Rangeland Ecology & Management 69 (2016) 206–214

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Compensatory Photosynthesis, Water-Use Efficiency, and Biomass Allocation of Defoliated Exotic and Native Bunchgrass Seedlings[☆]

Erik P. Hamerlynck [a,*], Brenda S. Smith [b], Roger L. Sheley [c], Tony J. Svejcar [d]

[a] Research Ecologist, U.S. Department of Agriculture (USDA)-Agricultural Research Service Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA
[b] Education/Outreach Project Coordinator, U.S. Department of Agriculture (USDA)-Agricultural Research Service Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA
[c] Weed Scientist, U.S. Department of Agriculture (USDA)-Agricultural Research Service Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA
[d] Research Leader, U.S. Department of Agriculture (USDA)-Agricultural Research Service Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA

ARTICLE INFO

Article history:
Received 14 September 2015
Received in revised form 14 December 2015
Accepted 30 December 2015
Available online 6 April 2016

Key Words:
bluebunch wheatgrass
crested wheatgrass
herbivory
photosynthesis
root-shoot ratios
sagebrush steppe

ABSTRACT

Compensatory increases in net photosynthetic assimilation rates (A_{net}) following herbivory are well documented in adult rangeland grasses but have not been quantified in bunchgrass seedlings, which may be more sensitive to tissue loss than established plants. To address this, we twice removed 30% and 70% leaf area of seedlings of crested wheatgrass (*Agropyron cristatum* [L.] Gaertn., var. Hycrest II) and the native bluebunch wheatgrass (*Psuedoroegnaria spicata* [Pursh] Á. Love, var Anatone) and compared A_{net} and aboveground and belowground growth of these to unclipped control plants. Compensatory A_{net} occurred only after the second clipping, roughly 1 month after the first, and was similar in magnitude and duration between species and treatments, ca. 26% higher than control plant A_{net} for 2 weeks following clipping. Despite similar compensatory A_{net} between species, increases in A_{net} were more proportional with increased stomatal conductance to water vapor (g_s) in crested wheatgrass. This resulted in higher intrinsic water use efficiency ($WUE_i = A_{net}/g_s$) integrated across the post-clipping recovery period compared with WUE_i of bluebunch seedlings, which declined with clipping. Differences in WUE_i were attributable to differences in root-to-shoot ratios and root tissue quality (specific root mass; g dry mass $\cdot$ m^{-2} root area), which were lower in crested wheatgrass. We concluded that compensatory photosynthesis is an important component of seedling herbivory tolerance, and that observed differences in post-herbivory WUE_i could help improve management strategies by informing seedling selection criteria to help develop methods aimed at minimizing impacts of herbivory during the seedling stage.

Published by Elsevier Inc. on behalf of The Society for Range Management.

Introduction

The stability and productivity of North American sagebrush steppe are threatened by increasing spread of invasive annual grasses, and establishing perennial grasses is the best long-term solution to restore fully degraded and invaded sagebrush steppe (Davies et al. 2010, 2011). Critical to the success of sagebrush steppe restoration efforts is a thorough understanding of seedling performance, especially perennial grass seedlings (James et al. 2011, 2012, and 2013). Seedling herbivory of native perennial bunchgrasses is a major impediment to their establishment in sagebrush steppe (Pyke 1986; Archer and Pyke 1991). Herbivory is prevalent throughout the plant life cycle and plays a critical role in determining trajectories of rangeland plant community dynamics (Crisp 1978; Oesterheld and Sala 1990; Milchunas et al., 1988, 1992; Augustine and McNaughton 1998; Maron and Crone 2006). Seedling herbivory can be fatal, as photosynthetic tissue loss makes maintaining the positive carbon balance needed to sustain seedling growth difficult to sustain, especially if parentally derived seed reserves are limited or fully exhausted (Fenner 1987; Hanley et al. 2004; Kitajima and Myers 2008). Quantifying seedling ecophysiological responses to environmental stresses, both biotic and abiotic, is a critical need for extending our understanding the role seedlings play in ecological and evolutionary processes (Parker et al. 2008), and such knowledge could improve our ability to restore degraded rangeland. Frameworks developed from large mammal grazing on adult plants (Heitschmidt and Taylor 1991) provide a scientific basis for developing hypotheses on seedling responses to herbivory. As seedlings gain in number of leaves and leaf area, their ability to survive defoliation, as in adult plants, depends upon how much and how frequently plant material is removed, and whether or not the plants can compensate for defoliation by increasing its photosynthetic rate (Heitschmidt and Taylor 1991).

The ability of established perennial bunchgrasses species in arid and semi-arid rangeland ecosystems to increase net photosynthetic assimilation rates (A_{net}) following defoliation is well documented (Caldwell et al. 1981; Painter and Detling 1981; Detling and Painter

---

[*] Correspondence: Erik Hamerlynck, USDA-ARS Eastern Oregon Agricultural Research Center, 67826-A, Highway 205, Burns, OR 97720, USA.
E-mail address: erik.hamerlynck@oregonstate.edu (E.P. Hamerlynck).

http://dx.doi.org/10.1016/j.rama.2015.12.007
1550-7424/ Published by Elsevier Inc. on behalf of The Society for Range Management.

1983; Nowak and Caldwell 1984; Wallace et al. 1984; Senock et al. 1991; Doescher et al. 1997; Zhao et al. 2008). At plant community and ecosystem scales, altered root-to-shoot ratios from grazing can enhance soil water availability (McNaughton 1983), and under such conditions, compensatory increases in A_{net} are usually concurrent with stomatal opening and higher stomatal conductance to water vapor (g_s) (Painter and Detling 1981; Detling and Painter 1983; Wallace et al. 1984; Doescher et al. 1997; but see Nowak and Caldwell 1986 and Senock et al., 1991); however, compensatory photosynthesis has not been found to originate from any direct improvement to plant water relations (Nowak and Caldwell 1984; Senock et al., 1991; Doescher et al. 1997). Other factors contributing to compensatory photosynthesis vary from enhanced light penetration through the canopy (Senock et al. 1991) to reallocation of resources to ungrazed tissue (Caldwell et al. 1981; Nowak and Caldwell 1984). In adult plants, compensatory A_{net} tends to be restricted to a relatively small proportion of active leaves; thus, its importance to overall total plant tolerance to herbivory is not as clear as those attained via reallocation of nutrient and energetic resources to ungrazed and newly produced tissue (Nowak and Caldwell 1984; Oesterheld and McNaughton 1988; Noy-Meir 1993; Ferraro and Oesterheld 2002; Mukherjee et al. 2015). However, because seedlings are as—if not more—likely to experience grazing but do not have the full suite of whole-plant mechanisms available to established adult plants to tolerate defoliation, the ability to perform compensatory A_{net} may be highly important in their ability to successfully grow and establish.

In woody species, many seedlings display compensatory photosynthetic activity similar to levels in adult plants after defoliation (Anten et al., 2003; Lovelock et al. 1999; Ozaki et al. 2004; Pepin et al. 2002) but for seedlings of semi-arid and aridland grass species, these responses have not been well documented. Nowak and Caldwell (1984) and Zhao et al. (2008) both found clipping stimulated A_{net} in the remaining tissue of established juvenile grasses. However, the postdefoliation responses of small emergent seedlings, the critical demographic phase in establishing stable perennial bunchgrass populations in semiarid rangelands (James et al. 2011, 2012, 2013; Gornish et al. 2015), is currently unknown. To address this, we performed a study quantifying the leaf-level gas exchange and plant growth responses of emergent seedlings of two perennial bunchgrass to defoliation; the exotic crested wheatgrass (*Agropyron cristatum* L. var. Hycrest II) and the native bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve, var. Anatone). Both species are cool season perennial bunchgrasses, are important components of sagebrush steppe communities, and are widely planted in sagebrush steppe restoration efforts (James et al. 2011, 2012). Well-established plants of both species are capable of increasing A_{net} in response to tissue loss (Caldwell et al. 1981; Nowak and Caldwell 1984; Doescher et al. 1997), though this is not always expressed (Nowak and Caldwell 1986). Adult plants also vary in their responses to grazing; crested wheatgrass allocates more resources to leaf growth following defoliation and produces less energetically costly tissue with low specific mass ($g \cdot m^{-2}$), especially in roots, compared with bluebunch wheatgrass (Jackson and Caldwell 1989; Meays et al. 2000; Leffler et al. 2013). The growth pattern in adult plants is similar to those in seedlings, where crested wheatgrass seedlings have more rapid overall growth, and produce more leaf area per unit root development, facilitating greater soil water extraction compared with bluebunch wheatgrass (Aguirre and Johnson 1991a, 1991b; Arredondo et al. 1998). In adult bunchgrasses, these characteristics are associated with high A_{net} and g_s, but at a cost of lower water-use efficiency (WUE) (Anderson and Toft 1993). On the basis of this information, we expected seedlings of both species would exhibit increased photosynthetic rates following tissue removal but that the exotic, crested wheatgrass, would show more marked compensatory response to defoliation and that this would result in lower intrinsic water-use efficiency (WUE_i; A_{net}/g_s) integrated over the postdefoliation recovery period.

Methods

This study was conducted from March 20 to July 31, 2014 in a plastic-covered hoop-house frame structure at the Eastern Oregon Agricultural Research Center (43°31′3.16″N, 119°1′19.37″W, 1 261.3 m ASL) located ca. 8.0 km SSE of Burns, OR. This facility is located in North American sagebrush steppe and experiences typical cold desert seasonal climate conditions. Mean annual precipitation is 278.4 mm, with the bulk of this (70.6%) distributed fairly evenly through the cool season (November to May), primarily in the form of rain, with occasional snowfall over the coldest months, and with some years having additional early (October) and/or late (June) rainfall. Mean annual temperature is 14.8°C, ranging from average daily maximums in July (28.7) to daily minimum of −7.1°C in January. Monthly average maximum temperatures over the plant active portion of our study were 12.1, 13.9, 18.9, and 24.0°C for March, April, May, and June, 2014, respectively, with corresponding and average minimum temperatures of −3.8, −1.8, 2.3, and 5.7°C, all close to long-term averages (9.5/−3.7, 13.8/−1.5, 18.8/2.4, and 23.9/5.3 max/min for March, April, May, and June, respectively) (NOAA NWS data, Western Regional Climate Center, http://www.wrcc.dri.edu). Both sides and one end wall of the hoop-house were left open over the duration of the experiment, with a fan programmed to aspirate the structure with outside air when temperatures reached 32°C, allowing interior temperatures to follow external ambient temperatures during the daylight period (data not shown). Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn., var Hycrest II) seeds were obtained from Maple Leaf Seed (Ephraim, UT; Lot 1480-BBHY0A) and bluebunch wheatgrass (*Psuedoroegnaria spicata* [Pursh] Á. Love, var. Anatone) seeds were obtained from Western Reclamation Inc. (Eltopia, WA; Lot 1406812); commercial source populations for both species are located in Washington state. Seeds were first pregerminated on moist blotting paper on a warming tray for 24−72 h, then ca. 10 germinated seeds were planted into pots (5.4 cm dia. × 10.8 h) containing a 50:50 mixture of native soils, consisting of a Gradon series gravelly fine sandy loam (collected from the Northern Great Basin Experimental Range, 16 km SE of Riley, OR, 43°27'58.37"N, 119°41'49.15"W), and a Dog Mountain series gravelly loam (collected 24 km S of Burns, OR, 43°21'36.15"N, 119°6'56.77"W) that had been uniformly mixed in a small portable cement mixer. Pot bottoms were covered with mesh to prevent soil loss, then filled with the mixed soil, and weights were recorded before and after watering to field capacity. Pots were kept uniformly moist until the grasses reached the two true-leaf stage when each pot was thinned to three plants of uniform height.

After thinning to three plants of even size, the first experimental defoliation (Clip 1) occurred on May 14, 2014 at the two-leaf stage. Eight pots for each species were assigned randomly into three clipping treatments: no defoliation (control), 30%, and 70% length of each leaf blade removed (total $n = 48$). Starting after the first clipping, volumetric soil moisture (θ) in half the pots was allowed to decline from 10% to 5% before rewatering, with the remaining pots kept near 10%, with θ measured daily with a Hydrosense time domain reflectometry (TDR) soil moisture probe (Campbell Scientific, Logan, UT). The purpose of these two watering treatments was to realistically vary soil moisture and induce a dynamic range of photosynthetic gas exchange across the duration of the experiment, not to assess the effects of soil water deficit on plant ecophysiological performance. Approximately 4 weeks after the first clipping, half of the 30% and 70% clipped plants were clipped again at the same removal levels (Clip 2; June 12, 2014).

Photosynthetic gas exchange was measured on intact, healthy leaves of a single individual for each species and clipping treatment using a portable photosynthesis system (LI-COR 6400, LI-COR Biosciences, Lincoln, NE). Light was provided by an opaque red/blue LED attached to the upper half of the leaf cuvette. Photosynthetic photon flux density (PPFD) was set to 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, as measured with an internal gallium arsenide photodiode, with this matching typical high PPFD in the greenhouse measured with a leveled silicon photodiode attached