (Schmidt & Stubbendieck 1993) and the Great Plains (McKinley & Blair 2008; Willson *et al.* 2008). *J. virginiana* was characterized by Schmidt & Stubbendieck (1993) as 'the most rapidly expanding woody species on rangelands in the Great Plains,' invading more than 20,000 ha of grasslands in western Nebraska in the last 10 years (US Forest Service), affecting approximately 7 million ha of grasslands in its western distribution of the eastern Great Plains (McKinley *et al.* 2008), and resulting in complete conversion to closed-canopy forests in as little as 40 years (Hoch 2000). Altered fire regimes (Bond *et al.* 2005; McKinley & Blair 2008), climate change (Bradley & Fleishman 2008), atmospheric nitrogen deposition, and changing land-use practices are implicated in the increased success of woody species over native grasses in semiarid grasslands in the USA and elsewhere (Scholes & Archer 1997; McCarron & Knapp 2001; Briggs *et al.* 2002; Fuhlendorf *et al.* 2008).

Soil moisture deficit has been reported to be one of the key factors limiting plant growth and ecosystem productivity worldwide (Chaves *et al.* 2003; Duursma *et al.* 2008), and is a key determinant of vegetation type, including relative abundance of grasses and woody species in semiarid grasslands like the Nebraska Sandhills (Huxman *et al.* 2005; Darrouzet-Nardi