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NOTES

SPATIAL VARIATION IN GERMINATION OF TWO ANNUAL BROME SPECIES IN THE NORTHERN GREAT PLAINS—Downy brome or cheat grass (*Bromus tectorum* L.) and field brome (*B. arvensis* L.; Synonym = *Bromus japonicus* Thunb. ex Murr.; Japanese brome) are two annual exotic species that have increased the intensity and frequency of fire cycles in the Intermountain West of the United States, with millions of dollars in associated costs (DiTomaso 2000). These invasive brome species have a different impact in the Northern Great Plains of North America where they commonly co-occur in disturbed sites (White and Currie 1983, Haferkamp et al. 1993). In these mixed-grass prairie rangelands, annual bromes compete against other forage species (Haferkamp et al. 1997) and reduce litter decomposition rates (Ogle et al. 2003), which negatively impacts ecosystem services of biomass production and soil nutrient availability. In central plains croplands, downy brome invades alfalfa fields (Kapusta and Strieker 1975), wheat fields (Wicks 1984, Ostlie and Howatt 2013), and perennial grass pastures and seed production areas (Wicks 1984). Downy brome is a regulated plant in Montana (Montana Noxious Weed List, December 2013) and has been found in all counties of Montana since 1950 (Menalled et al. 2008). Field brome is found in all North American states and provinces (USDA Plants Database http://plants.usda.gov). It is used as a winter cover crop in vegetable plots and orchards in the Northeastern United States (NRCS 2006). Field brome has no formal designation in the state of Montana, although downy brome and field brome are commonly grouped together and are referred to colloquially as "cheatgrass" in the state.

Downy brome and field brome are predominantly self-fertilizing winter annuals (Oja et al. 2003, but see Leger et al. 2009), and both species require an after-ripening period after seed shatter to remove dormancy (Baskin and Baskin 1981, Smith et al 2008). Because pre-emergent grass seedlings are highly susceptible to mortality (James et al. 2011), understanding spatial and temporal variability in germination has direct application to managing populations of invasive annual weeds (Mack and Pyke 1983). A recent publication from the Northern Great Plains has shown that reduction in one annual brome species results in the increase in the other (Espeland and Kilian 2015); the dominance of each species within the above-ground and below-ground (i.e. seed) annual grass community changes from year to year. This dominance trade-off could be supported by different germination cues for the two species (as in Facelli et al. 2005). Germination conditions for downy brome and field brome have been studied, however the degree to which the existing literature can be applied to managing populations of the two species in the Northern Great Plains is unclear. In the Intermountain West, downy brome germinates in either fall or spring; although some populations germinate in a single season, many populations have both fall- and spring- germinating cohorts (Mack and Pyke 1983). Laboratory studies on Kentucky collections of field brome show it germinates reliably in the fall and undergoes secondary dormancy in spring (Baskin and Baskin 1981). Factors that vary among years (such as rainfall timing and temperature) are important to germination in North American populations in Saskatchewan (Chepil 1946) and among-year variation is more important than among-microenvironment variation in the Intermountain West (Mack and Pyke 1983). These findings underscore the importance of climatic cues for germination in this species.

The bulk of laboratory germination in Intermountain West accessions of downy brome occurs in less than 3 days (Leger et al. 2009), indicating that annual bromes are capable of germinating *en masse* after a significant rainfall event. If germination is predictable at the population level *in situ* for downy brome and field brome with populations germinating reliably in fall and/or spring, chemical control may be achieved with one or two entries (Whitson and Koch 1998, Elseroad and Rudd 2011). To examine *in situ* germination in fall and spring in the Northern Great Plains, we conducted seed bank excavations in three annual brome patches in each of two populations in fall of 2011, spring of 2012, and fall of 2012. Our objective was to determine if populations mass-germinate seasonally, and if field brome and downy brome have similar germination patterns.

We collected data from two populations in eastern Montana, USA. We defined a population at the scale of putative management: at the pasture level. The Carson population (47°23' N 104°43' W) east of Bloomfield, Montana is within a field that was seeded with native grasses, crested wheatgrass and alfalfa prior to 2000 and has not been grazed by livestock since the time of seeding. Perennial grass cover is 50% at this site. The Wibaux population south of Wibaux, Montana (46°38' N 34°75' W) is a pasture that was set aside from livestock grazing for this experiment. This site has never been cultivated and is dominated by native perennial grasses and sedges at cover level of over 90%. Cover of downy brome and field brome averaged less than 10% at each site. Distribution of annual bromes in eastern Montana can be patchy: in each population we located three high-density patches where annual brome cover was greater than 1% within a 0.01km^2 area. Areas between patches (0.01 km^2 areas) had negligible densities of annual bromes. All patches were in flat areas and co-occurring vegetation among patches within populations was similar. At Wibaux, twenty-one 3 m × 7 m plots were arranged within each patch, resulting in a total of 63 plots. Buffers between plots ranged from 1.5 to 2 m. Seven plots in Patch 2 were lost in spring 2012 and seed bank data were not collected from these seven plots in spring or fall 2012. At Carson, the three 0.01 km^2 patches were at least 400 m apart from one another; we placed 8 plots within each patch, resulting in 24 plots in this population. Plot size and within-patch spacing in Carson was the same as Wibaux. To test for the potential effects of different sample sizes and patch spacings on observed variation in the populations, we calculated population-wide CVs (coefficients of variation) of all germination rates and found that Carson had a CV of 0.57 and Wibaux was 0.79; temperature and precipitation data from locations near the populations are shown in Fig. 1.

Carryover seed banks in downy brome are documented at about 0–30% of the total seed population (Chepil 1948, Mack and Pyke 1983, Smith et al. 2008). Each germination event would therefore largely include recently-produced seeds, with a small percentage of seeds produced in previous years: a fall germination event in 2011 would largely be from seeds produced in 2011. Because of longer after-ripening requirements, much of the field brome seed bank is likely to be from seeds produced the previous year (Baskin and Baskin 1981): a fall germination event in 2011 would largely be from seeds produced in 2010. Temperature and precipitation patterns over the course of the experiment were close to 30 year averages (Figure 1), except the extremely wet spring of 2011 which may have delayed seed maturation that summer. There was sufficient precipitation prior to each collection event to support the expectation that seeds had germinated in the months prior to collection. Samples to measure summer / fall germination were collected on 7 and 17 September 2011 (63 plots at Wibaux, 24 at Carson), and 24 and 28 September 2012 (56 plots at Wibaux, 24 at Carson). Samples to measure winter/spring germination were collected on 11 May 2012 (56 plots at Wibaux, 24 at Carson) when we collected surface soil and litter to a depth of 5 cm from two locations within each plot using a tulip bulb planter (11-cm tall: base and top diameter 6 cm and 7.5 cm, respectively). Soils were sieved, and all *Bromus* seeds were counted and visually examined. Seeds with radicles protruding were labeled “germinated,” and seeds that appeared intact (filled seeds without radicle protrusion) were categorized as “ungerminated.” The number of emerged seedlings (radicle protruding and coleoptile visible) at each collection date was negligible. The average number of seeds per cm^3 for downy brome was 10 at Carson and 3 at Wibaux; field brome was 1 and 4 respectively.

We used generalized linear mixed models (binomial distribution with loglink function, *glmer* in R package lme4) to analyze the influence of population, patch (within population), collection timing, and the interaction between patch

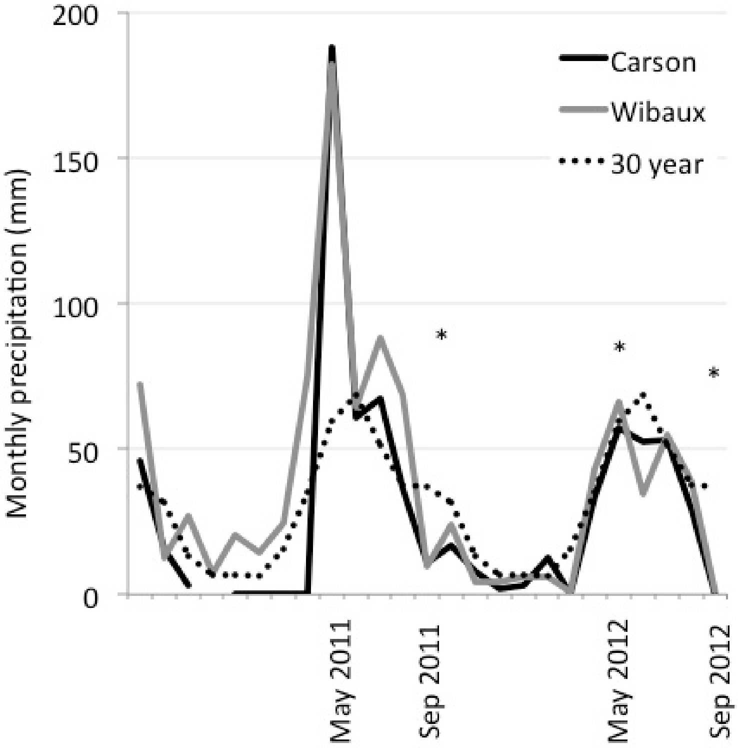

Figure 1. Climate data for Wibaux and Carson sites and 30 year normals from Wibaux. (A) Monthly precipitation from the Wibaux NOAA weather station (46°59’ N 104°09’ W), from the site nearest to Carson (Lindsay, 47°14’ N 105°09 W). (B) Average monthly temperature from the Wibaux weather station (temperature unavailable from Lindsay). Dotted line indicates 30 year normal. * indicates sample collection event.

and collection timing on the germinated fraction of each annual brome species. Because between population differences in relative germination were strong ($P < 0.001$), we analyzed populations separately to maximize our ability to distinguish patch and collection timing effects. For each species in each population, we examined differences among patches and time periods in germination, with plot ID as a random effect. When significant effects had greater than two levels, we used multiple contrasts within the model (*glht* in R package multcomp) to determine differences among factor levels. Three plots in the field brome Carson population had no seeds: these plots are responsible for an uneven number of plots between downy brome and field brome analyses.

Patch was always a significant main effect (Wibaux downy brome $\chi^2_{1,56} = 14.91$, $P < 0.001$; Wibaux field brome $\chi^2_{1,56} = 7.047$, $P < 0.03$; Carson downy brome $\chi^2_{1,24} = 10.58$, $P < 0.01$; Carson field brome $\chi^2_{1,21} = 6.341$, $p < 0.05$) and collection timing was a significant main effect for each population (Wibaux downy brome $\chi^2_{2,56} = 760.0$, $P < 0.001$; Wibaux field brome $\chi^2_{2,56} = 1449$, $P < 0.001$; Carson downy brome $\chi^2_{2,24} = 178.72$, $P < 0.001$) except Carson field brome ($\chi^2_{2,21} = 0.0282$, $P > 0.98$). The largest germination fraction for all populations was at the summer/fall collection event (Table 1), although it was not always significantly largest.

When germination is predictable for each population of each species, we expect no patch by collection timing interaction: patches within populations should respond the same way to climate. The interaction between collection timing and patch was a significant main effect for each population (Wibaux downy brome $\chi^2_{4,56} = 403.6$, $P < 0.001$; Wibaux field brome $\chi^2_{4,56} = 127.3$, $P < 0.0001$; Carson downy brome $\chi^2_{4,24} = 15.78$, $P < 0.01$) except Carson field brome ($\chi^2_{4,21} = 0.0282$, $P > 0.20$). Of the 18 possible 2-way interactions in the Wibaux populations, 11 were significant for downy brome and 15 were significant for field brome. Of the 18 possible 2-way interactions in the Carson populations, 6 were significant for downy brome and none were significant for field brome. Within each collection date, there were differences among patches at Wibaux for downy brome (Fig. 2a) and field brome (Fig. 2b). There were significant differences among patches for downy brome at Carson (Fig. 2c). There was no consistency in the differences among patches; no patch was always highest or lowest across collection dates.

In Northern Great Plains, the reduction of one annual brome species is associated with an increase in the other (Espeland and Kilian 2015), however, we find that this dynamic is not explained by opposite germination cues: only in winter/spring of 2012 does the highest germination rate shift between species across patches (Fig. 2a, 2b). We found that, on the population scale, overall germination rates of the two species can be similar: downy brome and field brome had similar germinated fractions at Wibaux in both winter/spring 2012 and summer/fall 2012 (Table 1).

Significant variation among patches in both Wibaux and Carson populations of downy brome indicates that germination cues and/or responses are influenced by microenvironment and that control of downy brome is unlikely without repeated herbicide application throughout the year. The micro-environmental factors that affect germination change across years and seasons. Overall, there was less variation among patches in the Carson populations of downy brome and field brome. Very low germination rates at Carson for field brome contributed to the lack of differences between collection timings. Lower variation at Carson could be due to its relatively recent cultivation history: formerly plowed sites have different community assembly mechanisms than unplowed sites (Morris et al. 2011). In addition, cultivated sites tend to be more homogeneous in soil conditions than uncultivated ones (e.g. Paz-Gonzalez et al. 2000).

Spatial differences in germination patterns could be explained by the mediation of germination rates by abiotic conditions such as soil water holding capacity (Coffin and Laurenroth 1989, Benvenuti 2003) or by sensitivity to soil biology (Hamman et al. 2002, Espeland 2015). Environmental conditions experienced by the maternal plant that affect seed sizes can have large effects on germination rates in weedy annual grasses (Leger et al. 2009, Dyer et al. 2010): different patterns of maternal responses or maternal effects could be a factor in creating spatial patterns in germination.

Our results agree with others (Chepil 1946, Mack and Pyke 1983) that have found that variation among years has a larger effect on germination in these species than spatial variation. Differences in germination fractions among collection dates (Table 1) are much greater than differences among patches within collection dates (Figure 2).

Herbicide control of annual bromes in pastures is difficult and has variable efficacy (Espeland and Kilian 2015). The variation we found in germination of both annual *Bromus* species indicates another reason why they may be so difficult to control in rangelands. Timing control activities to the most vulnerable life history stage is very difficult when germination occurs throughout the year and when germination is variable in space. None of the populations appeared to be reliably spring- or fall- germinating.

Biological control exploration for downy brome focuses on increasing seed and post-emergent mortality through soilborne pathogens (Kennedy et al. 1991, Meyer et al. 2007) and our study adds to the evidence that efficacy of biological control may differ among sites (Finch et al. 2013, Espeland 2015). Biological and chemical control may be more feasible, or at least more uniform, in recently-cultivated lands compared to native prairie.

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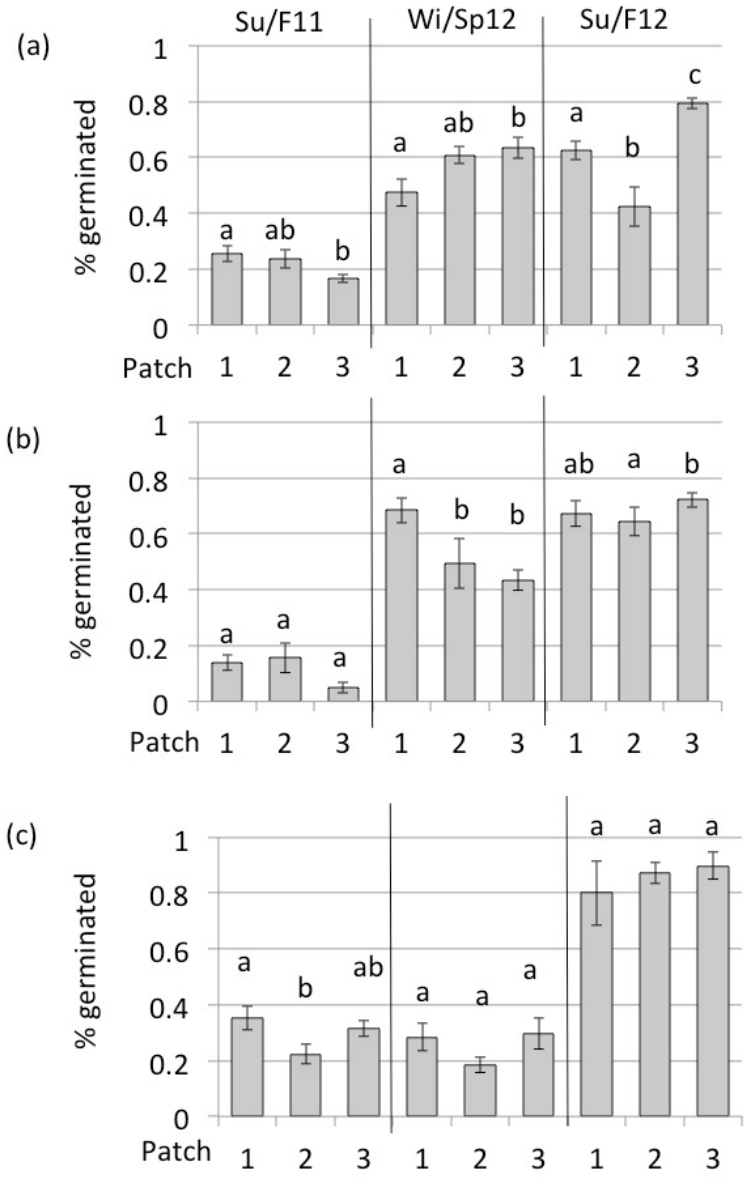

Figure 2. Percent germination by patch by population: a) downy brome at Wibaux, b) field brome at Wibaux, c) downy brome at Carson. X-axis collection dates are in chronological order: summer/fall 2011, winter/spring 2012, and summer/fall 2012. Bars are one standard error. Different letters indicate significant differences among patches within collection dates using multiple comparisons ($P < 0.05$).

Table 1. Percent germination of each population by collection timing: average (one standard deviation). Different letters indicate significant differences within populations across collection dates using multiple comparisons ($P < 0.05$).

	Carson		Wibaux	
	Downy brome	Field brome	Downy brome	Field brome
Summer/fall2011	30 (11)^{A}	1.5 (3.4)^{A}	22 (12)^{A}	11 (14)^{A}
Winter/spring2012	26 (13)^{B}	0.6 (1.5)^{A}	57 (19)^{B}	54 (25)^{B}
Summer/fall2012	86 (21)^{C}	35 (37)^{B}	64 (22)^{C}	68 (18)^{C}

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