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Abstract: The generalist fungal pathogen *Pyrenophora semeniperda* occurs primarily in cheatgrass (*Bromus tectorum*) seed banks, where it causes high mortality. We investigated the relationship between this pathogen and its cheatgrass host in the context of fire, asking whether burning would facilitate host escape from the pathogen or increase host vulnerability. We used a series of laboratory and field experiments to address the ability of host seeds and pathogen life stages to survive fire. First, we determined the thermal death point (TDP50; temperature causing 50% mortality) of seeds and pathogen propagules at two time intervals using a muffle furnace. We then measured peak fire temperatures in prescribed burns at sites in Utah and Washington, and quantified seed and fungal propagule survival using pre- and post-burn seed bank sampling and inoculum bioassays. Last, we investigated the survival of both seeds and pathogen after wildfires. We found that radiant heat generated by both prescribed and wild cheatgrass monoculture fires was generally not sufficient to kill either host seeds or pathogen propagules; most mortality was apparently due to direct consumption by flames. The 5-minute mean TDP50 was 164°C for pathogen propagules and 148°C for host seeds, indicating that the pathogen is more likely to survive fire than the seeds. Peak fire temperature at the surface in the prescribed burns averaged 130°C. Fire directly consumed 85-98% of the viable seed bank, but prescribed burns and wildfires generally did not lead to dramatic reductions in pathogen inoculum loads. We conclude that the net effect of fire on this pathosystem is not large. Rapid post-burn recovery of both host and associated pathogen populations is the predicted outcome. Post-fire management of residual cheatgrass seed banks should be facilitated by the persistent presence of this seed bank pathogen.

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1 **Fire effects on the cheatgrass seed bank pathogen *Pyrenophora semeniperda***

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ABSTRACT

21
22 The generalist fungal pathogen *Pyrenophora semeniperda* occurs primarily in cheatgrass
23 (*Bromus tectorum*) seed banks, where it causes high mortality. We investigated the relationship
24 between this pathogen and its cheatgrass host in the context of fire, asking whether burning
25 would facilitate host escape from the pathogen or increase host vulnerability. We used a series
26 of laboratory and field experiments to address the ability of host seeds and pathogen life stages to
27 survive fire. First, we determined the thermal death point (TDP₅₀; temperature causing 50%
28 mortality) of seeds and pathogen propagules at two time intervals using a muffle furnace. We
29 then measured peak fire temperatures in prescribed burns at sites in Utah and Washington, and
30 quantified seed and fungal propagule survival using pre- and post-burn seed bank sampling and
31 inoculum bioassays. Last, we investigated the survival of both seeds and pathogen after
32 wildfires. We found that radiant heat generated by both prescribed and wild cheatgrass
33 monoculture fires was generally not sufficient to kill either host seeds or pathogen propagules;
34 most mortality was apparently due to direct consumption by flames. The 5-minute mean TDP₅₀
35 was 164°C for pathogen propagules and 148°C for host seeds, indicating that the pathogen is
36 more likely to survive fire than the seeds. Peak fire temperature at the surface in the prescribed
37 burns averaged 130°C. Fire directly consumed 85-98% of the viable seed bank, but prescribed
38 burns and wildfires generally did not lead to dramatic reductions in pathogen inoculum loads.
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40 recovery of both host and associated pathogen populations is the predicted outcome. Post-fire
41 management of residual cheatgrass seed banks should be facilitated by the persistent presence of
42 this seed bank pathogen.

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KEY WORDS45 biological invasion, *Bromus tectorum*, natural enemies, plant-microbial interactions,46 *Pyrenophora semeniperda*, thermal death point

47

INTRODUCTION48 The cheatgrass (*Bromus tectorum* L.) invasion of vast areas of the Intermountain West is

49 uniquely intertwined with fire. Cheatgrass has increased the frequency and size of wildfires, and

50 these fires have in turn allowed cheatgrass to expand its dominance (Whisenant 1990; D'Antonio

51 and Vitousek 1992; Rotenberry and Knick 1997; Chambers et al. 2007). Cheatgrass typically

52 completes its life cycle as a winter annual. It produces highly flammable standing dead biomass

53 in early summer following seed production, greatly increasing the likelihood of subsequent fire

54 (Blank et al. 2006). Following burning, these wildlands often persist as cheatgrass-dominated

55 areas, threatening the existence of many native plants and animals (Baker 2006; Humple and

56 Holmes 2006; Keeley 2006; Larrucea and Brussard 2008). Even prescribed shrubland burns that

57 aim to increase forage for livestock often result in an expansion in annual grass invasion,

58 especially on more arid sites in the shrub steppe (Keeley 2006).

59 A key component of the cheatgrass-fire cycle is the fact that a fraction of the cheatgrass

60 seed bank can survive fire (Humphrey and Schupp 2001; Young et al. 1976), thus allowing for

61 its recovery following fire and its eventual domination of burned sites. Several factors can

62 influence the number of cheatgrass seeds surviving a fire. Seed mortality is greatest with fires

63 that burn while seeds are still attached to the plant, especially just before seed shatter in the

64 summer (Brooks 2002). Higher seed mortality has also been reported for fires that burn at higher

65 temperatures (Brooks 2002), either due to exceptionally high density of standing dead biomass

66 (Humphrey and Schupp 2001) or to the presence of woody plants (Brooks 2002). Although most
67 factors influencing the number of cheatgrass seeds surviving fires are abiotic (as listed above),
68 biotic factors may also affect cheatgrass ability to recover following fire.

69 Cheatgrass-associated fire can potentially have profound effects on the soil microbial
70 community. This may be important for understanding the cheatgrass-fire cycle because changes
71 in plant-microbe interactions, both positive and negative, may influence native species recovery
72 following fire. If burning reduces plant-suppressive microbes or pathogens that provide biotic
73 resistance to cheatgrass, or reduces beneficial mycorrhizae that facilitate native species
74 establishment, then the post-fire period can provide a window that favors cheatgrass expansion
75 over native species establishment. The positive plant-microbe interactions in cheatgrass-invaded
76 shrub steppe, specifically those involving mycorrhizae, have been examined by Rowe et al.
77 (2007). The effects of fire on negative plant-microbe interactions in the shrub steppe remain
78 largely unexplored. However, Kinter et al. (2007) found that rush skeletonweed (*Chondrilla*
79 *juncea*) seeds had higher emergence in field-burned cheatgrass-invaded soils than in unburned
80 soils, suggesting that perhaps soil organisms with a negative impact on rush skeletonweed may
81 themselves be negatively impacted by fire. The soil microbes in the Kinter et al. (2007) study
82 were not identified.

83 An important soil microbial organism of cheatgrass-invaded sites is the ascomycete seed
84 bank pathogen *Pyrenophora semeniperda* (Brittlebank and Adam) Shoemaker (anamorph
85 *Drechslera campanulata* (Lév.) B. Sutton). Seed infection is usually initiated by asexually
86 produced spores (conidia), which germinate on the surface, penetrate the coverings, and then
87 ramify as mycelium inside the seed (Beckstead et al. 2007). As the seed is consumed, the fungus
88 initiates sporulation by producing elongate black stromata (i.e., sporocarps) that protrude through

89 the seed coverings. These stromata then produce another generation of conidial spores that are
90 released into the seed bank. *Pyrenophora semeniperda* frequently kills large numbers of
91 cheatgrass seeds in field seed banks. Meyer et al. (2007) obtained densities of field-killed
92 cheatgrass seeds with distinctive *P. semeniperda* stromata as high as 20,000 seeds per m² at cold
93 desert sites in Utah and Idaho. *Pyrenophora semeniperda* usually has greater impacts on
94 cheatgrass seed banks at drier sites, where the secondarily dormant seeds in the spring seed bank
95 that are its primary host are likely to be present in higher densities (Beckstead et al. 2007). Soil
96 seed banks dominated by cheatgrass maintain much higher inoculum levels of this generalist
97 seed pathogen than native grass seed banks (Beckstead et al. 2010).

98 The primary question addressed in our study is how fire impacts survival of *P.*
99 *semeniperda* and seeds of its cheatgrass host. If fire completely destroys the pathogen, then
100 cheatgrass seeds surviving the fire would be able to establish free of this natural enemy.
101 Conversely, if the pathogen has high post-burn survival, then cheatgrass recovery from the seed
102 bank could be negatively impacted. We investigated this question and these hypotheses in a
103 series of laboratory and field studies. First, we quantified the thermal death point (temperature at
104 which 50% of the individuals experience death) for three life stages of *P. semeniperda* (i.e.,
105 conidia, mycelium, and stromata) and for cheatgrass seeds. Second, we measured the
106 temperature of prescribed cheatgrass fires in the field and compared field temperatures with the
107 thermal death points. Third, we determined the ability of *P. semeniperda* propagules and
108 cheatgrass seeds to survive both prescribed fires and natural wildfires.

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METHODS

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113 **Thermal Death Point Determination**

114 To determine the thermal death point (TDP₅₀, temperature causing 50% mortality) for cheatgrass
115 seeds and for three life stages of the pathogen, we subjected them to a range of temperatures in a
116 muffle furnace (20 (control), 65, 100, 125, 150, 200 and 300°C) for 5 or 15 minutes (to simulate
117 fast vs. slow-burning fires), and performed subsequent survivability assessment. First, to obtain
118 the three life stages of the pathogen, we used conidial inoculum obtained from a *P. semeniperda*
119 isolate from Tenmile Creek, Box Elder County, Utah USA (see Beckstead et al. 2010 for
120 inoculum production methods). We inoculated groups of 15 healthy, viable cheatgrass seeds
121 with 0.001 g of dry conidial inoculum by placing seeds and inoculum together in glass vials (4
122 ml) and shaking vigorously for one minute using a hand-held shaker. For the conidial stage,
123 inoculated seeds were placed immediately into the heat treatment. To produce the mycelial and
124 stromatal life stages, inoculated seeds were incubated for 4 and 14 days, respectively, in
125 individual Petri dishes (100 x 15 mm) on moist germination blotters (Anchor Paper, St. Paul,
126 MN, USA) in a dark 20°C incubator. The seeds with mycelium or stromata were then allowed to
127 air-dry prior to heat treatment. Fifteen replicate seeds in individual Petri dishes for each fungal
128 stage treatment (uninoculated, with conidia, with mycelium, and with stromata) were subjected
129 to each heat treatment.

130 To assess pathogen survival following the heat treatment, an uninfected host seed from
131 the same seed collection was placed on each side of the inoculated, heat-treated seed, as a 'bait'
132 for the pathogen. The dishes were incubated at 20°C in the dark for 4 weeks and scored for
133 development of stromata on at least one bait seed, indicating survival of the pathogen to

134 infection. For the seed survival assessment, uninoculated, non-dormant heat-treated seeds were
135 incubated as described above and scored for germination.

136 The effect of temperature treatment on survival of pathogen life stages and cheatgrass
137 seeds was analyzed using logistic regression (LOGIT; JMP, Version 8.0.1, SAS Institute Inc.,
138 Cary, NC, USA). Model optimal predictability was determined by Receiver Operating
139 Characteristic (ROC) curve area and was satisfactory for each analysis (DeLong et al. 1988).
140 Inverse prediction set at 50% was used to calculate TDP₅₀. This experiment included 15
141 replicated seeds for each of the pathogen life stages and cheatgrass seeds subjected to each of
142 seven heat treatments at two time intervals, for a total of 840 experimental units.

143 **Prescribed Burn Studies**

144 We utilized sites at Whiterocks in Skull Valley, Utah USA (40°32' N 112°77' W, 1450 m
145 elevation) and at Haven Flats on the Hanford Reach National Monument in Washington USA
146 (46°39' N, 119°40' W, 96 m elevation) for prescribed burn studies. These studies combined
147 evaluation of peak fire temperatures using pyrometers, a bioassay technique for assessment of
148 inoculum loads of *P. semeniperda*, and direct examination of pre-burn and post-burn seed banks
149 (Beckstead et al. 2010). The design included twenty burned plots (0.10 m²) at each site. Each
150 plot was sampled before and after burning for the inoculum load and seed bank studies; peak fire
151 temperatures were measured on each plot during the burn.

152 The prescribed burns were applied differently at the two sites, but both took place in
153 near-monocultures of cheatgrass (>85 % cover). At the Haven Flat site, the plots were burned as
154 part of a prescribed fire (743 m²) carried out in conjunction with associated field inoculation
155 studies (P. Allen, unpublished data). The fire crew used a backing-fire technique to burn into the

156 wind, resulting in a low rate of spread (8 chains per hour). Pre-burn sampling took place on
157 April 19, 2008, the burn took place on June 8, 2008, and post-burn sampling took place on June
158 12, 2008. The twenty 0.10 m²-sampling plots were randomly chosen along five randomly
159 chosen transects; plots sampled were a minimum of 2 m apart.

160 At Whiterocks, we were unable to carry out our large-scale prescribed burn in a timely
161 manner. Instead, individual plots were burned using a burn-barrel technique (Korfmacher et al.
162 2003), which is appropriate for field studies where precise knowledge of timing and magnitude
163 of temperature changes are not needed. We utilized a steel burn-barrel 1 m in diameter, which
164 enclosed the sampling plot (0.10 m²) with at least a 20-cm buffer from the edge of the barrel and
165 which included slots around the bottom to permit air intake during the burn. Conditions during
166 the burn were hot, windy, and dry, resulting in very rapid fuel consumption after ignition within
167 each barrel placement, with a flame duration of <30 seconds. The pre-burn samples were taken
168 on May 20, 2008, the burn took place on July 8, 2008, and the post-burn samples were taken on
169 July 8, 2008. The 1-m burn-barrel plots were laid out at 1.5 m between-plot intervals along two
170 transects spaced 2 m apart.

171 **Peak Fire Temperature Measurement.** At the center of each of twenty sampling plots
172 (0.10 m²) at a given site, we installed pyrometers at four vertical positions to measure relative
173 peak fire temperature: 5 cm above the soil surface, at the soil surface, and at 1 cm and at 3 cm
174 below the soil surface. Pyrometers were constructed using industrial temperature-indicating
175 lacquer paints (Tempilaq, Tempil, Inc., South Plainfield, NJ, USA) applied to thin copper oval
176 tags (90 mm x 19 mm x 0.125 mm; National Band and Tag Co., Newport, KY, USA) using
177 methods similar to those of Wally et al. (2006). The tags were painted with eight Tempilaq
178 paints melting at 52, 56, 79, 93, 121, 177, 232, and 288°C, painted in 10 mm streaks with 5 mm

179 between streaks. The temperatures selected encompass the expected range of cheatgrass-
180 associated fires and mirror those measured by Brooks (2002). After drying, the painted surface
181 was covered with another copper tag and secured with wire through the tag eyelet and a staple.
182 Pyrometers were exhumed on the same date that inoculum bioassay samples were taken and
183 evaluated visually to estimate peak burn temperature.

184 We analyzed the peak fire temperature experiment as a mixed model ANOVA with block
185 nested within site as the random effect (Proc Mixed; SAS Version 8.1, SAS Institute Inc., Cary,
186 NC, USA). Site and pyrometer position were considered fixed effects. The response variable
187 (peak fire temperature) was transformed to improve homogeneity of variance. This experiment
188 included 20 replicated plots at each of four pyrometer positions at each of two field sites for a
189 total of 160 experimental units.

190 **Pathogen Inoculum Bioassay.** The two inoculum bioassay sample points (i.e., pre- and
191 post-burn) in each plot were consistently located relative to pyrometer placement. We took
192 samples by pounding a steel ring (10 cm diameter and 2.5 cm deep) into the soil until it was flush
193 with the surface. A mason's trowel was then used to lift the ring with its surface litter and
194 underlying soil layer intact (i.e., an intact sample of the seed zone). Twenty ring samples, one
195 from each sampling point, were then placed in Petri dishes (15 × 100 mm), bound with rubber
196 bands and transported to the laboratory. This procedure was carried out both before and after
197 burning, for a total of 40 ring samples from each site.

198 Inoculum bioassays were conducted by planting dormant cheatgrass seeds into the seed-
199 zone rings and monitoring *P. semeniperda*-caused disease. Within three weeks of field
200 collection, each seed-zone ring was planted with twenty-five surface-sterilized and safranin-dyed

201 dormant cheatgrass seeds (dyed to distinguish them from *in situ* seeds; see Beckstead et al. 2010
202 for methods). Bioassay rings were incubated for 4 weeks at 20°C without lights; rings were
203 randomized weekly and watered as needed. Coleoptiles of any emerged seedlings were kept
204 clipped to 2-5 cm. On day 28, all safranin-dyed seeds were exhumed and examined for
205 germination and for presence of disease (*P. semeniperda* stromata). Seeds were classified as
206 germinated without stromata, germinated with stromata, ungerminated without stromata, and
207 ungerminated with stromata. All seeds that developed stromata, whether they germinated or not,
208 were presumed to have been infected by the pathogen (Beckstead et al. 2007). All ungerminated
209 seeds lacking fungal stromata were checked for viability using a cut test (Ooi et al. 2004). There
210 was little or no loss of viability due to causes other than *P. semeniperda*.

211 We analyzed the inoculum bioassay experiment as a mixed model ANOVA with block
212 nested within site as the random effect in SAS Proc Mixed as described earlier. Site and burn
213 treatment were fixed effects. The response variable (proportion of seeds infected) was
214 transformed to improve homogeneity of variance. This experiment contained 20 replicated field-
215 collected seed-zone sample (each planted with 25 seeds) for each of the burn treatments (pre-
216 and post-burn) at each of two study sites, for a total of 80 experimental units.

217 **Seed Bank Quantification.** We also monitored the effects of the prescribed burn
218 treatments described earlier on cheatgrass seed banks. Pre- and post-burn seed bank samples
219 were collected from the same plots on the same dates as the bioassay ring samples. Seed bank
220 samples were collected using a steel can 6 cm in diameter and 4 cm deep, which was inverted
221 and pressed into the soil until flush with the soil surface, then lifted out with a mason trowel and
222 its contents emptied into a labeled paper sack. Samples were air-dried, screened, and hand-
223 processed to remove all apparently viable and field-killed cheatgrass seeds (see Beckstead et al.

224 2010 for methods). Apparently viable seeds were incubated for 4 weeks at 20°C and scored as
225 germinated, viable but dormant, killed in incubation by the pathogen, or nonviable/unfilled.
226 From this incubation test, we determined the following response variables: viable seed density
227 (i.e., living, free of disease, the sum of germinated and dormant seeds), field-killed seed density
228 (i.e., recently killed by *P. semeniperda* in the field and exhibiting stromata), and incubation-
229 killed seeds (i.e., seeds obtained from field that were pre-infected with *P. semeniperda* and that
230 developed disease signs in incubation).

231 For Whiterocks, we included a third sample data set in the seed bank analysis. These
232 samples were taken from a closely adjacent area (within 50 m of the burn study) as part of a
233 different study. Samples were taken from 20 blocks in an unburned area on August 27, 2008,
234 and processed and evaluated as described above. The reason for including this third data set was
235 to obtain an estimate of seed survival after burning. Because initial sampling on the burn plots
236 took place before seed dispersal, but both burning and post-burn sampling were delayed until
237 after seed dispersal, sampling from an adjacent unburned area was necessary to obtain an
238 estimate of seed rain prior to the burn. Field-killed seed densities were expected to be the same
239 for pre-burn and unburned plots, as these are not likely to change during summer; the only
240 variable expected to change between pre-burn (and pre-seed-dispersal) plots and unburned plots
241 was viable seed density.

242 We had a similar problem estimating seed survival after burning at Haven Flats, but we
243 did not have a seed bank data set from an unburned area for comparison purposes. Instead, we
244 used a data set for cheatgrass density on burned vs. unburned plots obtained as part of an
245 adjacent field inoculation study (P. Allen, unpublished data) to indirectly estimate seed survival
246 after burning. The difference in plant density on burned and unburned plots was assumed to be

247 directly related to the variable of interest, namely the difference in seed density with and without
248 burning. These data were obtained the spring following the same prescribed burn described
249 above for Haven Flats. Fifteen 0.10 m² uninoculated control plots from adjacent unburned and
250 burned areas at the Haven Flats site were randomly chosen. Each of these plots had received
251 approximately 250 supplemental seeds the previous fall (i.e., post-burn). Although these seed
252 additions complicate the purpose of the present study, we were still able to detect the relative
253 effect of prescribed burning on seed survival, as indicated by post-burn plant density. Both
254 burned and unburned plots received the same seed additions, and these additions were not
255 sufficient to swamp out the effect of burn treatment on the seed bank. To estimate seed survival,
256 density of individual plants was obtained by hand-counting in the field, when cheatgrass was at
257 the early seed production stage. We also counted individual tillers, and biomass per plot was
258 measured by collecting aboveground plant shoots, drying them at 60°C for 72 hours, and
259 weighing. From these measures we calculated plant density, tillers per plant, biomass per plant,
260 and biomass per plot for each of the 30 plots.

261 The analyses for the effect of prescribed burning on the seed bank were different for
262 Whiterocks and Haven Flats. We chose to exclude the seed bank data from Haven Flats because
263 of problems with sampling dates described above. The Whiterocks seed bank data were
264 analyzed using ANOVA in SAS for a completely randomized design with burn treatment (pre-
265 burn, post-burn, and unburned) as the fixed effect. The experiment could not be considered
266 blocked because the unburned treatment was not included in the original block design. Response
267 variables were viable seed density, field-killed seed density, and density of incubation-killed
268 seeds as described earlier; these were log-transformed prior to analysis. We included twenty
269 replications in each of the three burn treatments for a total of 60 experimental units.

270 For the Haven Flats site, the effect of the prescribed burn treatment on plant density,
271 tillers per plant, biomass per plant, and biomass per plot were analyzed using a completely
272 randomized ANOVA design in SAS as described above. The response variables were log-
273 transformed to improve homogeneity of variance prior to analysis. We included 15 replicates for
274 each of the two burn treatments for a total of 30 experimental units.

275 **Wildfire Seed Bank Studies**

276 We took advantage of natural August 2007 burns in cheatgrass monocultures on West Mountain
277 in northern Utah (40.13851 N 111.80478 W, 1390 m elevation) and at Rattlesnake Mountain on
278 the Hanford Reach National Monument in Washington (46.22573 N 83.30382 W, 732 m
279 elevation) to evaluate the effect of wildfire on both cheatgrass seed banks and *P. semeniperda*
280 abundance. Sampling took place within one month of each burn and prior to any cheatgrass
281 autumn germination. On the West Mountain burn, we selected a site where an elongate island of
282 unburned cheatgrass remained in the center of a burned area. This island apparently remained
283 unburned because of wind shifts during the fire and not because of any obvious topographical or
284 soil difference. At 5-m intervals along the boundary of the unburned area, we sampled at a
285 distance of 2 m from the edge of the burn on both the burned and unburned sides. Ten seed bank
286 samples each from burned and unburned areas were obtained. Seed bank samples were taken as
287 described earlier. A similar protocol was followed at the Rattlesnake Mountain site, except the
288 burned and unburned areas were located on opposite sides of a dirt road, 20 samples each from
289 burned and unburned areas were obtained, and a small hand shovel was used instead of a can
290 (although area sampled was roughly the same). Soil seed bank samples were processed and
291 evaluated as described above.

292 Data sets from the two sites were combined for analysis of variance (ANOVA) for a
293 randomized design. We used SAS Proc GLM because of unequal replication between sites.
294 Fixed main effects specified in the ANOVA were site (West Mountain vs. Rattlesnake
295 Mountain) and burn treatment (burned vs. unburned). The response variables were density of
296 viable seeds, density of field-killed seeds and density of incubation-killed seeds; these were log-
297 transformed for analysis to increase homogeneity of variance. This experiment included either 10
298 (West Mountain) or 20 (Rattlesnake Mountain) replicated field-collected seed bank samples for
299 each of the burn treatments for a total of 60 experimental units.

300 RESULTS

301 Thermal Death Point Determination

302 The ability of the seed pathogen *P. semeniperda* to survive high temperature and subsequently
303 infect adjacent host seeds decreased with increasing temperature and varied among life stages
304 after the 5-minute heat treatment (Figure 1a; temperature main effect: Chi-square = 225.27, df =
305 1, $P < 0.0001$; life stage main effect: Chi-square = 6.71, df = 2, $P = 0.03$). The conidial stage
306 experienced 50% mortality at a lower temperature than the mycelial and stromatal stages
307 (conidial stage $TDP_{50} = 141.36^{\circ}\text{C}$, mycelial stage $TDP_{50} = 174.57^{\circ}\text{C}$, stromatal stage $TDP_{50} =$
308 178.34°C).

309 After the 15-minute heat treatment, pathogen survival was again significantly affected by
310 temperature, but the difference between life stages was only marginally significant (Figure 1b;
311 temperature main effect: Chi-square = 227.87; df = 1; $P < 0.0001$; life stage main effect: Chi-
312 square = 5.52; df = 2; $P = 0.06$). Mean thermal death point across life stages was 14% lower for

313 the longer-duration heat treatment (15-minute overall $TDP_{50} = 141.60^{\circ}\text{C}$ and 5-minute overall
314 $TDP_{50} = 164.21^{\circ}\text{C}$), indicating lower survival after a longer heat treatment period.

315 The ability of cheatgrass seeds to survive high temperature also decreased with increasing
316 temperature and showed a similar pattern after 5- and 15-minute heat treatment durations (Figure
317 1c; 5-minute treatment: Chi-square = 126.32, $df = 1$, $P < 0.0001$; 15-minute treatment: Chi-
318 square = 129.78, $df = 1$, $P < 0.0001$). The TDP_{50} for cheatgrass seeds was 10% lower than the
319 mean TDP_{50} for the pathogen at each of the two treatment durations, indicating that the seeds
320 would be killed at a lower temperature than the pathogen (for seeds: TDP_{50} at 5-minute interval =
321 147.64°C and TDP_{50} at 15-minute interval = 127.33°C).

322 **Prescribed Burn Studies**

323 **Peak Fire Temperature Measurement.** Prescribed burn peak fire temperature varied
324 with height above or below the soil surface. The highest flame temperatures were measured at
325 and above the soil surface, averaging around 144°C , whereas fire temperatures were lower below
326 the soil surface, averaging around 63°C (Figure 2; pyrometer position main effect: $df = 3$, 152; F
327 = 74.44; $P < 0.0001$). There was no significant difference in overall peak fire temperature
328 between the two sites (Figure 2; site main effect: $df = 1$, 152; $F = 1.67$; $P = 0.20$). There was
329 however a significant site x pyrometer position treatment interaction ($df = 3$, 152; $F = 5.92$; $P =$
330 0.0008), indicating that soil properties and/or aboveground litter were different between sites,
331 resulting in different peak fire temperature patterns. The fire burned substantially hotter at and
332 above the soil surface at Haven Flats, whereas subsurface temperatures during the burn were
333 slightly higher at Whiterocks.

334 **Pathogen Inoculum Load Bioassay.** Laboratory experiments with field-collected seed-
335 zone samples from pre-burn and post-burn plots at the two sites demonstrated significant
336 differences between sites in the fraction of planted cheatgrass seeds infected by *P. semeniperda*
337 (Figure 3). Mean disease incidence was 25% for Whiterocks Utah but only 13% for Haven Flats
338 (site main effect: $df = 1,76$, $F = 23.48$, $P < 0.0001$). Mean disease incidence did not vary
339 significantly between burn treatments, indicating that pathogen inoculum was generally able to
340 survive fire (burn treatment main effect: $df = 1,76$; $F = 0.14$; $P = 0.71$). There was a significant
341 site x burn treatment interaction, however ($df = 1,76$; $F = 10.57$; $P = 0.002$). This interaction
342 was significant because samples at the Haven Flats site demonstrated a decrease in seed infection
343 following the burn, whereas samples from the Whiterocks site actually showed an increase in
344 post-burn seed infection.

345 **Seed Bank Quantification.** The prescribed burn treatment at the Whiterocks site had a
346 very large impact on viable seed density in the cheatgrass seed bank (Figure 4a; $df = 2,57$; $F =$
347 30.90 ; $P < 0.0001$). Fire drastically reduced the cheatgrass seed bank; only an estimated 12%
348 survived the burn (mean of 30,400 seeds/m² in the unburned plots vs. 3600 seeds/m² in the post-
349 burn plots). The majority (97%) of the seed bank present at the time of the burn was from
350 current-year seed production, as the carryover present prior to both seed shatter and burning was
351 only 800 seeds/m². Fire had a similar impact on field-killed seed density (Figure 4b; $df = 2,57$; F
352 $= 15.68$; $P < 0.0001$). Post-burn density of only 1400 field-killed seeds/m², compared to 7650
353 and 8940 killed seeds/m² in the pre-burned and unburned plots, respectively, or an average burn
354 survival of 17% (Figure 4b). As expected, field-killed seed density did not differ significantly
355 between the unburned area and the pre-burn plots, evidence that these plots represented two sets
356 of samples from essentially the same population (Figure 4b). In contrast to viable and field-

357 killed seed density, the density of seeds killed in incubation did not differ significantly among
358 burn treatments (Figure 4c; d.f. = 2, 57, $F = 0.82$, $P = 0.44$), and for samples from the same plots,
359 the means were very similar (pre-burn 850 vs. post-burn 810 seeds/m²). The density was
360 somewhat higher in the unburned plots, but because of high variance this difference was not
361 significant. Incubation-killed seeds are seeds that were already infected by the pathogen at the
362 time of seed bank drying in late spring, so that the ability of the pathogen to grow out of these
363 seeds following burning indicates that the mycelial stage inside the host seed was able to survive
364 the fire.

365 Prescribed burning at the Haven Flats site also had a large impact on several cheatgrass
366 density and biomass measures taken the following spring. Fire reduced plant density by 96%
367 (Figure 5a; $df = 1,21$; $F = 372.18$; $P < 0.0001$). However, the plants on burned plots had 3x as
368 many tillers as plants on unburned plots (Figure 5b; $df = 1,21$; $F = 114.61$; $P < 0.0001$).
369 Although density varied greatly between burn treatments, biomass per plot did not differ
370 significantly (Figure 5c; $df = 1,28$; $F = 1.11$; $P = 0.30$). Individual plants on burned plots were
371 20x larger on average than plants on unburned plots (Figure 5d; $df = 1,21$; $F = 311.06$; $P <$
372 0.0001).

373 **Wildfire Seed Bank Studies**

374 In the wildfire seed bank studies, density of viable cheatgrass seeds differed between sites and as
375 a function of wildfire (Figure 6a; Table 1). The West Mountain, Utah site had 1.4x as many
376 viable seeds per m² as the Rattlesnake Mountain, Washington site, though both sites had viable
377 seed densities of over 10,000/m² in the unburned treatment. Wildfire dramatically reduced
378 viable seed density at both sites; the Rattlesnake Mountain site had a 98% reduction, while the

379 West Mountain site had an 85% reduction. This difference in seed survival (2 vs. 15%) was
380 reflected in a significant site by burn interaction (Table 1).

381 The potential inoculum load for *P. semeniperda* measured as the density of field-killed
382 cheatgrass seeds with stromata varied significantly between sites; the West Mountain site had a
383 field-killed seed density 20x higher than the Rattlesnake Mountain site (Figure 6b; Table 1).
384 Overall, fire reduced the density of field-killed seeds from 890 to 680 killed seeds/m², a
385 difference that was only marginally significant. The ability of the pathogen to survive fire at the
386 mycelial stage, internally in seeds, was once again indicated by the lack of any significant
387 difference between burn treatments in density of incubation-killed seeds. The West Mountain
388 site had much higher densities of incubation-killed seeds overall (1190 vs. 130/m²), a result
389 similar to the result for field-killed seeds (Figure 6c).

390 DISCUSSION

391 The hypothesis that fire creates a window for cheatgrass expansion by eliminating the natural
392 enemy *P. semeniperda* was not supported. We also found that fires in cheatgrass monocultures
393 destroyed most of the current-year seed production through direct flame consumption, but that
394 fires rarely burned hot enough to kill seeds via radiant heat. In the laboratory experiment, seeds
395 had to be exposed to temperatures greater than 150°C for 5 minutes to result in high mortality. In
396 the prescribed burn experiments seeds at the soil surface or above (i.e., in the litter layer) did
397 experience temperatures around 150°C (duration less than 5 minutes) and would also experience
398 direct flame consumption. However, seeds 1 cm below the soil surface only experienced fire
399 temperature less than 70°C; not hot enough to kill seeds via radiant heat. Similarly, *P.*
400 *semeniperda* inoculum on or in seeds or in the litter may be consumed directly by fire along with

401 host seeds, but if not directly consumed, the pathogen frequently survives. Although both
402 cheatgrass seeds and *P. semeniperda* can survive fire, they do not survive to the same degree; the
403 pathogen exhibited higher post-burn survival than cheatgrass seeds (e.g., Figure 1, Figure 6).

404 Comparison of the thermal death point (TDP₅₀) for pathogen life stages with fire
405 temperatures measured during prescribed burns explains why radiant heat during the cheatgrass
406 burns apparently had little impact on pathogen viability. Laboratory measurements of TDP₅₀ for
407 the pathogen predicted that temperatures above 164°C for 5 minutes were needed for mortality,
408 whereas predicted peak fire temperature for seed mortality was 148°C for 5 minutes. TDP₅₀ was
409 thus higher for the pathogen, indicating that hotter fires would be needed to kill the pathogen
410 than host seeds. The mycelial and stromatal stages of the fungus survived high temperatures
411 better than the conidial stage. Field-measured peak aboveground fire temperatures ranged from
412 about 120°C to 170°C, suggesting that particularly the hotter fire at Haven Flats could have killed
413 some seeds and pathogen propagules via radiant heat. These temperatures are slightly higher
414 than those reported for annual grassland burns in the arid western Mojave Desert (Brooks 2002)
415 but similar to those reported for grassland fires of the Canadian prairies (Bailey and Anderson
416 1980). However, it is likely that peak temperatures during cheatgrass fires usually last only a
417 few seconds, and only rarely as long as five minutes (Stinson and Wright 1969; M. Brooks,
418 personal communication, February 2010). This suggests that TDP₅₀ values for peak temperatures
419 at the short durations experienced in field burns would be even higher, further explaining the low
420 mortality from radiant heat in our field studies. Our data do predict that somewhat hotter fires,
421 as when shrublands first burn (Bailey and Anderson 1980) or when there is exceptionally heavy
422 standing litter (Humphrey and Schupp 2001) could eliminate this pathogen and create a

423 temporary “enemy-free” zone. However, under these hot fire conditions our data predict that it
424 is likely that most if not all cheatgrass seeds would be killed as well.

425 In general, we saw higher seed mortality than pathogen mortality as a consequence of
426 fire, particularly when the pathogen was in the mycelial life stage within seeds. This could be
427 partly due to the superior ability of the pathogen to survive radiant heat. It could also be related
428 to the vertical position of healthy viable seeds versus infected or killed seeds in the seed bank.
429 Most of the viable seeds were recently dispersed and probably located on the surface of the litter,
430 where they would be more likely to be directly consumed by fire. In contrast, infected and killed
431 seeds were carryover seeds that would be likely to be buried deeper in the litter or located at the
432 interface with mineral soil, where they would be less likely to be consumed directly by fire and
433 also less likely to experience lethal doses of radiant heat.

434 From the seed pathogen perspective, prescribed fires and wildfires did not lead to
435 dramatic reductions in infection or inoculum loads; the one exception was the Haven Flats
436 prescribed burn where surface fire temperatures were high, reducing infection by 56%. At
437 Whiterocks, there was no evidence for an inoculum decrease; mortality in the seed bioassay test
438 was actually greater in the post-burn samples. The reason for this is unknown, but it could be
439 related to differences in the phenology of conidial production at the two sites. Cheatgrass at
440 other sites on the Hanford Reach National Monument, where Haven Flats is located, generally
441 have advanced phenology relative to Whiterocks, because the springs are warmer and drier there
442 (Beckstead et al. 2010). It is likely that this relative difference in phenology is present for
443 pathogen conidial production as well. Most infection in seed bioassays is probably due to
444 conidial inoculum. If conidial production had not yet taken place at the time of pre-burn
445 sampling at Whiterocks, this could have reduced infection in the inoculum bioassay test relative

446 to post-burn levels, which in turn were not much impacted by the burn itself because of cooler
447 surface fire temperatures.

448 Integrating our laboratory thermal death point measurements with the field-measured fire
449 intensities, it is clear that annual grassland fires in our study, whether prescribed burns or
450 wildfires, were not hot enough to eliminate *P. semeniperda* from the seed zone. Although spores
451 have been found to be fire-resistant fungal propagules primarily for mycorrhizae (Baar et al.
452 1999; Pattinson et al. 1999; Bruns et al. 2002), other studies support our findings of resistant
453 mycelium embedded within plant tissues. For example, pathogenic fungi such as *Phellinus*
454 *weirii* (Dickman and Cook 1989) and *Phanerochaete raduloides* (Penttilä and Kotiranta 1996)
455 appear to persist as latent mycelium and to spread within living trees after fire. Sporocarps, such
456 as stromata, are often thought to protect fungi during fire (Pattinson et al. 1999), and this idea
457 was also supported by our study. In several of the studies examining fungal life stages and fire,
458 it was found that newly dispersed fungal spores moved on to burned sites and were the primary
459 source of fungal colonization (Wicklow 1975; Johannesson et al. 2001; Bruns et al. 2002).
460 While this process is also likely to occur with *P. semeniperda*, it cannot explain the high level of
461 inoculum found post-burn at Whiterocks, because the samples were taken immediately after
462 burning, so that dispersal onto the site could not yet have taken place.

463 We found that both prescribed fires and wildfire had a dramatic impact on the cheatgrass
464 seed bank. In our quantification of pre- and post-burn viable seed densities, only 2-15% of the
465 seed bank survived fire, values similar to those from prior studies (3 to 20%; Young and Evans
466 1976; Humphrey and Schupp 2001). However, evidence from Haven Flats indicated that
467 cheatgrass was able to compensate for a large reduction in plant density the spring following fire
468 with much larger biomass per individual in burned versus unburned plots. These findings are

469 similar to those for a closely related species, *Bromus rubens*. Brooks (2002) found that biomass
470 per *B. rubens* individual was 5-100x larger in burned than unburned plots, depending on burn
471 treatment and microhabitat, showing the tremendous phenotypic plasticity in response to
472 resource availability. Density and biomass of annual bromes can increase or decrease in the first
473 few years post-fire (Brooks 2002). However, eventually *Bromus* dominates burned sites, and it
474 does so across a wide range of community types throughout the Mojave Desert and Great Basin
475 (Young et al. 1976; Hunter 1991).

476 **IMPLICATIONS**

477 The pathogen *P. semeniperda* can destroy a large fraction of the cheatgrass seed bank, up to 50%
478 of the seeds produced each year (Meyer et al. 2007). The demonstrated ability of this pathogen to
479 survive fire means that pathogen-caused mortality will continue unabated, whether or not a site
480 burns. High mortality from this pathogen appears to have minimal demographic consequences
481 for its annual grass host, however. These minimal consequences result both from prolific host
482 seed production (up to 30,000 seeds/m²; Smith et al. 2008) and because rapid germination of the
483 first seedling cohort each year virtually guarantees that numerous host seeds escape from the
484 pathogen and establish as seedlings that produce seeds the following spring (Beckstead et al.
485 2007). This assures the continued existence of both host and pathogen through time regardless
486 of the frequency of burning. Our studies predict rapid post-burn recovery of both host and
487 associated pathogen populations after fire. Post-fire management of residual cheatgrass seed
488 banks may be facilitated by the persistent presence of this seed bank pathogen. Pathogen attack
489 has the potential to reduce viable cheatgrass seed density, which will likely already be quite low
490 following fire, to levels that could permit post-burn establishment of seeded species.

491

492

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501

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585 Figure captions

586 Figure 1. Thermal death curves showing the effect of radiant heat after 5- and 15-minute heat
587 treatments on survival of *Pyrenophora semeniperda* life stages (a, b) and cheatgrass (*Bromus*
588 *tectorum*) seeds (c) (n = 15 seeds). Thermal death points (TDP₅₀; temperature at which 50% of
589 the individuals experience death) are indicated for the average of all pathogen life stages after 5
590 minutes (a; TDP₅₀ = 164°C), for the average of all pathogen life stages after 15 minutes (b;
591 TDP₅₀ = 142°C), and for cheatgrass seeds after 5 and 15 minutes (c; TDP₅₀ = 148°C and 127°C,
592 respectively).

593 Figure 2. The peak fire temperatures measured during prescribed burns using pyrometers with
594 temperature-indicating paints placed at positions above, at, or below the soil surface at the Haven
595 Flats, Washington and Whiterocks, Utah study sites (mean + 1 SE). Data represent twenty
596 replicated pyrometers for each site by pyrometer position combination.

597 Figure 3. The percentage of cheatgrass (*Bromus tectorum*) seeds infected by the seed pathogen
598 *Pyrenophora semeniperda* after planting into field-collected seed-zone samples collected from
599 twenty burn plots prior to and after burning at each of two prescribed burn sites: Haven Flats,
600 Washington and Whiterocks, Utah (mean + 1 SE). Each replicate included twenty-five planted
601 seeds.

602 Figure 4. Seed bank density of (a) viable seeds (i.e., living, free of disease), (b) field-killed seeds
603 (i.e., recently killed by *Pyrenophora semeniperda* in the field and exhibiting stromata), and (c)
604 incubation-killed seeds (i.e., seeds obtained from field that are pre-infected with *P. semeniperda*
605 and that develop disease signs in incubation) for cheatgrass (*Bromus tectorum*) at Whiterocks,
606 Utah in each of three burn treatments (pre-burn, post-burn, and adjacent unburned; mean + 1

607 SE). Bars capped by the same letter are not significantly different at the $P = 0.05$ level according
608 to a Duncan multiple range test. Data represent twenty-replicated soil seed bank samples
609 obtained from each burn treatment.

610 Figure 5. Effects of a prescribed burn at Haven Flats, Washington on cheatgrass (*Bromus*
611 *tectorum*): (a) density, (b) biomass per unit area, (c) tillers per plant, and (d) biomass per plant
612 (mean + SE). Data represent means from fifteen plots per burn treatment sampled in late spring
613 following prescribed fire the previous summer.

614 Figure 6. Effects of wildfires at Rattlesnake Mountain, Washington and West Mountain, Utah
615 on cheatgrass (*Bromus tectorum*) seed bank (a) viable seed density (i.e., living, free of disease),
616 (b) field-killed seed density (i.e., recently killed by *Pyrenophora semeniperda* in the field and
617 exhibiting stromata), and (c) density of seeds killed in incubation (i.e., seeds obtained from field
618 that are pre-infected with *P. semeniperda* and that develop disease signs in incubation); mean + 1
619 SE. Data represent ten (West Mountain) or twenty (Rattlesnake Mountain) soil samples
620 collected from each treatment combination.

621

622 Table 1. ANOVA results for the effects of site and wildfire burn treatments on seed bank
 623 components, including cheatgrass (*Bromus tectorum*) viable seed density (i.e., living, free of
 624 disease), field-killed seed density (i.e., recently killed by *Pyrenophora semeniperda* in the field
 625 and exhibiting stromata), and density of seeds killed in incubation (i.e., seeds obtained from field
 626 that are pre-infected with *P. semeniperda* and that develop disease signs in incubation).

Source	df	Viable seed		Field-killed seed		Incubation-	
		density	density	density	density	killed seed	killed seed
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Site	1, 56	14.21	0.0004	65.50	0.0001	35.64	0.0001
Burn	1, 56	86.67	0.0001	3.75	0.0578	0.13	0.7214
Site x burn	1, 56	7.63	0.0078	0.05	0.8225	0.04	0.8519

627

Figure 1

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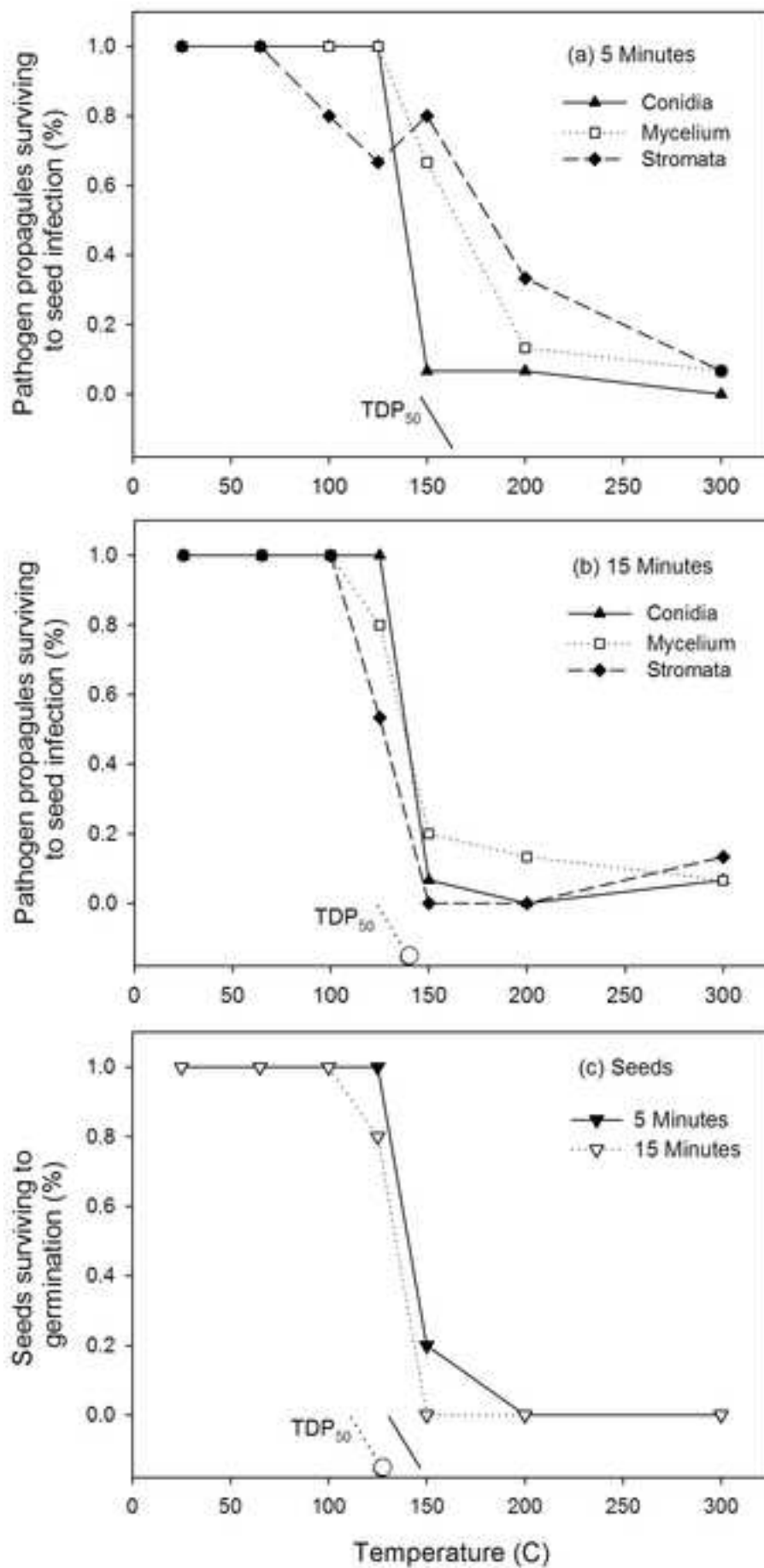


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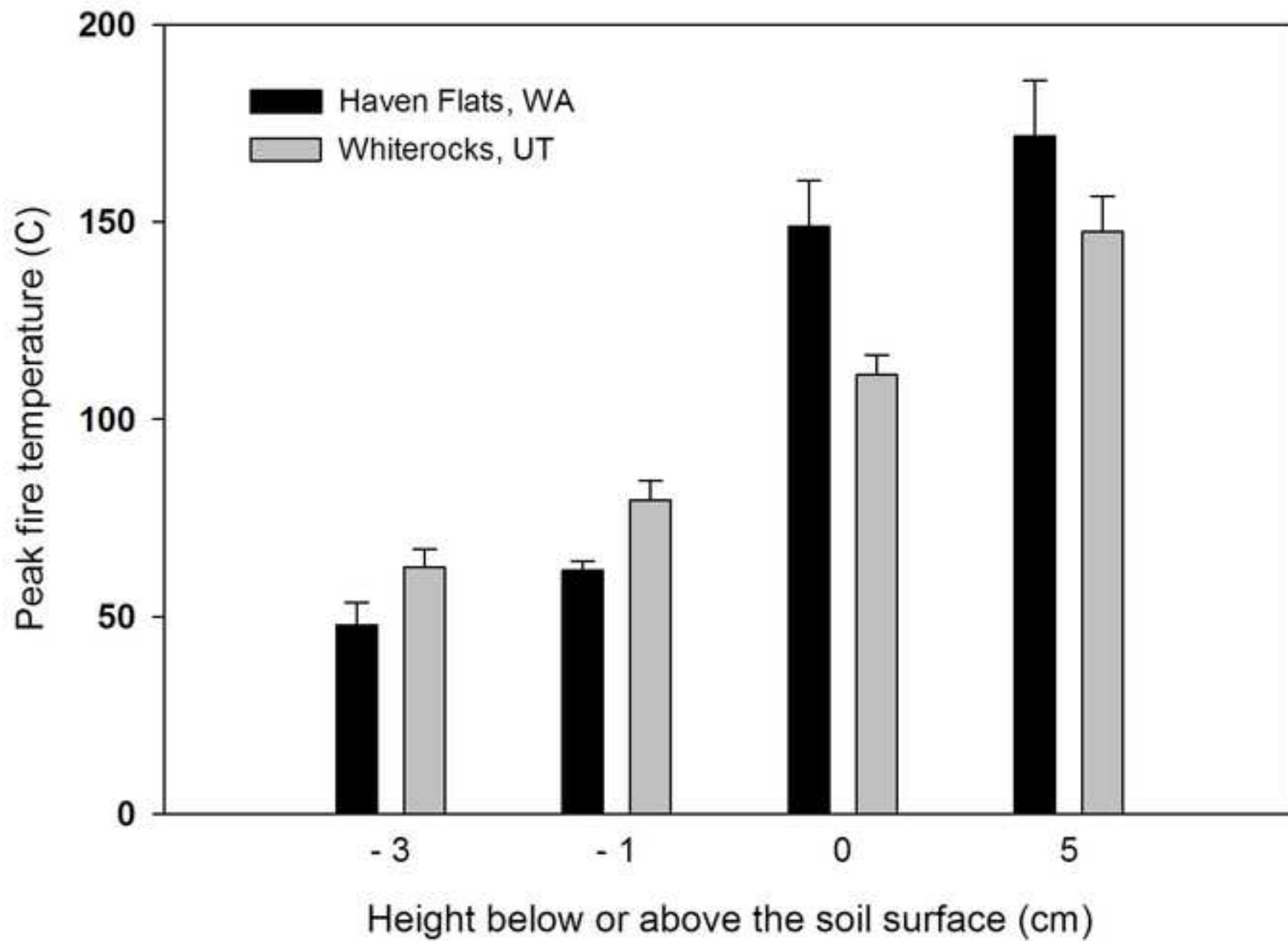


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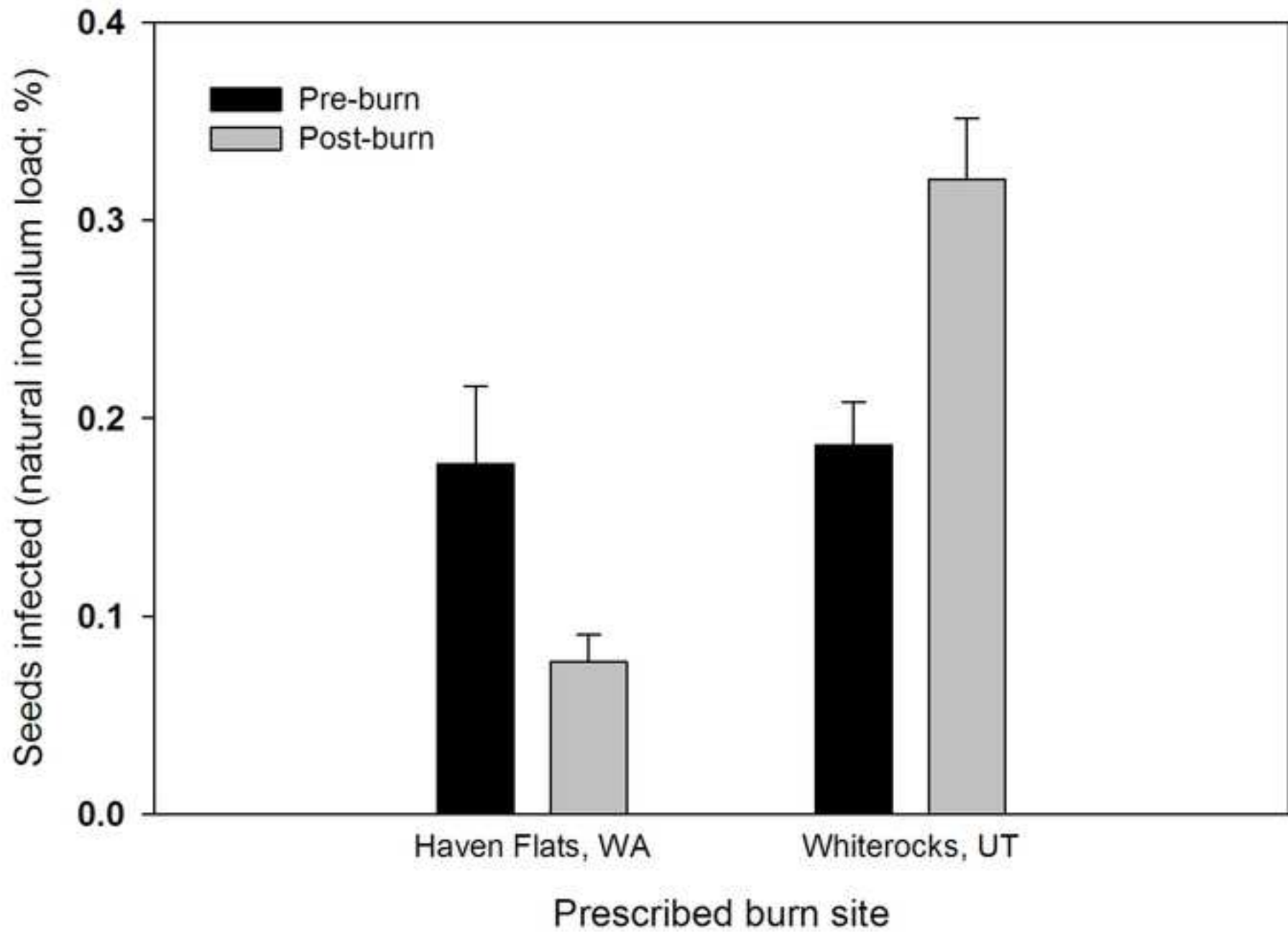


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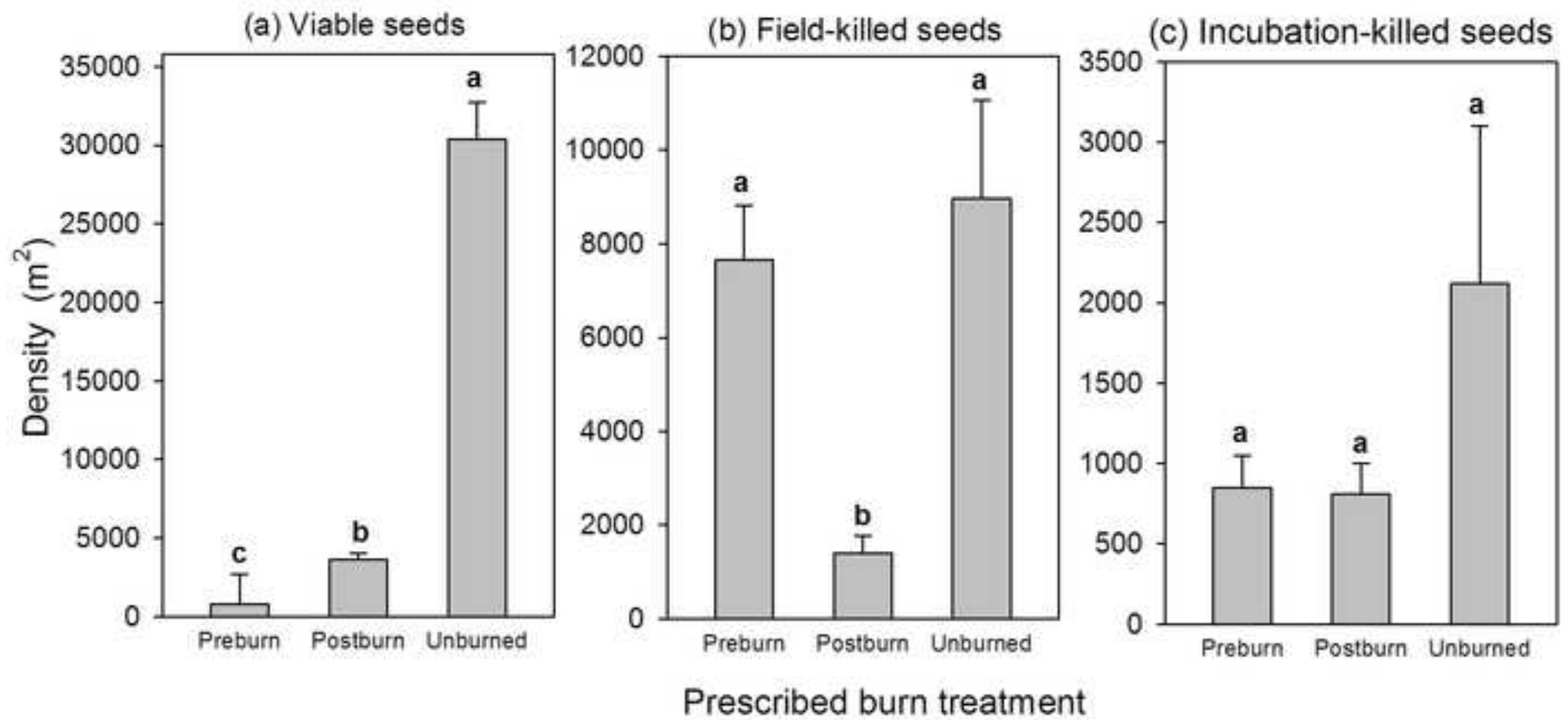


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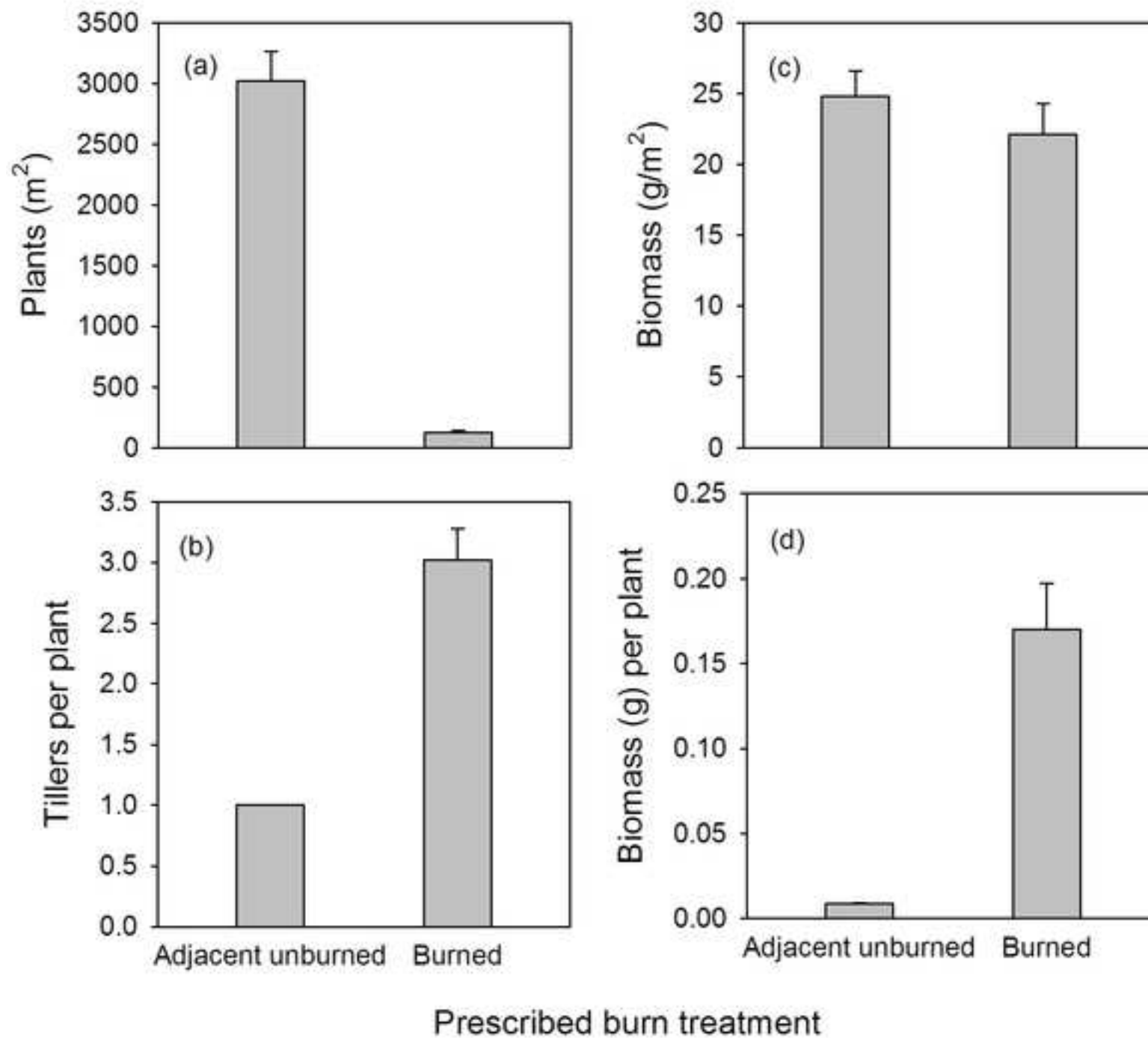


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