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



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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 (*Psuedoroegneria 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 · 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.

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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; Oosterheld 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

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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 (*Pseudoroegneria 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 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, as measured with an internal gallium arsenide photodiode, with this matching typical high PPFD in the greenhouse measured with a leveled silicon photodiode attached

to the exterior of the cuvette. Leaf temperature was measured with a fine-wire type-T (copper/constantan) thermocouple pressed to the underside of the leaf. The temperature of the block housing the reference and sample infrared gas analyzers (IRGAs) was maintained at 25°C with a Pelletier heat exchange system attached to the block exterior. Bulk flow rate through the system was set to 200 mL · s⁻¹; with this block temperature control and flow rate, cuvette conditions ranged between 25% and 48% relative humidity, with leaf temperatures ranging from 17° to 29°C, and leaf-to-atmosphere vapor pressure deficit (VPD_l) from 1.1 to 3.0 kPa. Reference cell [CO₂] was set to 400 ppm, with sample cell [CO₂] departing from this depending on leaf photosynthetic CO₂ uptake. Before enclosing in the cuvette, leaf area (cm²) was calculated by measuring the length and width of each leaf enclosed in the cuvette. Leaf area corrected net photosynthetic assimilation rate (A_{net} ; $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and stomatal conductance to water vapor (g_s ; $\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) were calculated and logged by the system software after the summed coefficients of variation (CV) of [CO₂], [H₂O], and flow rate regressed against time was less than 1.0%. Gas exchange was measured over five time periods for both Clip 1 and Clip 2: preclip (1–2 days prior) and +1, +4, +10, and +17 days following tissue removal. Care was taken following Clip 1 to ensure only leaves that had been clipped were sampled, as marked tillering and new leaf production occurred between the 17th and 24th days following tissue removal.

Split-plot repeated-measures analysis of variance (split-plot RM-ANOVA) was used to test for differences in A_{net} responses to clipping in crested and bluebunch wheatgrasses across the two post-clip sampling periods (Statistix v8.0, Analytical Software, Tallahassee, FL). Species was the whole-plot between-treatment factor, with the species-by-replicate interaction as the F-test error term. The subplot, within-species factors were clipping (control, 30% and 70%), five sampling periods (pre, +1, +4, +10, and +17 days after clipping), and all two-way and three-way interaction effects, using the species-by-clipping-by-period-by-replicate interaction effect as the subplot F-test error term. Separate RM-ANOVAs were run for the first and second clipping; of specific interest were the species-by-clipping and species-by-clipping-by-period interactions; the first interaction would test for species-specific responses to clipping, the second for temporal differences in species-specific responses to clipping. General linear contrasts (Scheffe's F, Statistix v8.0) were used to test for specific pairwise comparisons that may underlie any significant interaction effects. To determine intrinsic water use efficiency (WUE_i), we regressed A_{net} against g_s across for each clipping/species combination over each sampling period (linear regression, Statistix v8.0), with the obtained slope used to determine WUE_i. First, species comparisons pooled across all clipping treatments were made by testing differences in fitted slopes using an F-test (Statistix v8.0), then testing for differences in slopes of different clipping treatments within species. If the clipping treatment slopes were found to differ, we performed pair-wise slope comparisons via Tukey HSD, with a critical q value of 3.35 ($P < 0.05$), using the more conservative pair-wise specific standard error rather than the more liberal pooled standard error estimation to calculate q (Zar 1974).

On July 8, 2014, after the final set of gas exchange measurements were completed, all plants were removed from the pots and roots were washed to remove soil. Total number of tillers was recorded, and then the aboveground and belowground portions were separated for each pot. Aboveground and belowground portions were subsequently kept refrigerated and hydrated before scanning on a flat-bed scanner, with the resulting images analyzed using WinRHIZO software (WinRHIZO v.2005, Regent Instruments, Inc, Quebec City, Quebec, Canada), which calculated total projected areas (cm²) of culms and leaves for each pot, which were then combined and divided by three to estimate average per plant photosynthetic area. The software calculated total projected root cylindrical area (cm²) from total root lengths and diameters of different root size classes it automatically generated for each scanned pot; this total root area was divided by three to estimate average per plant root areas. Following scanning, plant material was dried at 65°C

for 48 hours for estimation of specific mass ($\text{g} \cdot \text{m}^{-2}$) of leaf, culm, and roots, as well as to determine root-to-shoot ratios on a per-mass basis and per-area basis. Two-way ANOVA was used to test for differences in all growth and allocation parameters between species, clipping treatment, and the species-by-clipping interaction, using least significant difference (LSD) for post-hoc α -adjusted pairwise means testing; all ratio and proportional data (specific mass, root-to-shoot ratios) were log- and arcsine-transformed to meet ANOVA data distribution assumptions.

Results

The first clipping treatment did not induce any significant compensatory A_{net} response, with no clipping or clip-by-time interaction, though there was a species-by-time interaction (Table 1). This was due to crested wheatgrass having significantly higher A_{net} rates ($21.1 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 1.14 \text{ SE}$) for the preclipping sampling compared with rates attained by bluebunch wheatgrass ($16.1 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 1.33 \text{ SE}$; Scheffe's $F = 3.19$; $P = 0.02$). Over the first postclipping period, there were no differences between species A_{net} pooled across clipping treatments on any sampling date (Fig. 1a). The significant time period effect over this sampling period (see Table 1) was due to declines in A_{net} from preclipping to day 17 (Fig. 1a, b), most likely due to the effects of the variable watering regimen imposed on half the seedlings (data not shown). For second clipping sampling period 1 month later, there was evidence of compensatory photosynthesis, with significant clipping, period, and clip-by-period interaction effects to A_{net} (see Table 1). Photosynthetic compensation was not species specific, as there was no significant species, species-by-clipping, or species-by-clipping-by-period interactions (see Table 1). Pooled across both species, A_{net} in plants with 30% clipping ($15.9 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 0.71 \text{ SE}$) and 70% tissue removal ($15.8 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 0.66 \text{ SE}$) did not differ significantly (Scheffe's $F = 2.83$; $P = 0.07$), with these A_{net} rates significantly higher than those of control plants ($12.6 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 0.48 \text{ SE}$; Scheffe's $F = 26.5$; $P < 0.001$). The time period effect was due to similar A_{net} in plants over the preclipping ($11.4 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 0.60$) and 1 day postclipping ($11.9 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 0.61 \text{ SE}$; Scheffe's $F = 0.1$; $P = 0.98$); A_{net} over these two periods were significantly lower than higher A_{net} attained 4 days ($19.0 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 0.86 \text{ SE}$) and 10 days ($17.8 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 0.86 \text{ SE}$) following clipping (Scheffe's $F = 300.39$; $P < 0.001$). Seventeen days after clipping, A_{net} declined to rates similar to those on the pre- and 1-day samplings ($13.7 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 0.56$; Scheffe's $F = 2.16$; $P = 0.09$). The clipping-by-period interaction was in part due to varying clipping treatment effects within specific sampling dates; for instance, 4 days after clipping, the 70% clipped plants A_{net} ($22.4 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 1.32$) and 30% clipped plant A_{net} ($21.0 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 0.72$) were similar (Scheffe's $F = 0.13$; $P = 1.00$), but 10 days after clipping, A_{net} in 30% clipped plants ($20.8 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 1.89 \text{ SE}$) was significantly higher than rates attained in 70% clipped plants ($18.5 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} + 1.16 \text{ SE}$; Scheffe $F = 5.16$; $P = 0.001$; Fig. 1c, d). In addition, there were clipping-treatment specific differences between sampling dates; in

Table 1

Repeated-measures analysis of variance F-test results comparing leaf-level net photosynthetic assimilation rates (A_{net}) of crested wheatgrass and bluebunch wheatgrass seedlings before (preclipping) and after (+1, +4, +10, and +17 days) experimental defoliation (0%, 30%, and 70% clipping) on May 14 (first clipping) and June 12, 2014 (second clipping). Degrees freedom for each F-test are presented parenthetically; bold F-test results are significant at $P < 0.05$.

| Effect | 1st Clipping | 2nd Clipping |
|--|--------------------|--------------------|
| Species _(1,14) (Spp) | 0.68 ^{ns} | 0.07 ^{ns} |
| Clip percent _(2,195) (Clip) | 0.10 ^{ns} | 11.50 |
| Sample period _(4,195) (Per) | 17.92 | 24.61 |
| Spp × Clip _(2,195) | 0.16 ^{ns} | 2.05 ^{ns} |
| Spp × Per _(4,195) | 3.56 | 1.19 ^{ns} |
| Clip × Per _(8,195) | 0.61 ^{ns} | 3.72 |
| Spp × Clip × Per _(8,195) | 0.68 ^{ns} | 1.00 ^{ns} |

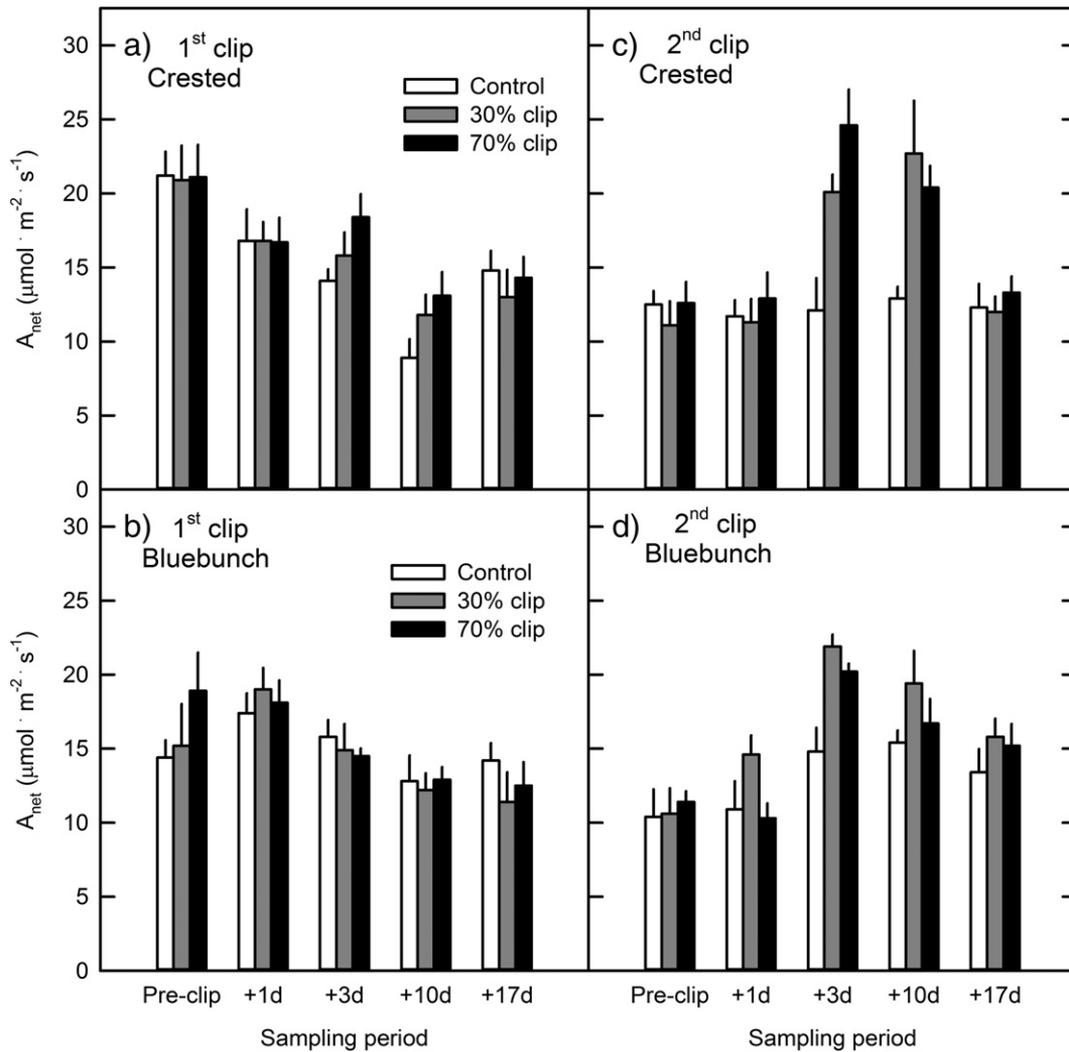


Figure 1. Net photosynthetic assimilation (A_{net}) following clipping at two-leaf stage seedlings of (a) crested wheatgrass, (b) bluebunch wheatgrass, and following a second clip 1 month later (c and d for crested and bluebunch wheatgrass, respectively). Please note that “preclip” for the second clipping is +24 days after first clipping. Each bar is the mean of eight independent measurements. Error bars are \pm one SE of the mean.

70% clipped plants, A_{net} declined significantly from 4 to 10 days following clipping (Scheffe’s $F = 2.66$; $P = 0.015$). That was not the case in 30% clipped plants (Scheffe’s $F = 1.00$; $P = 0.45$). Also, control plant A_{net} did not significantly differ across periods (Scheffe’s $F = 1.25$; $P = 0.31$; Fig. 1c, d).

With the absence of compensatory photosynthesis response in first clipping (Fig. 1a, b), the slope of $A_{net}:g_s$ relationship (WUE_i) of crested wheatgrass ($35.2 \mu\text{mol} \cdot \text{mol}^{-1}$; 11.73 MSE), though higher than in bluebunch wheatgrass ($28.3 \mu\text{mol} \cdot \text{mol}^{-1}$; 14.54 MSE), did not significantly differ ($F_{1,188} = 3.05$; $P = 0.082$), and WUE_i did not differ between clipping treatments in crested ($F_{2,90} = 0.33$; $P = 0.72$; Fig. 2a) or bluebunch wheatgrass ($F_{2,90} = 0.24$; $P = 0.78$; Fig. 2b). In contrast, when clipping induced a compensatory photosynthetic response in both species (Fig. 1c, d), the slope of the $A_{net}:g_s$ relationship showed that WUE_i of crested wheatgrass pooled across all clipping treatments ($39.6 \mu\text{mol} \cdot \text{mol}^{-1}$; 10.35 MSE) was significantly greater than WUE_i in bluebunch wheatgrass ($28.3 \mu\text{mol} \cdot \text{mol}^{-1}$; 10.54 MSE; $F_{1,236} = 14.49$; $P = 0.0002$), with significant differences in WUE_i between clipping treatments in crested wheatgrass ($F_{2,113} = 4.33$; $P = 0.016$; Fig. 2c) and bluebunch wheatgrass ($F_{2,115} = 9.64$; $P = 0.0001$; Fig. 2d). Pairwise comparisons showed the two species had distinctly different WUE_i responses between clipping treatments (Fig. 2c, d). In crested wheatgrass, WUE_i of unclipped controls ($32.3 \mu\text{mol} \cdot \text{mol}^{-1}$;

7.45 MSE) and 70% clipped plants ($35.0 \mu\text{mol} \cdot \text{mol}^{-1}$; 13.04 MSE) did not significantly differ (HSD = 2.84; $P > 0.05$), with WUE_i of both significantly lower than WUE_i in 30% clipped plants ($50.4 \mu\text{mol} \cdot \text{mol}^{-1}$; 8.55 MSE; HSD = 11.29; $P < 0.05$ for control vs. 30% clipped, and HSD = 15.95; $P < 0.05$ for 70% vs. 30% clipped plants, respectively; Fig. 2c). In bluebunch wheatgrass, WUE_i of control plants ($45.3 \mu\text{mol} \cdot \text{mol}^{-1}$; 6.11 MSE) was significantly higher than 30% clipped plants ($34.2 \mu\text{mol} \cdot \text{mol}^{-1}$; 10.70 MSE; HSD = 7.66; $P < 0.05$), which in turn had significantly higher WUE_i than 70% clipped plants ($22.2 \mu\text{mol} \cdot \text{mol}^{-1}$; 8.16 MSE; HSD = 9.27; $P < 0.05$) (Fig. 2d). As an additional analysis, we performed individual linear regressions comparing species within each clipping treatment; in unclipped controls, bluebunch wheatgrass seedlings had higher WUE_i compared with crested wheatgrass controls, but this was not significant at our chosen probability level ($F_{1,76} = 3.59$; $P = 0.062$), while crested wheatgrass seedlings had higher WUE_i compared with bluebunch wheatgrass counterparts in the 30% ($F_{1,76} = 8.44$; $P = 0.0048$) and 70% clipping treatments ($F_{1,76} = 9.17$; $P = 0.0034$) (Fig. 2c, d).

Experimental clipping had no significant effect on total numbers of tillers produced per plant by the end of the experiment, with a significant difference in tiller production between the species, with no species-by-clipping interaction (Table 2). Pooled across clipping treatments, crested wheatgrass produced fewer tillers per plant ($2.6 \text{ plant}^{-1} + 0.10 \text{ SE}$) compared with bluebunch wheatgrass seedlings

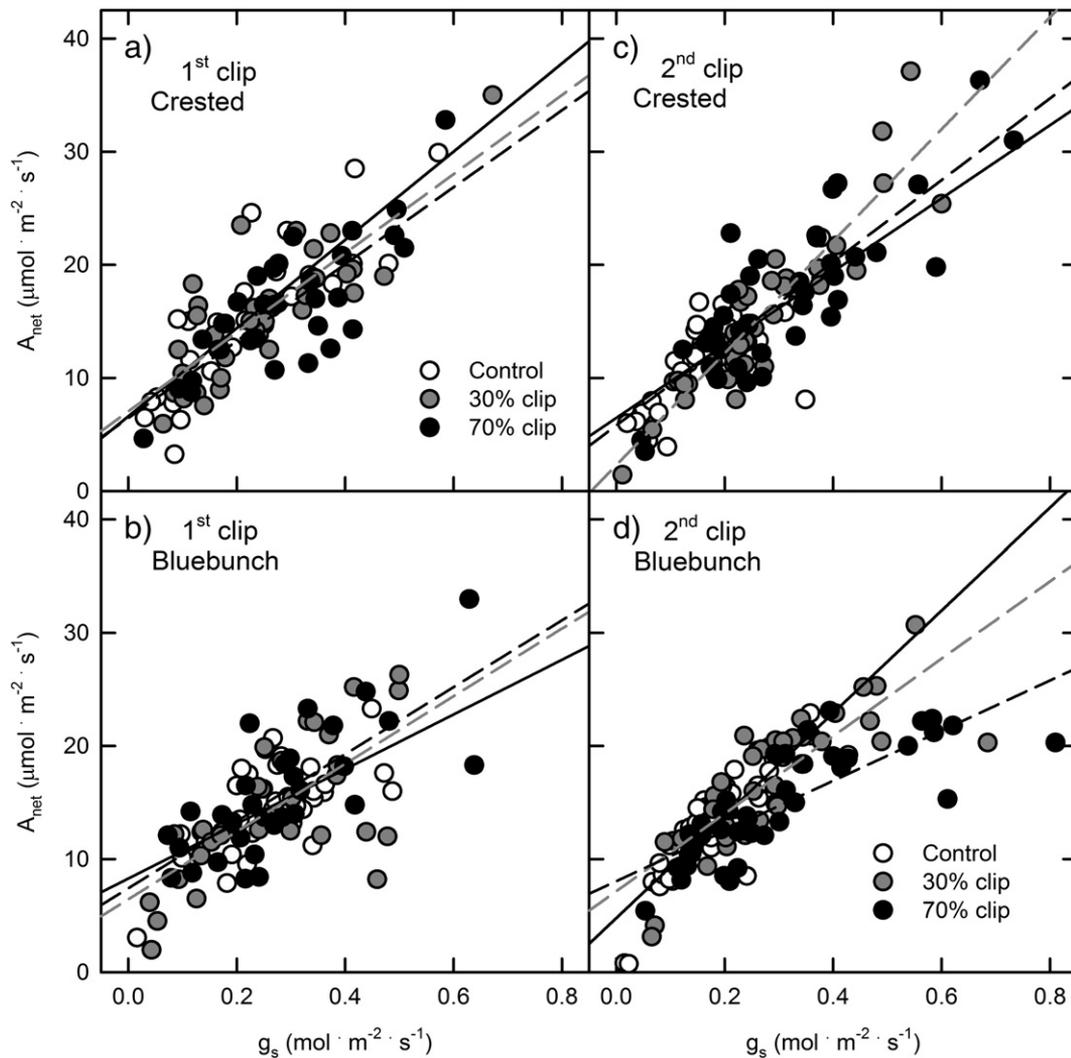


Figure 2. Relationship between net photosynthetic assimilation rate (A_{net}) and stomatal conductance to water vapor (g_s) for unclipped controls (open symbols), 30%- (gray symbols) and 70%-clipping treatments (black symbols) for crested and bluebunch wheatgrass seedlings following the first (a and b, respectively) and second clipping treatments (c and d, respectively). Slopes of control (solid lines), 30% clipping (dashed gray), and 70% clipping (dashed black) were used to determine intrinsic water use efficiency (WUE_i) from linear regressions fitted to data pooled across the preclipping to +17 days postclipping periods were used to determine intrinsic water use efficiency (WUE_i); all regressions are significant at $P < 0.05$.

($3.6 \text{ plant}^{-1} + 0.12 \text{ SE}$). Total leaf area per plant did not significantly vary between species, clipping treatments, with no species-by-clipping treatment interaction (see Table 2; Fig. 3a). Despite

Table 2

Two-way analysis of variance F-test results for final aboveground and belowground growth parameters of crested wheatgrass and bluebunch wheatgrass seedlings treated with three levels of experimental defoliation (unclipped controls, 30% and 70% aboveground tissue removal), with clipping treatments occurring twice (May 14 and June 12, 2014) over the experimental period (March 20 to July 30, 2014). Bold F-test results are significant at $P < 0.05$; degrees of freedom are presented parenthetically.

| Variable | Spp _(1,42) | Clipping _(2,42) | Spp × clip _(2,42) |
|---|-----------------------|----------------------------|------------------------------|
| Tillers (no. plant ⁻¹) | 39.35 | 0.16 ^{ns} | 2.70 ^{ns} |
| Leaf area (cm ² plant ⁻¹) | 3.12 ^{ns} | 0.05 ^{ns} | 0.03 ^{ns} |
| Culm area (cm ² plant ⁻¹) | 13.60 | 1.64 ^{ns} | 0.04 ^{ns} |
| Total area (cm ² plant ⁻¹) | 0.19 ^{ns} | 0.32 ^{ns} | 0.02 ^{ns} |
| Root length (cm plant ⁻¹) | 4.89 | 1.98 ^{ns} | 0.40 ^{ns} |
| Root mass (g plant ⁻¹) | 4.14 | 3.94 | 0.51 ^{ns} |
| Root area (cm ² plant ⁻¹) | 2.91 ^{ns} | 2.26 ^{ns} | 0.39 ^{ns} |
| Specific leaf mass (g m ⁻²) | 1.82 ^{ns} | 1.78 ^{ns} | 1.22 ^{ns} |
| Specific culm mass (g m ⁻²) | 103.35 | 5.13 | 1.87 ^{ns} |
| Specific root mass (g m ⁻²) | 55.80 | 1.95 ^{ns} | 0.71 ^{ns} |
| Root-to-shoot ratio (g g ⁻¹) | 18.85 | 4.63 | 0.10 ^{ns} |

significantly higher culm area per plant in crested wheatgrass ($5.0 \text{ cm}^2 \cdot \text{plant}^{-1} + 0.28 \text{ SE}$) compared with bluebunch wheatgrass ($3.7 \text{ cm}^2 \cdot \text{plant}^{-1} + 0.23 \text{ SE}$; Fig. 3b), the consistent slightly lower leaf area per plant in crested wheatgrass, though not significant (see Table 2; Fig. 3a), resulted in similar total photosynthetic tissue area between species and clipping treatments (see Table 2; Fig. 3c).

Pooled across all clipping treatments, total root length per plant was greater in crested wheatgrass ($1466.6 \text{ cm} \cdot \text{plant}^{-1} + 106.32 \text{ SE}$) compared with root lengths in bluebunch seedlings ($1166.9 \text{ cm} \cdot \text{plant}^{-1} + 85.93 \text{ SE}$; Table 2), with no significant differences between clipping treatments (see Table 2), despite a general declining trend from unclipped controls to 70% removal treatments (Fig. 3d). Crested wheatgrass had lower root mass per plant pooled across clipping treatments ($100.5 \text{ mg} \cdot \text{plant}^{-1} + 5.78 \text{ SE}$) than masses attained in bluebunch seedlings ($122.5 \text{ mg} \cdot \text{plant}^{-1} + 9.79 \text{ SE}$). Clipping treatment significantly affected root mass per plant (see Table 2), with control plants ($120.6 \text{ mg} \cdot \text{plant}^{-1} + 8.61 \text{ SE}$) and 30% removal plants ($123.8 \text{ mg} \cdot \text{plant}^{-1} + 11.84 \text{ SE}$) having similar root masses that were significantly greater than root mass in 70% removal plants ($90.1 \text{ mg} \cdot \text{plant}^{-1} + 7.82 \text{ SE}$; Fig. 3e). Despite significantly longer roots in crested wheatgrass (see Table 2; Fig. 3d), total projected root area did not significantly differ between species (see Table 2;

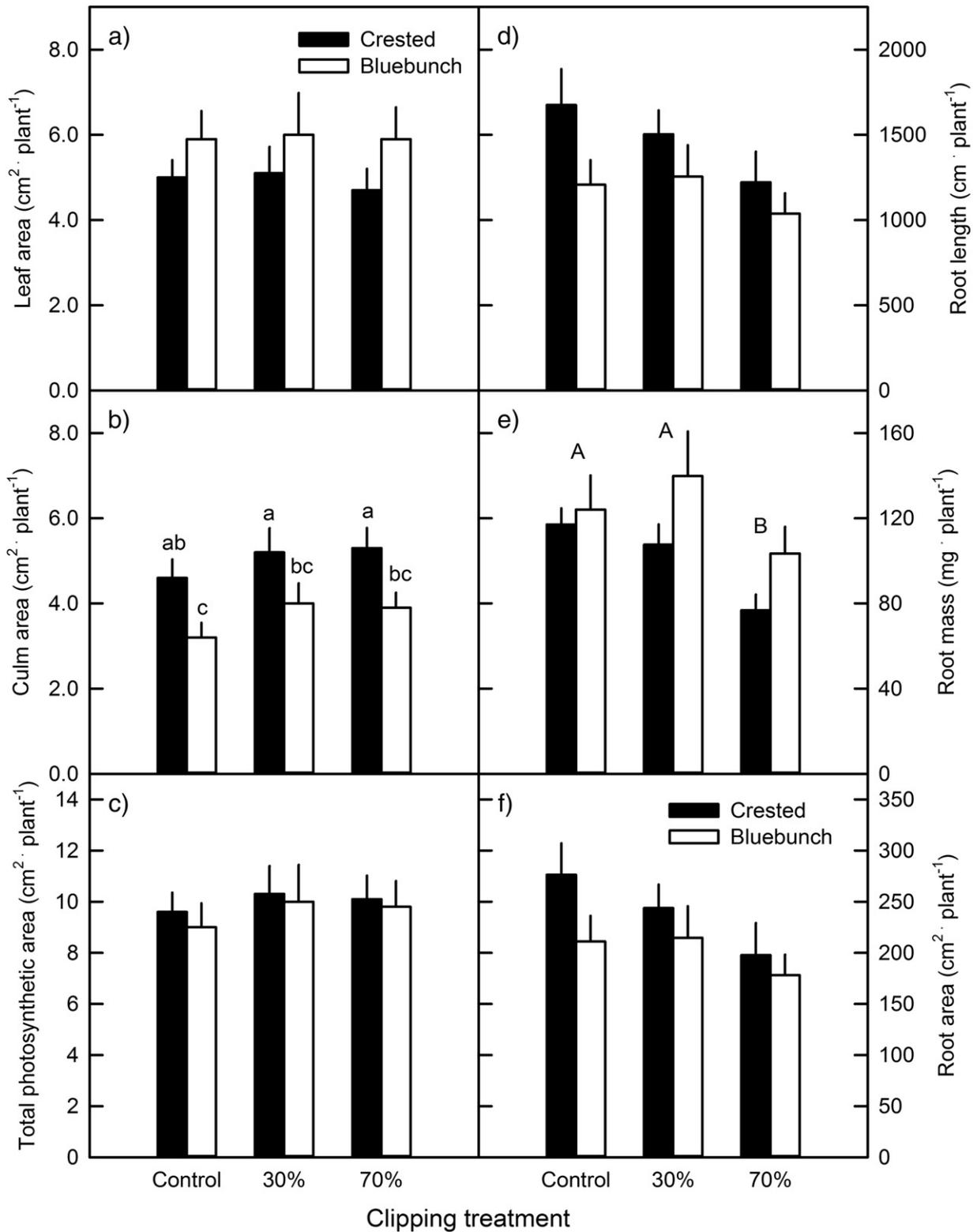


Figure 3. Average plant (a) leaf area, (b) culm area, (c) total photosynthetic area, and (d) root length, (e) root mass, and (f) root area of crested and bluebunch wheatgrass seedlings in control, 30%, and 70% clip treatments. Each bar is the mean of eight independent measurements. Error bars are + one SE of the mean. Letters differ at $P < 0.05$ (LSD).

$P = 0.095$), or clipping treatments (see Table 2; Fig. 3f), likely due to the relatively invariant root lengths in bluebunch wheatgrass (Fig. 3d).

Specific leaf mass did not vary significantly between species or clipping treatment, with no species-by-clipping treatment interaction (see Table 2; Fig. 4a), while specific mass of culms and roots significantly

differed between species (see Table 2). Specific culm mass was significantly higher in crested ($104.3 \text{ g} \cdot \text{m}^{-2} + 2.90 \text{ SE}$) than in bluebunch ($72.9 \text{ g} \cdot \text{m}^{-2} + 1.79 \text{ SE}$; Fig. 4b), while crested wheatgrass attained lower specific root mass ($4.4 \text{ g} \cdot \text{m}^{-2} + 0.17 \text{ SE}$) than levels in bluebunch pooled across all clipping treatments ($6.1 \text{ g} \cdot \text{m}^{-2} + 0.16 \text{ SE}$; Fig. 4c). Specific culm mass also significantly differed between clipping treatments

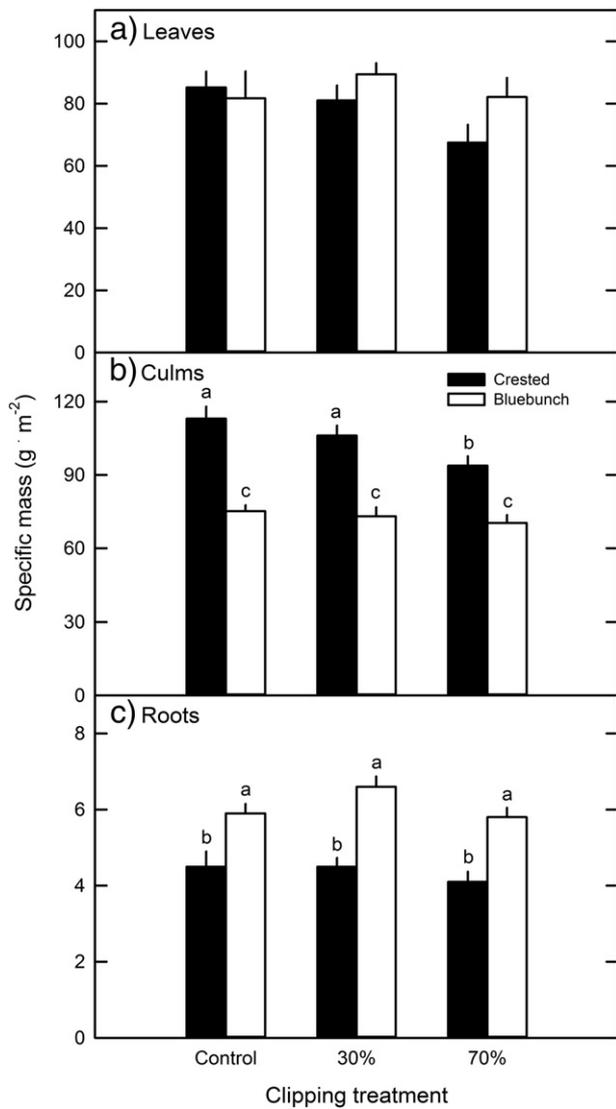


Figure 4. Specific mass of (a) leaves, (b) culms, and (c) roots of crested and bluebunch wheatgrass plants in control, 30%, and 70% clipping treatments. Each bar is the mean of eight independent measurements. Error bars are + one SE of the mean. Letters differ at $P < 0.05$ (LSD).

(see Table 2), primarily due to declines in crested wheatgrass specific culm mass with increasing clipping (Fig. 4b). Specific root mass did not significantly vary between clipping treatments (see Table 2; Fig. 4c). On a per-mass basis, root-to-shoot ratios significantly differed between species and clipping treatments, with no species-by-clipping treatment interaction (see Table 2). Bluebunch wheatgrass had higher overall root-to-shoot ratios ($1.42 \text{ g} \cdot \text{g}^{-1} + 0.060 \text{ SE}$) compared with crested wheatgrass ($1.07 \text{ g} \cdot \text{g}^{-1} + 0.061 \text{ SE}$). Pooled across species, controls and 30% clipping treatments had similar root-to-shoot ratios ($1.37 \text{ g} \cdot \text{g}^{-1} + 0.104 \text{ SE}$ and $1.30 + 0.079 \text{ SE}$, respectively), markedly higher than those in 70% clipping treatments ($1.08 \text{ g} \cdot \text{g}^{-1} + 0.053 \text{ SE}$); decreases in root-to-shoot ratios with clipping were more marked in crested wheatgrass, while changes in ratios in bluebunch wheatgrass were not as pronounced (Fig. 5).

Discussion

As we expected, seedlings of these two bunchgrass species did have the ability to up-regulate photosynthetic activity in response to defoliation, but this was not apparent following both clips (see Fig. 1). By the time of the second clipping, clipped plants were considerably larger

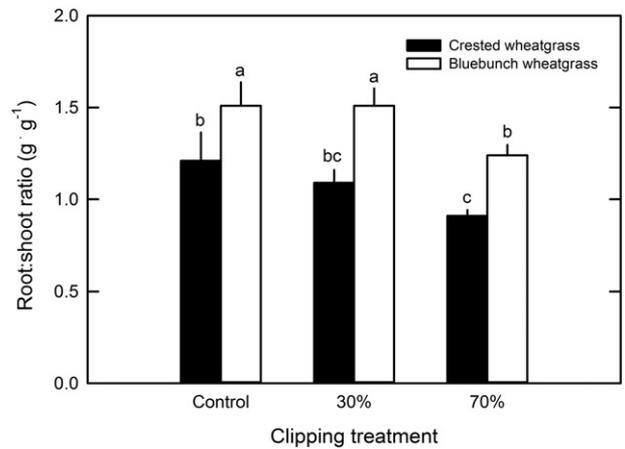


Figure 5. Root-to-shoot ratios of crested wheatgrass and bluebunch wheatgrass treated with varying degrees of aboveground tissue removal. Each bar is the mean of eight independent measurements. Error bars are + one SE of the mean. Letters differ at $P < 0.05$ (LSD).

than their initial size at the first clip (data not shown), and this growth may have facilitated the ability to increase A_{net} following the second clipping (see Fig. 1c, d). Contrary to our hypothesis, seedlings of the exotic bunchgrass crested wheatgrass did not show more pronounced compensatory photosynthesis compared with the native bluebunch wheatgrass (see Fig. 1). This somewhat stands in contrast to earlier work on adult plants, which found that when no photosynthetic compensation occurs, both species have remarkably similar A_{net} and g_s in early- and mid-growing season leaves (Nowak and Caldwell 1986), but that bluebunch wheatgrass has a more positive postclipping response than crested wheatgrass when photosynthetic compensation is observed (Nowak and Caldwell 1984).

Also contrary to our expectations, compensatory photosynthesis did not lower water use efficiency of crested wheatgrass; indeed, clipping either enhanced or had no marked effect on WUE_i (see Fig. 2c). Rather, the pattern we expected to be expressed in crested wheatgrass was more clearly apparent in bluebunch seedlings, where increased A_{net} following defoliation led to WUE_i consistently reducing from control plant levels with increasing defoliation severity (see Fig. 2d). These differences in WUE_i could be an important feature in seedling establishment, as soil water deficit is a seasonal feature modulating the success of bunchgrass seedling emergence and establishment in sagebrush steppe ecosystems (James et al. 2011, 2012). In some cases, higher WUE_i is thought to contribute to the invasive success of exotic species, but this is usually associated with a more conservative approach to WUE_i , with the benefit of more sustained relative growth rates under drier soil moisture conditions associated with a cost of greater stomatal limitations to photosynthesis under more favorable moisture conditions (Anderson and Toft, 1993; Kimball et al. 2014). The divergent WUE_i responses noted in our study suggest crested wheatgrass seedlings could have a distinct carbon-gain advantage following grazing over a broader range of soil moisture conditions than bluebunch wheatgrass at the seedling stage.

In both crested and bluebunch wheatgrass, higher A_{net} was accompanied by increased stomatal conductance (g_s); indeed, control plant g_s did not exceed $0.400 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in unclipped control plants, even though these received identical watering regimens as the clipping treatment plants (see Fig. 2c, d). In established plants, stomatal opening is a common response with compensatory photosynthesis (Caldwell et al. 1981; Painter and Detling 1981; Detling and Painter 1983; Wallace et al. 1984; Doescher et al. 1997). However, A_{net} changed almost linearly with increasing g_s in crested wheatgrass seedlings (see Fig. 2c), while A_{net} in clipped bluebunch seedlings reached an asymptote with increasing g_s , especially in 70% clipping treatment plants (Fig. 2d). These

findings show crested wheatgrass and bluebunch wheatgrass seedlings are indeed capable of compensatory photosynthesis, but that crested wheatgrass seedlings have the ability to better coordinate stomatal supply with photosynthetic demand to maintain or even increase WUE_i over the postherbivore recovery period (see Fig. 2).

These leaf-level dynamics may reflect species-specific differences in the proportional aboveground and belowground growth of these seedlings. Such allocation patterns are often critical determinants in the responses of aridland grasses to environmental variability (Fernandez and Reynolds 2000). Compared with bluebunch wheatgrass, crested wheatgrass had lower root-to-shoot ratios (see Fig. 5), due to lower total root mass per plant (see Fig. 3e) comprising longer roots (see Fig. 3d) of low specific root mass (see Fig. 4c). These findings are in agreement with those showing that the lower energetic costs in producing belowground structures allow crested wheatgrass to more rapidly acquire soil resources to support proportionally more aboveground growth (Jackson and Caldwell 1989; Aguirre and Johnson 1991a, b; Meays et al. 2000). This could very likely facilitate more rapid coordination and optimization of photosynthetic demand and stomatal supply functions (Smith et al. 1997). These “belowground savings” in total root mass and specific root mass (see Fig. 3) were eventually expressed aboveground in our study as higher A_{net} in crested wheatgrass before clipping early in the study (see Fig. 1a, b) and higher WUE_i in clipped crested wheatgrass seedlings compared with lower WUE_i in bluebunch counterparts following the second clipping (see Fig. 2c, d). It would also be interesting to see if aboveground and belowground growth and tissue-level allocation patterns were consistent between the first and second clippings, as WUE_i in bluebunch wheatgrass controls increased markedly between these periods (see Fig. 2b and d), while WUE_i in crested wheatgrass controls did not vary markedly (see Fig. 2a and c), or if this was due to other developmental processes in these seedlings.

Total photosynthetic area did not differ between clipping treatments by the end of the experiment in both species (see Fig. 3c), highly indicative of compensatory regrowth in both species (McNaughton 1983; Ferraro and Oesterheld 2002). At first glance, our data suggest these species' seedlings have similar relative growth rates, as previous research suggests (Arredondo et al. 1998). However, we do not know if the final sizes of both species were attained at the same time before the final harvest. In field studies of adult plants in established plant communities, compensatory regrowth and photosynthesis are commonly associated with increased root-to-shoot ratios that reflect the degree of long-term grazing pressure and altered soil moisture conditions (Detling and Painter 1983; Wallace et al. 1984; Doescher et al. 1997). In our seedlings, however, compensatory photosynthesis was associated with decreased root-to-shoot ratios (see Fig. 5). In adult plants, compensatory photosynthesis is not considered to be a major determinant of herbivory tolerance, as it occurs in a small proportion leaves in the plant canopy (Nowak and Caldwell 1984), and adult plants have sufficient energetic resources to allocate to aboveground regrowth and recover from grazing loss (Meays et al. 2000). This is not the case with seedlings, which have very limited resources to mobilize in response to tissue loss (Hanley et al. 2004). In our study, the size of the leaf-level gas exchange samples made ($0.5\text{--}2.0\text{ cm}^2$) was a significant proportion of the total plant leaf area and likely is representative of whole-plant carbon uptake response to tissue loss.

Our study suggests compensatory photosynthesis is an important component of herbivore recovery and tolerance in the demographically critical seedling stage of bunchgrass life cycles. Seedlings have small masses and limited carbon reserves (Kitajima and Myers 2008) and produce foliar tissue lacking high defensive compounds, making seedling tissue particularly palatable and highly likely targets for herbivory (Fenner et al. 1999). In addition to herbivory pressure, seedlings in sagebrush steppe ecosystems face short and highly variable growing seasons, particularly prone to limiting soil moisture conditions and hot and cold temperature extremes (Mack and Pyke 1984; Pyke 1986; Smith et al. 1997; James et al. 2011; Gornish et al. 2015). The

photosynthetic compensatory responses we have quantified here, in addition to their relationship to WUE_i and plant biomass and tissue allocation, may reflect two distinct strategies for dealing with these pressures. Moreover, our results suggest the compensatory photosynthetic responses in adult plants may reflect a demographic “carry-over” from the seedling stage. Outer-canopy leaves, which represent a relatively small fraction of the total grass canopy (Smith et al. 1997), typically experience the greatest degree of environmental variation and herbivory (Nowak and Caldwell 1986), putting them in a similar environmental context to seedlings. Possibly, exposure to defoliation in the seedling stage induces a compensatory photosynthesis response that continues to be expressed in leaves similar in age and microenvironment within adult plant canopies.

Implications

In addition to implementing practices that affect adult plant populations, understanding seed and seedling ecology is essential to the successful matching of species to environmental conditions to successfully restore and preserve the stability of sagebrush steppe rangelands (Meays et al. 2000; James et al. 2013). Range grass seedlings are faced with a diverse array of invertebrate and vertebrate herbivores, including granivores (Pyke 1986; Archer and Pyke 1991). Accounting for the nature of these herbivory agents, as well as their effects on seedling performance, could help improve successful establishment of desirable native sagebrush steppe grasses. This study improves our understanding of the consequences of seedling-level herbivory and demonstrates how seedling herbivory can affect plant processes important to maintaining positive carbon balance. Compensatory photosynthesis in crested wheatgrass resulted in increased WUE_i across the establishment period. This, along with the ability of adult plants to optimize carbohydrate allocation after grazing (Meays et al. 2000), likely contributes to the high success rate of crested wheatgrass in degraded sagebrush steppe rangelands dominated by invasive annual grasses across a wide range of conditions (Davies et al. 2010). However, for the native bluebunch wheatgrass, compensatory photosynthesis reduced WUE_i , which may limit the range of conditions that this species may successfully establish. Our results suggest that, if warranted, reducing herbivory impacts via such techniques as spraying for insects, applying antipalatability agents, or even rodent control to reduce the effects of seedling herbivory may be important considerations in enhancing the eventual success in establishing this native grass.

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