Field growth comparisons of invasive alien annual and native perennial grasses in monocultures

S. Mangla[a, *], R. L. Sheley[b] and J. J. James[b]

[a] *Graduate Research Assistant, Environmental Science, Oregon State University, Corvallis, OR 97331, USA*

[b] *Weed Ecologist and Plant Physiologist, USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center, 67826-A Hwy 205, Burns, OR 97720, USA*

* Corresponding author: Tel.: + 1 541 732 8475; fax: + 1 541 737 1393

E-mail address: seema.mangla@oregonstate.edu (S. Mangla).

Abstract

Throughout the western United States, the invasive annual grass, medusahead (*Taeniatherum caput-medusae* L. Nevski), is rapidly invading grasslands once dominated by native perennial grasses, such as bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A). It is also invading grasslands dominated by less undesirable invasive annual grasses, especially cheatgrass (*Bromus tectorum* L.). Understanding medusahead growth dynamics relative to native perennial grasses and cheatgrass is central to predicting and managing medusahead invasion. We hypothesized that medusahead would have a higher relative growth rate (RGR), a longer period of growth, and as a consequence, more total biomass at the end of the growing season than the native perennial grass and cheatgrass. In 2008 (dry conditions), 250 seeds and in 2009 (wet conditions), 250 and 100 seeds of each species were sown in 1 m^2 plots with 5 replicates. Shoots were harvested on 3-25 day intervals throughout the growing season. The native perennial grass had more biomass and higher RGR than medusahead in the dry year, but the relationship was reversed in the wet year. Precipitation in 2008 was well-below average and this level of drought is very infrequent based on historical weather data. Medusahead had a longer period of growth and more total biomass than cheatgrass for both years. We expect that medusahead will continue to invade both native perennial and less undesirable invasive annual grasslands because of its higher RGR and extended period of growth.

Keywords: Taeniatherum caput-medusae, Relative growth rate, Shoot weight, *Bromus tectorum*, *Pseudoroegneria spicata*

Introduction

Throughout the western United States, the exotic annual grasses, cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* L. Nevski), are expanding and dominating areas once dominated by native perennial grasses, such as bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A) (D'Antonio and Vitousek, 1992). Annual grass invasion is driving one of the largest changes in vegetation structure ever documented (D'Antonio and Vitousek, 1992). Vegetation dynamics involve deterioration of healthy intact shrub-steppe plant communities into annual grass monocultures. This conversion has major negative impacts on ecosystem function, wildlife, and fire regimes (Stohlgren et al., 1999; Vitousek et al., 1996).

In the Intermountain West, the exponential increase in dominance by medusahead has largely been at the expense of other annual grasses, especially cheatgrass (Bovey et al., 1961; Harris, 1977). In this scenario, medusahead either joins, replaces or displaces cheatgrass (Hironaka, 1989). From an agricultural and restorative perspective, conversion of cheatgrass grassland to predominantly medusahead grassland represents further deterioration beyond that of cheatgrass alone. Invasion by medusahead substantially reduces forage quality and amount, alters timing of forage availability, and increases year-to-year variation in forage production on grassland (Monaco et al., 2005).

Invasive species are hypothesized to share a host of plant traits that contribute to their success (Grotkopp and Rejmánek, 2007). One trait that seems to be particularly important is high relative growth rate (RGR, plant weight increase per unit biomass per unit of time) (Burns, 2006). A high RGR allows invasives to occupy space and capture resources quickly and reduces the time between vegetative growth and reproduction

(Poorter, 1989). Higher RGR provides an initial size advantage that allows invasives to capture more resources than natives, thus minimizing their exposure to drought stress (Grotkopp and Rejmánek, 2007).

While the potential for cheatgrass to achieve higher RGR is well documented (Arredondo et al., 1998; Humphrey and Schupp, 2004; James, 2008), less is known about RGR comparisons of medusahead with native grasses and cheatgrass. Only a few greenhouse studies provide evidence that differences exist in RGR between medusahead and co-occurring species (Arredondo et al., 1998; James, 2008). In spite of the importance of studying growth related traits under natural conditions (Villar et al., 2005), no field experiment has been conducted comparing RGR of medusahead with co-occurring species. Our objectives were to compare patterns and rate of growth by medusahead with bluebunch wheatgrass and cheatgrass in the field. We hypothesized that medusahead growing in monocultures would have a higher RGR, a longer period of growth, and as a consequence, more total biomass at the end of the growing season than bluebunch wheatgrass and cheatgrass.

Material and Methods

The study was conducted in 2008 and 2009 within a Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* [Beetle & A. Young] S.L. Welsh)-steppe community type in southeastern Oregon (43°32′ N, 118°9′ W), 106 km from Burns, Oregon, USA. Site elevation was 1229 m with a 20% southerly slope, consisting of a Risley cobley loam soil. Environmental conditions were monitored using HOBO data loggers. The solar radiation was similar for both years ranging from 6 to 8 KW-hr m^{-2} day^{-1} (data not shown). Long-term monthly precipitation (1897-2009) was compiled from the Western Regional Climate Center (NCDC, 2009; Fig. 1).

In spring 2008, before the experiment was initiated, we applied glyphosate [N-(phosphonomethyl) glycine] at the rate of 0.85 kg active ingredient per hectare to kill existing vegetation. After ten days, the site was rototilled to a depth of 100 mm. Large soil aggregates and dead plants were removed to facilitate plant establishment. The site had been moderately grazed (50% utilization) in the summer by cattle for over 50 years, but was fenced during the experiments.

On May 14, 2008, 250 individual seeds of invasive annual grasses (medusahead and cheatgrass) and the native perennial grass (bluebunch wheatgrass) were sown in completely-randomized $1m^2$ plots. A total of 5 replicates of each species were established separately providing a total of 15 plots spaced 200 mm apart. Seeds were randomly broadcasted and were lightly (<2 mm) covered with soil. Each seed was separated from the nearest neighbor to avoid clustering and provide uniform distribution. The surface soil was kept moist until emergence. No further water was added. This experiment was repeated in 2009. Additionally, in 2009, a similar experiment using 100 seeds in $1m^2$ plots were sown to compare plant growth at a slightly lower monoculture density.

Seedlings were harvested by randomly hand-removing 5 seedlings from each plot at an interval of 7-25 days for 126 days beginning 18 days after planting (DAP) for 2008. For 2009, seedlings were harvested for 131 days beginning 22 DAP at an interval of 3-7 days. Therefore, the densities declined over time as harvests continued and the days between harvests increased as the season progressed. Roots could not be retrieved intact given the rocky nature of the soil; therefore only shoots of each seedling were collected. Shoots were oven-dried at 65ºC for 48 hours before weighing.

Results

Shoot weight was plotted against DAP to determine the differences in growth. We calculated RGR using the classical plant growth analysis (Causton and Venus, 1981). As there were a series of successive harvests, functional plant growth analysis was also used to derive RGR (Hunt and Parson, 1974). For this purpose, HP curves were used (http://people.exeter.ac.uk/rh203/growth_analysis.html). The results were similar to those obtained with the classical approach, and therefore, functional growth analysis is presented. Without roots it was impossible to calculate the total plant weight, therefore the RGR calculated is essentially the shoot RGR (referred to as RGR *hereafter*). All data were subjected to ANOVA, and Tukey's test was used for pairwise comparisons (α = 0.05) using S-plus 7.0.2 statistical software (Insightful Corp., Seattle, WA, USA) for Windows. In 2009, no differences in shoot weight and RGR resulted with either 250 or 100 seeds per m^2 and therefore, results from 250 seeds per m^2 are presented.

As expected, temperature was lower early in the season than during middle and later portions of the season. The lowest temperature in 2008 was nearly 7ºC, while it dropped to 2ºC in 2009. The highest temperatures in 2008 and 2009 were nearly similar and recorded as 21ºC and 23ºC, respectively. Precipitation was lower in 2008 than 2009 with most occurring in early spring. In comparison, precipitation in 2009 was similar to the long-term average and was more evenly distributed throughout the season (Fig. 1).

In 2008, medusahead had greater shoot weight than cheatgrass for most harvests ($P < 0.05$, Fig. 2a); however, bluebunch wheatgrass had greater shoot weight than medusahead during all harvests ($P < 0.01$, Fig. 2a). During the last harvest, seedlings of bluebunch wheatgrass dried and were not harvestable; therefore, no comparison was possible at 126 DAP. Averaged across harvests excluding 126 DAP, bluebunch wheatgrass had 2 times higher shoot weight than medusahead ($P < 0.01$). However, in 2009, averaged across harvests, medusahead had 4 and 1.5 times higher shoot weight than bluebunch wheatgrass and cheatgrass, respectively ($P < 0.01$).

In 2008, during the first two harvests (18 and 28 DAP, $P < 0.01$); medusahead had higher RGR than bluebunch wheatgrass. However, during mid growth period (48-77 DAP); bluebunch wheatgrass resulted in tremendous increase in its RGR compared to medusahead. During the last two harvests for bluebunch wheatgrass (94 and 101 DAP), a negative RGR was recorded, which was significantly lower than the RGR for medusahead ($P < 0.01$, Fig. 3a). Comparing medusahead with cheatgrass, medusahead had significantly lower RGR than cheatgrass during the first two harvests ($P < 0.01$) while medusahead had higher RGR afterwards ($P < 0.01$) except at 48 and 101 DAP. At 126 DAP, both species had negative RGR.

In 2009, medusahead had greater RGR than bluebunch wheatgrass during the early growth period (22-62 DAP, $P < 0.01$). During the mid growth period (70-91 DAP, $P > 0.01$) no significant differences in RGR between the two species were observed, while during the later growth period (97-131 DAP, $P < 0.01$), medusahead had lower RGR than bluebunch wheatgrass. Medusahead had lower RGR than cheatgrass from 22-50 DAP ($P < 0.01$) while from 56-110 DAP, medusahead had greater RGR, however, no differences in RGR were recorded during 56 and 62 DAP ($P > 0.01$). Averaged across harvests, medusahead (0.066 ± 0.008 mg mg^{-1} d^{-1}) had higher RGR than bluebunch wheatgrass (0.049 ± 0.007 mg mg^{-1} d^{-1}) and cheatgrass (0.052 ± 0.004 mg mg^{-1} d^{-1}). From 117-131 DAP, negative RGR's were recorded.

Discussion

Duration of growth and greater biomass accumulation by invasives has been identified as important factors contributing to their success (Grotkopp and Rejmánek, 2007). Over the two years, our hypothesis that medusahead would have a longer period of growth than bluebunch wheatgrass, and as a consequence more total biomass at the end of the growing season, was partially supported. In 2008, bluebunch wheatgrass had more biomass than medusahead, but did not have a longer growing period. In 2009, medusahead had a slightly longer growing period and more biomass than bluebunch wheatgrass. We believe that differences in year-to-year precipitation patterns may be a possible reason for contrasting growth (Fig. 1). Environmental variability is a ubiquitous feature of arid systems, of which precipitation is a major driver of growth (Chambers et al., 2007). In our study, 2008 was drier than 2009 with most precipitation occurring early in the growing season. This is consistent with the work of Kiemnec et al. (2003) who reported that warm, dry conditions resulted in a slower growth rate by diffuse knapweed (*Centaurea diffusa* L). This suggests that biomass dynamics between study species is likely to be oscillatory based on the amount and timing of precipitation.

We believe that more biomass accumulated by bluebunch wheatgrass in 2008 and medusahead in 2009 is associated with their high RGR during the year that favored one species over the other. These contrasting results between two years provided only partial evidence for our hypothesis that medusahead growing in monocultures will have higher RGR than bluebunch wheatgrass. Variation in RGR amongst species could be achieved by having higher rates of photosynthesis and/or lower rates of respiration (high NAR, net assimilation rate), allocating more biomass to leaves (high LMR, leaf mass ratio), or producing thinner or less dense leaves resulting in more leaf area per unit leaf biomass (high SLA, specific leaf area) (Causton and Venus, 1981). Although we were not able to identify the components of RGR driving the differences, we speculate that year-to-year variation in environmental conditions may change the relative contribution of SLA or NAR to RGR as suggested by Loveys et al. (2002).

Medusahead matures 2 to 3 weeks later than cheatgrass (Bovey et al., 1961; Harris, 1977). Recently, James et al. (2008) measured leaf biomass over the growing season and found that medusahead maintained vegetative growth later in the growing season than cheatgrass. Consistent with these findings, data from this study supports our hypothesis that medusahead has a longer period of growth and more total biomass than cheatgrass. Possible explanations may be related to the ability of medusahead to maintain water uptake as upper soils dry compared to co-occurring species, especially cheatgrass (Harris, 1977). Cheatgrass roots have a relatively poorly developed endodermis layer to insulate against hot, dry soils, while medusahead roots have thicker cell walls, which allow it to conduct water throughout very dry soil horizons (Harris, 1977). Cheatgrass roots develop a more fragile root system than medusahead and this fragility increases as the roots grow older (Hironaka, 1961). Our findings tend to support the speculations of Hironaka (1989) that the sequence of species replacement among invasive annuals in the western United States would be from early maturing cheatgrass to later maturing medusahead.

We anticipated that differences in RGR between medusahead and cheatgrass could be one of the major factors for replacement of cheatgrass by medusahead. Consistent with our hypothesis, we found higher RGR by medusahead compared to cheatgrass for both years. However, the degree of differences in RGR between species varied between years. This contrasts with earlier work reporting a comparable RGR between medusahead and cheatgrass in a greenhouse experiment (James, 2008). This discrepancy may be related to the differences in importance of particular RGR component for a particular species. Contrasting growth condition between the present study and greenhouse experiments could affect RGR as suggested by Villar et al. (2005).

The RGR of annual and perennial grasses reached an inflection point when seedlings were young and then decreased over time. The general trend of decline in RGR with time for invasives and natives is consistent with the findings of several other studies (Causton and Venus, 1981; Villar et al., 2005). Ontogenic changes, higher allocation to low-efficiency tissues and self-shading are possible explanations of this reduction. However, we were surprised that both invasives and natives had negative RGR towards the end of the growing season for both years. Typically, species demonstrate a greater reduction in RGR with time without reaching negative values. We believe, fluctuating environmental conditions might have constrained plant growth. Absence or little precipitation coupled with high temperatures could have resulted in leaf desiccation and leaf senescence. Support for our results could be found in other ecosystems with invasives experiencing drought, burning and other treatments resulting in negative RGR (Bellingham et al., 2004; Golezani et al., 2009).

Recent modeling and empirical work suggests that seasonal patterns of precipitation input and temperature are key factors determining regional variation in the growth, seed production, and spread of invasives (Bradford and Lauenroth, 2006). Establishment of annual grasses is heavily influenced by year-to-year variations in precipitation timing and amounts (Chambers et al., 2007). In our study, medusahead had two times higher RGR in 2009 than in 2008 and consequently produced three times more biomass during the second growing season because precipitation was substantially higher that year. Precipitation in 2008 was well-below average and this level of drought is very infrequent based on historical data. Collectively, our results suggest that the continued invasion and dominance of medusahead onto native grasslands will continue to increase in severity because conditions that favor bluebunch wheatgrass over medusahead are rare.

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Figure captions

Fig. 1: Total precipitation (mm) and temperature (ºC) at the study site for year 2008 (a) and 2009 (b) during the studied period of growth. Additionally, monthly average precipitation for 2008, 2009 and long-term (1890-2009) were also determined (c).

Fig. 2: Shoot weight (mg) for cheatgrass, medusahead and bluebunch wheatgrass over all harvest intervals during the studied period of growth for 2008 (a) and 2009 (b). Bars represent mean ± SD (n = 25).

Fig. 3: Relative growth rate (RGR, $mg\ mg^{-1}\ d^{-1}$) for cheatgrass, medusahead and bluebunch wheatgrass over all harvest intervals during the studied period for 2008 (a) and 2009 (b). Bars represent mean ± SD (n = 25).

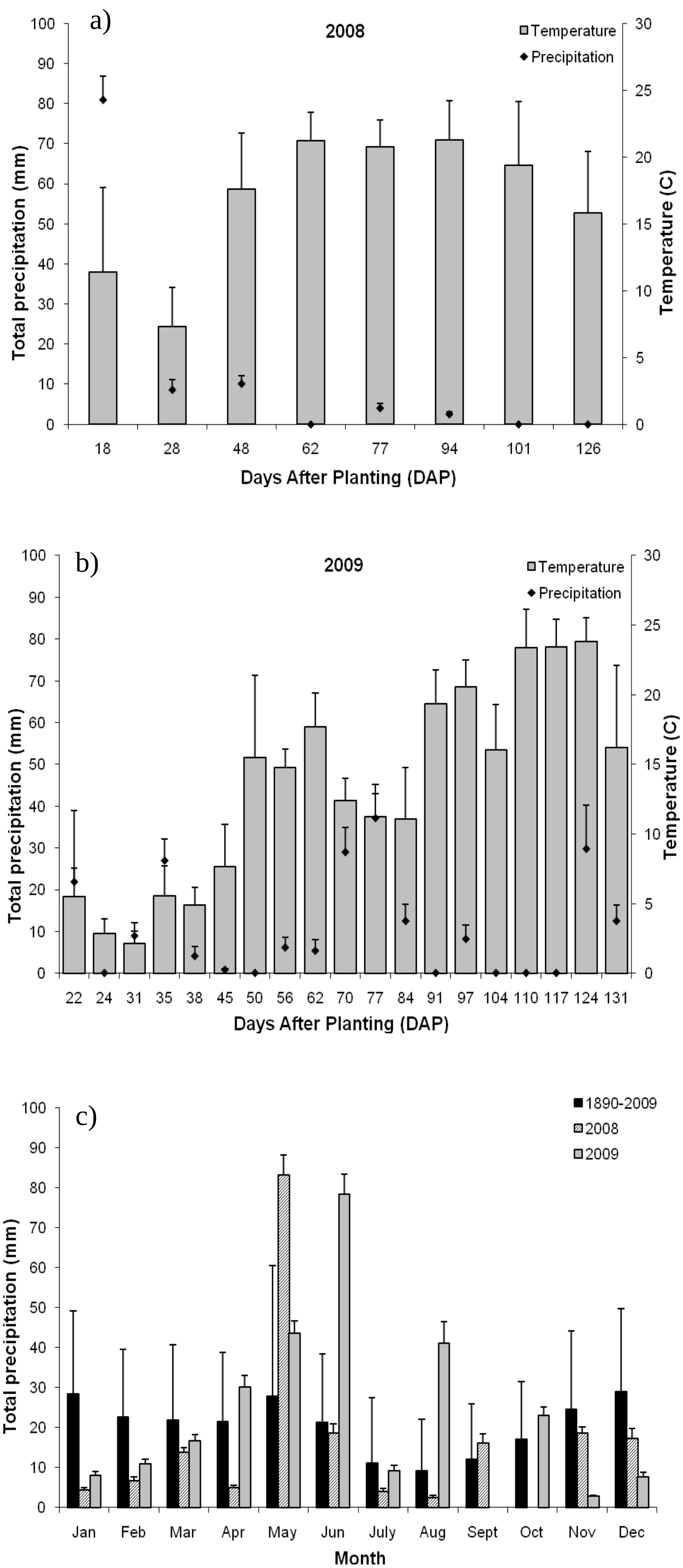
a)
2008
Temperature
Precipitation
Total precipitation (mm)
Temperature (C)
Days After Planting (DAP)
18 28 48 62 77 94 101 126
b)
2009
Temperature
Precipitation
Total precipitation (mm)
Temperature (C)
Days After Planting (DAP)
22 24 31 35 38 45 50 56 62 70 77 84 91 97 104 110 117 124 131
c)
1890-2009
2008
2009
Total precipitation (mm)
Month
Jan Feb Mar Apr May Jun July Aug Sept Oct Nov Dec

Fig. 1

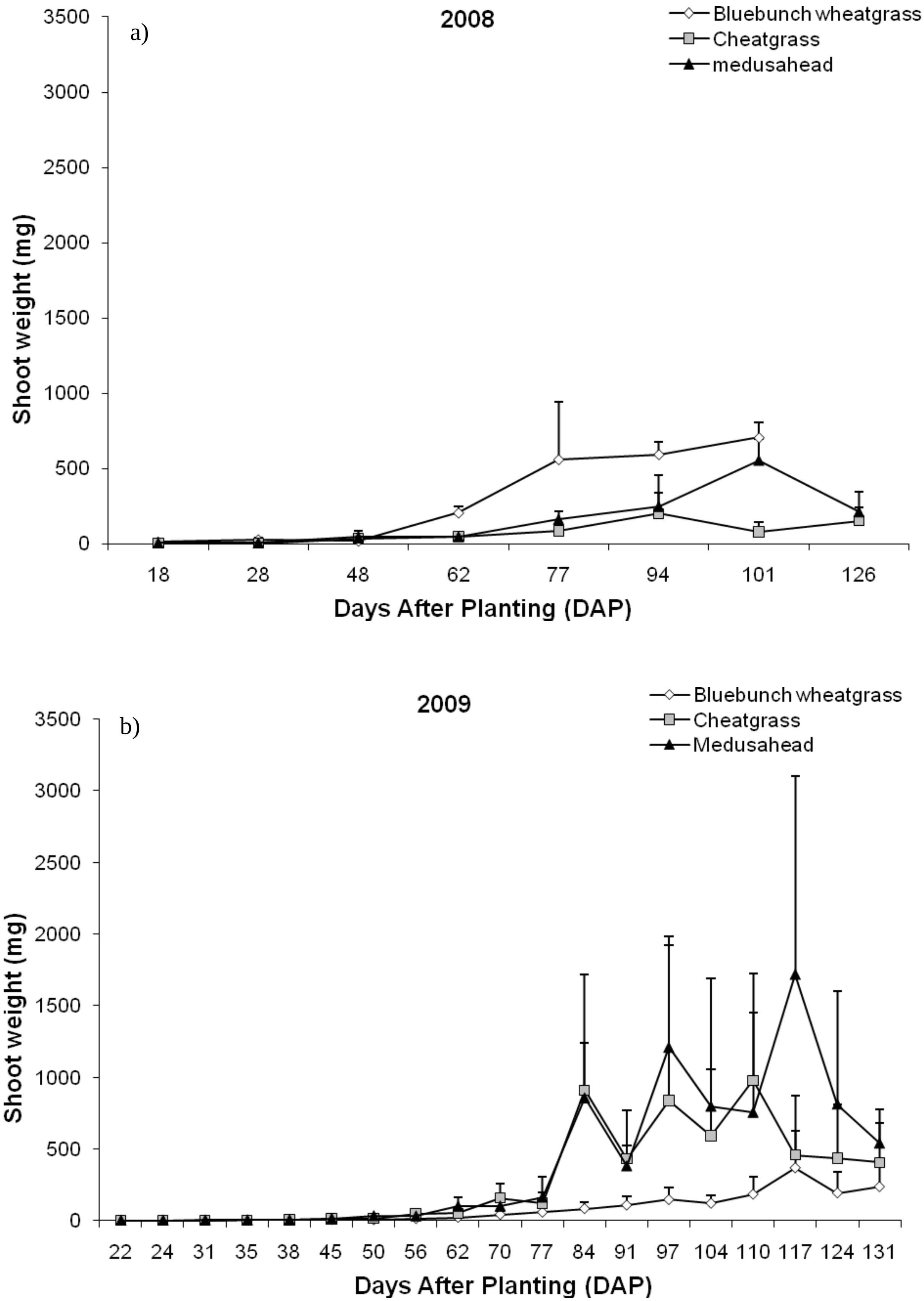
2008
a)
Bluebunch wheatgrass
Cheatgrass
medusahead
Shoot weight (mg)
3500
3000
2500
2000
1500
1000
500
0
18
28
48
62
77
94
101
126
Days After Planting (DAP)
2009
b)
Bluebunch wheatgrass
Cheatgrass
Medusahead
Shoot weight (mg)
3500
3000
2500
2000
1500
1000
500
0
22
24
31
35
38
45
50
56
62
70
77
84
91
97
104
110
117
124
131
Days After Planting (DAP)

Fig. 2

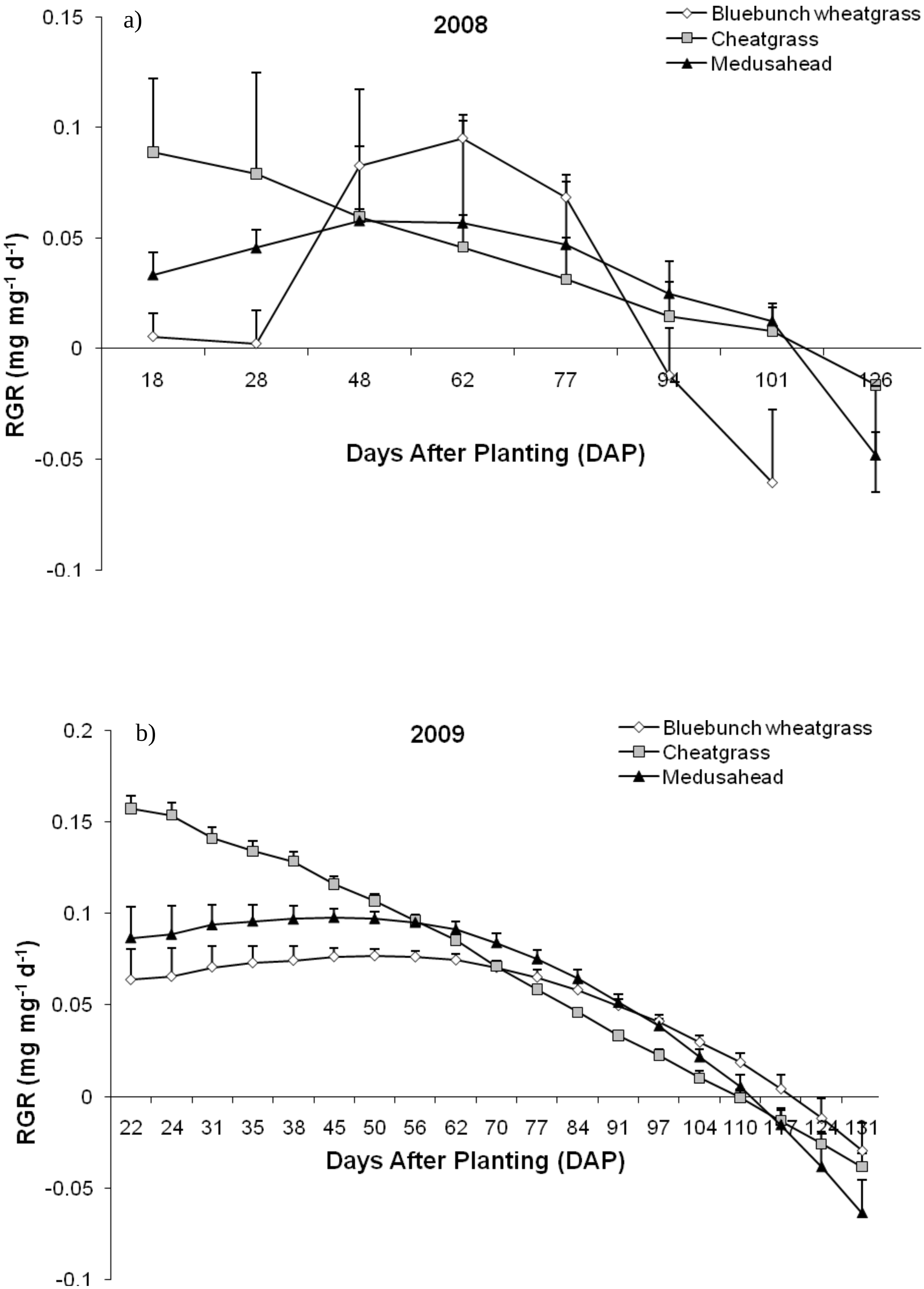
a)
2008
Bluebunch wheatgrass
Cheatgrass
Medusahead
RGR (mg mg-1 d-1)
0.15
0.1
0.05
0
-0.05
-0.1
18
28
48
62
77
94
101
126
Days After Planting (DAP)
b)
2009
Bluebunch wheatgrass
Cheatgrass
Medusahead
RGR (mg mg-1 d-1)
0.2
0.15
0.1
0.05
0
-0.05
-0.1
22 24 31 35 38 45 50 56 62 70 77 84 91 97 104 110 117 124 131
Days After Planting (DAP)

Fig. 3