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ABSTRACT

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Seeds sown in the fall to restore sagebrush (*Artemisia* spp.) steppe plant communities could experience high mortality when they germinate and seedlings freeze during the winter. Delaying germination until the risk of frost is past could increase seedling survival. We evaluated the use of abscisic acid (ABA) to delay germination of *Elymus elymoides*, *Pseudoroegneria spicata*, and *Linum lewisii*. The following treatments were applied: uncoated seed, seed coated with ABA at 2.2, 4.4, 8.8, 13.2, and 17.6 g of active ingredient kg^{-1} of seed, and seed coated with no ABA. The influence of seed treatments on germination were tested at five different incubation temperatures (5-25°C). The lowest application rate of ABA had no significant influence on germination percentage but higher application rates showed a decline. All concentrations of ABA tested delayed germination, especially at low incubation temperatures. For example, the time required for 50% of the seeds to germinate at 5°C was increased with the use of the lowest ABA application rate by 56, 61, and 14 days, for *E. elymoides*, *P. spicata*, and *L. lewisii,* respectively. Quadratic thermal accumulation regression models were developed for each species and treatment to predict progress toward germination. For the two grasses, models had sufficient accuracy (R^2 = 0.61- 0.97) to predict germination timing using field seedbed temperatures. Equations for *L. lewisii* were less accurate (R^2 = 0.03-0.70). Use of these models will allow testing whether ABA will delay germination sufficiently to avoid winter frost periods and provide the basis for future field tests.

Keywords: abscisic acid, seed coating, squirreltail, bluebunch wheatgrass, Lewis flax, rangeland restoration

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Introduction

Invasion and dominance of sagebrush (*Artemisia* spp.) communities across the Great Basin of North America by annual grasses, especially cheatgrass (*Bromus tectorum* L.), has increased fire frequency and perpetuated weed dominance (D'Antonio & Vitousek 1992; Miller et al. 2001; Balch et al. 2013). The fine and continuous fuels of cheatgrass increase fire frequency while its phenology lengthens the fire season (D'Antonio & Vitousek 1992; Bradley et al. 2006). The recurrent fire cycle caused by cheatgrass dominance negatively affects ecological processes (Miller et al. 2011). For example, dominance of cheatgrass decreases organic carbon stored in the soil (Rau et al. 2011). Annual grass fire cycles reduce habitat of wildlife species such as sage-grouse (*Centrocercus urophasianus*) that depend on the sagebrush steppe system (Knick et al. 2003). To reduce weed dominance and stabilize soils, native and introduced perennial species are seeded in fall after wildfires and other disturbances (Whisenant 1990; Richards et al. 1998; Crawford et al. 2004; Hardegree et al. 2011). However, consistent plant establishment from revegetation projects has been challenging (Mosley et al. 1999; Lysne & Pellant 2004; Knutson et al. 2014). James and Svejcar (2010) and Hardegree et al. (2011) stated that failure rates could be as high as 90%.

Although lack of precipitation is most commonly associated with limited seedling establishment on arid and semiarid rangelands (Hardegree et al. 2011), there is evidence that seedlings may also die from winter freezing. In the Great Basin, soil water recharge occurs in fall, winter, and spring (Roundy et al. 2014). Wildfires in sagebrush steppe generally occur during the hot and dry summers and rangelands are sown for fire rehabilitation in fall before winter snow and rain. The expectation is that germination will occur when temperatures warm in spring and winter soil moisture is still available for seedling growth. However, James et al.

(2011) and Boyd and James (2013) found that 80% of fall-seeded perennial grasses, such as *Pseudoroegneria spicata* (Pursh Á. Löve) (bluebunch wheatgrass) germinated prior to winter and seedling establishment the following spring was only 10-15% of germinated seeds. Those studies were conducted in an *Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young (Wyoming big sagebrush) plant community in the northern Great Basin in Oregon. They also found that freezing usually started in November and ended in March. The majority of freezing periods were < 1 day, and the number of days when freezing occurred ranged from 25 to 50, depending on the year. Roundy and Madsen (personal communication) reported an average of over 58 freeze-thaw periods for the upper 1-3 cm of soil occurring from October to mid-March across 3-4 years and 14 sagebrush steppe sites in the Great Basin. Even short-duration freezing (< 4 d) may significantly reduce seedling emergence and survival (Boyd & Lemos 2013). Seedlings are also susceptible to harmful pathogens (Gornish et al. 2015). Seedbed freezing conditions have been shown to limit natural establishment of big sagebrush (*Artemisia tridentata* Nutt.) (Loik & Redar 2003), which has been especially challenging to successfully establish in rangeland seedings (Arkle et al. 2014; Brabec et al. 2015).

One potential solution to the problem of seedling freezing mortality is to delay germination of fall-sown seeds until spring. The plant growth regulator, abscisic acid (ABA) has been identified as a seed treatment that can prevent germination when environmental conditions do not support seedling survival (Finch-Savage and Leubner-Metzger 2006). ABA radicle emergence (Leubner-Metzger 2006). ABA applications may help avoid seedling frost mortality by delaying seed germination of fall-sown seeds until spring.

The rate that ABA should be applied to delay seed germination has not been studied for application in rangeland systems. Germination timing of many nondormant seed populations is a

function of temperature accumulation when seeds are imbibed (Rawlins et al. 2011a). Hydrothermal models can be used to predict the timing and rate of seed germination based on time above temperature and water potential thresholds (Forcella et al. 2000; Vleeshouwers and Kropff 2000). Because soil water potentials near the soil surface are difficult to accurately measure (Taylor et al. 2007) and because seedbeds may quickly dry out, Roundy et al. (2007) proposed use of a wet thermal accumulation model to predict germination using soil water potentials measured by gypsum blocks (maximum soil matric potential range > -1.5 MPa). Rawlins et al. (2011b) found this model to accurately predict germination in seed bags 50-95% of the time, depending on the season.

Wet thermal accumulation models could be used as a first step in determining approximate ABA application rates. The objectives of this study were to: 1) assess the effect of ABA application rate on total germination percentage and germination rate or the inverse of days to 50% germination, under different constant temperatures, and 2) develop wet thermal accumulation models for different ABA application rates that could be used to predict seed germination timing in the field. Research was conducted on two perennial cool-season grasses and one forb species that are commonly used in seeding efforts in sagebrush communities in the Great Basin. Wet thermal accumulation models developed from this research could be applied to historical seedbed soil temperature and water potential data to predict when germination will occur (Roundy et al. 2007; Rawlins et al., 2011a,b). Application rates of ABA that are predicted to delay seed germination beyond the period when frost mortality occurs would be candidates for further testing in the field.

Materials and methods

Species tested and seed coating formulations

Test species used in the study included the perennial grasses, *P. spicata*, *Elymus elymoides* (Raf.) Swezey (bottlebrush squirreltail) and the perennial forb, *Linum lewisii* Pursh (Lewis flax). Seeds were obtained from certified seed lots purchased from Granite Seed (Lehi, Utah). The plant growth regulator ABA was obtained from Valent BioSciences Corporation (Libertyville, IL), which is sold under the trade name BioNik™. The following treatments were applied in the experiment to test ABA and coating effects: uncoated seed, seed coated with ABA at 2.2, 4.4, 8.8, 13.2, and 17.6 g of active ingredient (a.i.) kg^{-1} of seed, and seed coated with base materials but no ABA. Separate treatments were applied to 100 g of seed on a RP14DB rotary seed coater (Brace Works Automation and Electric, Lloydminster, SK, Canada) according to Table 1. The coating process was divided into two main steps. In the first step, a solution of ABA, distilled water, fungicides, and polymer binder was coated directly onto the seed. We varied the amount of water applied in the recipe so that as ABA application rates changed the total amount of liquid applied would stay the same (Table 1). The fungicides Maxim 4FS and Apron XL (Syngenta, Greensboro, NC), were applied at 2.6 and 20.9 ml kg^{-1} of seed, respectively. The polymer binder Opadry® II (Harleysville, PA) was added to provide stability within the coating. In the second step, we applied the same ingredients as applied in the first step, with the exception that ABA was not included and an equal proportion of water was added in its place so the total liquid amount delivered was the same as in step 1. During the application of liquid in step 2, we also simultaneously added 100 g of Silverline® 002 talcum powder (Imerys Talc, San Jose, CA). Treated seeds were immediately dried with a forced air dryer (Brace Works Automation and Electric, Lloydminster, SK, Canada) at 43 °C for approximately 5 min.

Germination experiment

Seed germination was assessed over a range of constant temperatures (5, 10, 15, 20, and 25 °C), in environmental growth chambers under (12 h/ 12 h) light/dark conditions. For each species and incubation temperature, seeds were germinated in six replicate 15-cm diameter petri dishes that each contained 25 seeds. Petri dishes had a single layer of blue blotter paper (Anchor Paper Co., St. Paul, MN), which was kept moist over the period of the study. Seed germination was counted every 48 hr; with seeds considered to have germinated when the radicle extended at least 2 mm out of the seed. After germination was identified, seedlings were removed from the petri dish. Each day that seed germination was assessed, petri dishes were rotated to a different shelf in the growth chamber.

Germination prediction for seedbed temperatures

Time to reach 50% germination (D50) was calculated as following:

$$\mathrm{T} = \left[\left(\frac{t_a - t_b}{n_a - n_b}\right)\ (N - n_b)\right] + t_b \qquad [1]$$

where: T is equal to time (days) to subpopulation germination, t_a is equal to the incubation day when subpopulation germination was reached, t_b is equal to the incubation day before subpopulation germination was reached, n_a is equal to the number of germinated seeds on the day that subpopulation germination was reached, n_b is equal to the number of germinated seeds on day before subpopulation germination was reached, and N is equal to the number of germinated seeds equal to 50% of the total population. Linear and curvilinear regression was used to construct models that estimate progress toward germination as a function of incubation temperature for each species and ABA concentration (Rawlins et al. 2011a). To improve model accuracy regression analysis was performed on germination rate or the inverse of days to 50% germination (D50). Models produced from 1/D50 can then be used to estimate progress toward

germination and expected day of germination from hourly soil water and temperature measurements in rangeland seedbeds (Roundy et al. 2007). Total germination percentage was also calculated as the ratio of the number of seeds germinated to the total number of seeds sown and was expressed as a percentage.

Statistical Analysis

Plotting both total germination percentage and germination rate (1/D50) for the different species and ABA concentrations indicated a quadratic response to incubation temperature for both variables. We used a completely random general linear model to first determine significance ($P<0.05$) of main effects and interactions of species and ABA concentration in relation to the linear and quadratic covariates of incubation temperature. When species, ABA, and temperature interactions proved significant, we developed a general linear model of covariance for each species separately. Using these models, we tested for differences in responses to ABA concentrations at the covariate incubation temperatures of 5, 10, 15, 20, and 25 C using a Tukey test ($P<0.05$). For germination rate, significant interactions of species, ABA concentration, and temperature led us to develop regression equations of germination rate as a quadratic function of incubation temperature for each species and ABA concentration. These regression equations can then be used to estimate timing of germination from hourly seedbed temperatures (Roundy et al. 2007; Rawlins et al. 2011b). The logit of total germination percentage was used to normalize the data, but transformation of the germination rate was not needed as indicated by viewing residuals.

Results

Total germination

Total germination percentage of uncoated and coated seeds with no added ABA was similar ($p < 0.05$) for all species and incubation temperatures. Germination of coated seeds with no ABA was generally greater than 80% for most species and incubation temperatures (Fig. 1). The four-way interaction of species and ABA treatment with the linear and quadratic effects of incubation temperature was significant ($p = 0.0175$) (Table 2). At the lowest ABA application rate (2.2 g a.i. kg^{-1} seed), seed germination was similar to seed without an ABA treatment. From 4.4-13.2 g a.i. kg^{-1} seed, significant declines in germination were primarily found at incubation temperatures of 5 and 25 °C (Fig. 1). When ABA was applied at 17.6 g g a.i. kg^{-1} seed, germination was reduced across all temperatures by 66% for *E. elymoides*, 69% for *P. spicata*, and 74% for *L. lewisii*, compared to no added ABA (Fig. 1). *Linum lewisii* germination was generally more sensitive to ABA than that of the grasses. The two grasses had maximum germination at 15 °C while *L. lewisii* maximum germination was at 10-15 °C.

Germination rate

Germination rates (1/D50) were similar ($p < 0.05$) for uncoated and coated seeds with no added ABA for all species and incubation temperatures. The one exception to this was that D50 was increased from 2.9 days for uncoated seeds to 4.1 days for coated seeds of *E. elymoides* at 25 °C. Addition of even the lowest concentration of ABA reduced germination rate and greatly increased D50 for all species (Fig. 2). The increase in D50 between ABA-treated seeds and those with no ABA became more pronounced with decreasing incubation temperature (Fig. 2). The four-way interaction of ABA treatment and species with the linear and quadratic effects of incubation temperature was highly significant (Table 3). Therefore, regression equations to

estimate 1/D50 from incubation temperatures were fit for each species and ABA concentration (Table 4). R^2 values indicated a better model fit for the grasses than *L. lewisii* and for some ABA concentrations than others. A major increase was observed in D50 with the addition of the lowest ABA addition when seeds were incubated at 5 ºC. Although D50 was increased by increasing concentrations of ABA for some species and incubation temperatures, the lowest concentration produced a major increase in D50 compared to no ABA (Figs. 2).

Discussion

The lowest application rate of ABA had no significant influence on germination percentage but higher application rates showed a decline. All concentrations of ABA tested showed a delay in the period required for germination. The influence of ABA was generally greatest at 5 and 25 ºC. (Fig. 1). Germination timing was more sensitive to lower ABA additions than was germination percentage (Fig. 1). The greatest delay in germination for the grasses was at 5 ºC, where even the lowest ABA addition greatly increased D50 to > 70 days (Fig. 2). Naturally-occurring ABA in the seed both induces and maintains dormancy during seed maturation (Leubner-Metzger 2006). ABA also inhibits germination of nondormant seeds of some species when applied exogenously (Baskin & Baskin 1998; Goggin et al. 2009). Temperature is involved in breaking of dormancy and regulating germination (Hilhorst et al. 2006). The three species studied were all nondormant as evidenced by high germination percentages for untreated seeds (Fig. 1). Little information is available on interactive effects of temperature and ABA, or the germination delay associated with ABA additions. Prechilling is associated with loss of both ABA and dormancy in some seeds (Baskin & Baskin 1998). However, our study is unique in modeling germination responses for nondormant seeds at varying incubation temperatures with seeds coated using different ABA concentrations.

Time-course germination models are especially useful in predicting germination timing for seeds in relation to continuous variables such as temperature and water potential (Rawlins et al. 2011a,b). These models have been applied to combinations of both ABA and water potential (Ni & Bradford 1993; Still & Bradford 1998). We have now successfully developed similar models to predict germination timing for three species and five ABA concentrations applied in seed coatings. We can use these models to predict germination timing under measured seedbed moisture and temperature conditions as demonstrated by Rawlins et al. (2011b). Such predictions will need to be validated with actual field studies. To determine the application of these models, a number of concerns will need to be addressed. One of these is the influence of environmental effects on ABA effectiveness, such as possible leaching and loss of ABA from seed coatings after planting. Also to be determined is the length of germination delay needed to avoid frost mortality and enhance seedling survival. Since higher concentrations of ABA reduced total germination in our study (Fig. 1), it would probably be best to use the lowest concentration of ABA required to avoid frost mortality. Subsequent studies should assess seed viability of non-germinated seeds. If germination is delayed too far into the spring, it will decrease the period that seedlings have access to available water and plants may not develop sufficiently before the onset of summer drought (Roundy & Madsen, personal communication).

Susceptibility of seedlings to freezing depends on frost dynamics in the environment, stage of seedling development, and inherent tolerance of the species. Both Boyd and Lemos (2013) and Roundy and Madsen (personal communication) found that in sagebrush steppe, numerous surface-soil frost periods, usually < 1 day in duration, occur between late October and mid-March. These studies also reported a wide range in the time that surface soils were continually frozen from 11 to 45 days. The length of the period when frost occurred varied

almost 3 months over a 4-year period across 14 sites (Roundy & Madsen, personal communication). Boyd and Lemos (2013) reported major reduction in emergence and tiller density for range grasses adapted to sagebrush steppe after exposure to only 4 days of freezing. The range of sub-zero temperatures over which seedlings can tolerate freezing can be quite narrow (Bois et al. 2006). Complexities of plant resistance to frequency, duration, and severity of freezing (Gusta & Wisniewski 2014), and the variation in frost dynamics in sagebrush steppe seedbeds suggest a number of possible strategies. A conservative strategy would be to coat seeds with enough ABA to avoid the longest-expected period in which freezing duration or intensity is sufficient to cause mortality (mid-October to late March). However, seedlings might be able to tolerate short duration freezing events or temperatures just below freezing, particularly in late winter or spring. Skinner and Bellinger (2010) reported that a freeze-thaw cycle helped acclimate winter wheat (*Triticum aestivum* L.) seedlings to subsequent freezing. Additional research is needed to quantify effects of duration, frequency, and intensity of freezing on seedlings in the field. ABA coatings could be tailored to work on specific sites known to have shorter or longer freezing periods, or to species with greater frost tolerance. Since it may be difficult to predict what the frost period will be for a given year, maybe a bet-hedging strategy could be employed where a combination of shorter and longer-delay coatings is used (Madsen et al. 2016).

Preliminary modeling of germination using field seedbed temperatures suggests that the delays shown by ABA in the laboratory should be sufficient to avoid sagebrush steppe frost periods. However, additional modeling and field experiments need to be conducted to determine effects of ABA on field germination and seedling survival. For example, if ABA delays germination until mid-late March, will soil moisture be available long enough for seedling

establishment? Cline (2014) characterized seedling root zone drying rates of sagebrush steppe communities. Water was readily available during initial spring drying periods and when temperatures were sufficient for root growth for 37.3 days at 3 cm to 87.3 days at 30 cm soil depth. Roundy et al. (2014) found that soil water was available for growth for an average of 74 days at 1-30 cm from March through June in pinyon-juniper (*Pinus* spp.- *Juniperus* spp.) woodlands that had encroached into sagebrush steppe. These studies suggest that seedlings could have sufficient time to establish, even after germination is delayed into March. The current study shows that effects of ABA in delaying seed germination can be modeled in relation to sagebrush steppe seedbed temperatures. Subsequent laboratory and field studies will need to be conducted to determine specific concentrations and effectiveness for increasing seedling establishment.

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Table 1. Seed coating recipe showing ingredients added during the coating process. Seed batch was equal to 100 g of seed.

Coating ID	ABA	Water	Opadry II	Maxim 4FS	Apron XL
	---------- g batch seed^{-1} ----------			---- ml batch seed^{-1} ----	
Blank	0	40.65	8.13	0.26	2.09
ABA-1	0.88	39.77	8.13	0.26	2.09
ABA-2	1.76	38.89	8.13	0.26	2.09
ABA-3	3.53	37.13	8.13	0.26	2.09
ABA-4	5.29	35.36	8.13	0.26	2.09
ABA-5	7.06	33.6	8.13	0.26	2.09

Table 2. Four-way general linear model analysis of total germination percentage with species (SPP), abscisic acid treatment (ABA), incubation temperature (T) and incubation temperature squared (T^2).

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SPP	2	0.6255339	0.31276695	3.17	0.043
ABA	6	10.82162181	1.80360364	18.26	<0.0001
SPP*ABA	12	2.27847564	0.18987297	1.92	0.0296
T	1	1.71235729	1.71235729	17.34	<0.0001
T*SPP	2	0.29112796	0.14556398	1.47	0.23
T*ABA	6	4.13752296	0.68958716	6.98	<0.0001
T*SPP*ABA	12	2.27131517	0.18927626	1.92	0.0302
T^2	1	0.48101261	0.48101261	4.87	0.0278
T^2*SPP	2	0.36142593	0.18071297	1.83	0.1615
T^2*ABA	6	3.04998091	0.50833015	5.15	<0.0001
T^2*SPP*ABA	12	2.34009854	0.19500821	1.97	0.0246
T*T^2	1	0.05810767	0.05810767	0.59	0.4434
T*T^2*SPP	2	0.38513573	0.19256786	1.95	0.1434
T*T^2*ABA	6	2.6376173	0.43960288	4.45	0.0002
T*T^2*SPP*ABA	12	2.45210046	0.2043417	2.07	0.0175

Table 3. Four-way analysis of germination rate (1/days to 50% germination) with species (SPP), abscisic acid treatment (ABA), incubation temperature (T) and incubation temperature squared (T^2).

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SPP	2	0.00130261	0.0006513	2.74	0.0654
ABA	6	0.0031355	0.00052258	2.2	0.0417
SPP*ABA	12	0.00882007	0.00073501	3.09	0.0003
T	1	0.00129572	0.00129572	5.46	0.0199
T*SPP	2	0.00135432	0.00067716	2.85	0.0587
T*ABA	6	0.00286306	0.00047718	2.01	0.0628
T*SPP*ABA	12	0.01311633	0.00109303	4.6	<0.0001
T^2	1	0.00574054	0.00574054	24.17	<0.0001
T^2*SPP	2	0.00253142	0.00126571	5.33	0.0051
T^2*ABA	6	0.00971935	0.00161989	6.82	<0.0001
T^2*SPP*ABA	12	0.01965642	0.00163803	6.9	<0.0001
T*T^2	1	0.00697802	0.00697802	29.38	<0.0001
T*T^2*SPP	2	0.00430362	0.00215181	9.06	0.0001
T*T^2*ABA	6	0.01419675	0.00236612	9.96	<0.0001
T*T^2*SPP*ABA	12	0.02789595	0.00232466	9.79	<0.0001

Table 4. Quadratic regression coefficients and fit statistics for estimating germination rate (1/days to 50% germination) from incubation temperatures (T and T^2) for uncoated seeds (control) and seeds coated with different concentrations of abscisic acid (ABA).

Common name/collection	Treatment	Intercept	T	T^2	Adj R^2	Pr >F
E. elymoides	0	0.03198	0.00063012	0.000463	0.9708	<.0001
	2.2	-0.03006	0.00797	-0.00016847	0.7922	<.0001
	4.4	-0.01328	0.00452	-0.00007093	0.8722	<.0001
	8.8	-0.00126	0.0022	-0.0000122	0.8359	<.0001
	13.2	-0.00364	0.00273	-0.00004659	0.7898	<.0001
	17.6	0.01182	-0.00033702	0.00004356	0.6102	<.0001
	control	-0.01508	0.01106	-0.00002824	0.9505	<.0001
P. spicata	0	-0.07109	0.02647	-0.00060682	0.7279	<.0001
	2.2	-0.04763	0.01296	-0.00035088	0.8669	<.0001
	4.4	-0.02654	0.00744	-0.00017626	0.7615	<.0001
	8.8	-0.01387	0.00479	-0.00009802	0.7237	<.0001
	13.2	-0.00415	0.00286	-0.00004402	0.7557	<.0001
	17.6	0.00967	0.0000804	0.00003098	0.6374	<.0001
	control	-0.076	0.02741	-0.00069102	0.65	<.0001
L. lewisii	0	-0.07185	0.02676	-0.00074439	0.6047	<.0001
	2.2	0.0294	0.00144	-0.00006049	0.0308	0.2583
	4.4	0.02509	0.00074596	-0.00004553	0.0409	0.2483
	8.8	0.03243	-0.00203	0.00006678	0.3094	0.0079
	13.2	0.04068	-0.00458	0.00018896	0.5171	0.0001
	17.6	0.01115	0.0007212	-0.00002387	0.0483	0.5921
	control	-0.11965	0.03616	-0.00113	0.6984	<.0001

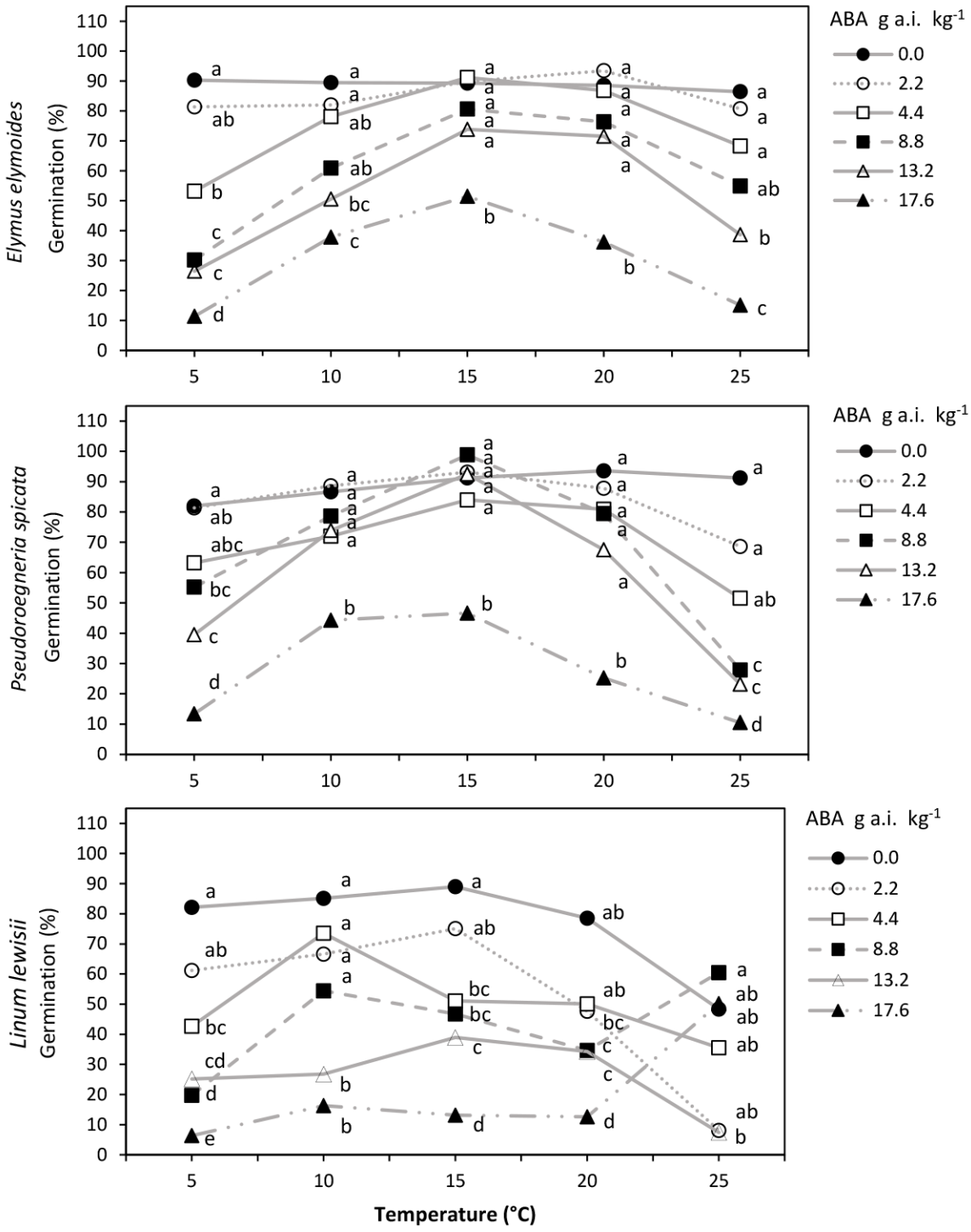

Figure 1. Influence of ABA concentrations on total germination percentages for all species and at each incubation temperature. Values within the same incubation temperature with different letters are significantly different ($P<0.05$) at that temperature.

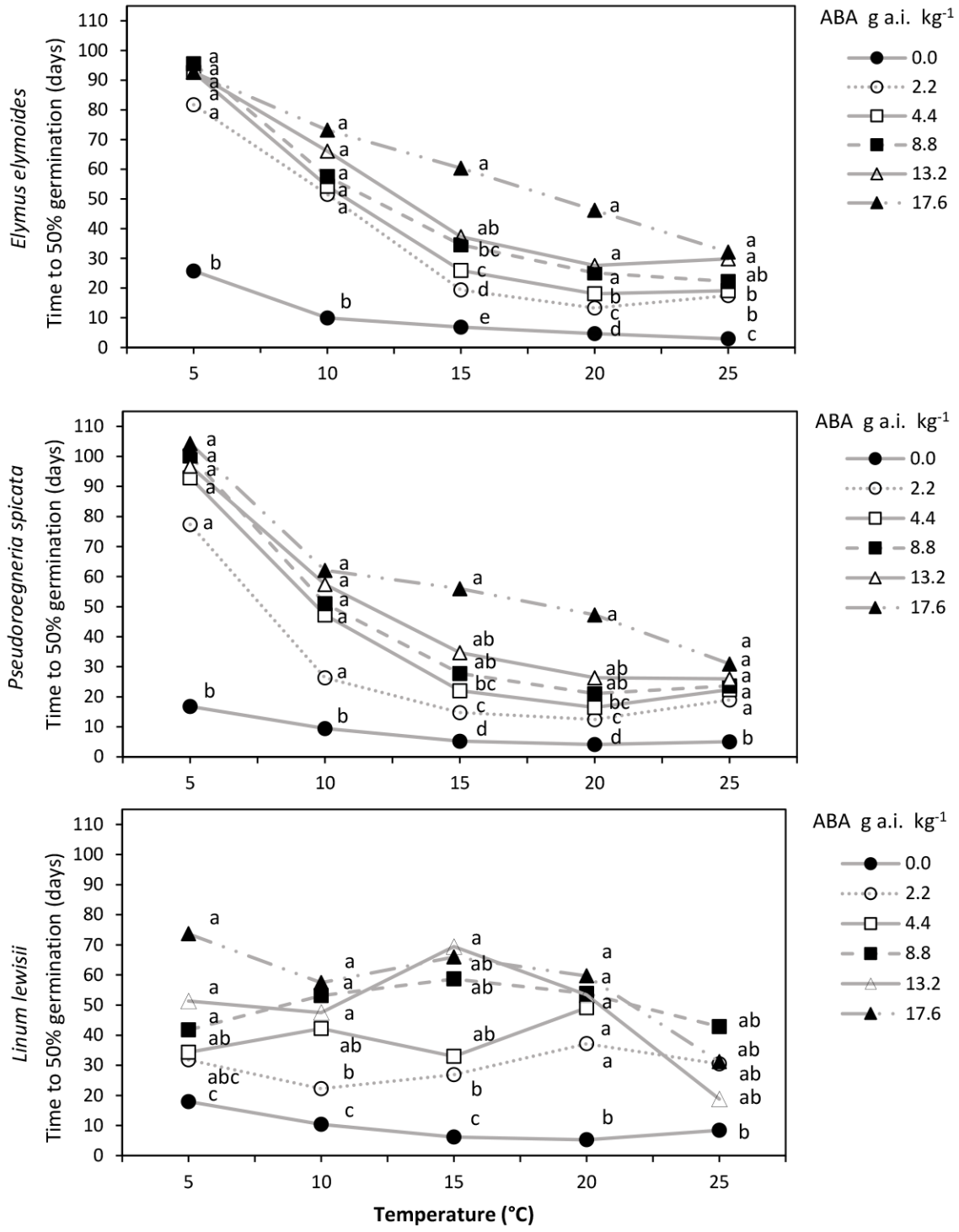

Figure 2. Influence of ABA concentrations on the time to 50% germination for all species and at each incubation temperature. Values within the same incubation temperature with different letters are significantly different ($P<0.05$) at that temperature.