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Photoinhibition of germination in grass seed – Implications for prairie revegetation

Federico P.O. Mollard [a,b,c,*], M. Anne Naeth [a,b]

[a] Department of Renewable Resources, University of Alberta, 751 GSB, Edmonton, AB T6G 2H1, Canada
[b] Land Reclamation International Graduate School, University of Alberta, 751 GSB, Edmonton, AB T6G 2H1, Canada
[c] Departamento de Biología Aplicada y Alimentos, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, Capital Federal 1417, Argentina

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ABSTRACT

Germination photoinhibition is not a recognized cause of revegetation failure; yet prolonged sunlight exposure can inhibit germination of several grass species. This research addressed susceptibility to photoinhibition of selected native grass species used to restore Canadian prairies, and reclamation treatments to alter environmental conditions in order to release seeds from photoinhibition. Under laboratory conditions effects of photoinhibition were tested on the ability of seeds to germinate at low water potential and effects of daily alternating temperatures and nitrates to break photoinhibition. Whether surficial mulch can release seeds from photoinhibition was assessed in a field experiment. Germination photoinhibition was evident in *Festuca hallii* and *Koeleria macrantha* seeds even under very low irradiances. The prolonged exposure to light decreased germination rates and ability of seeds to germinate at low water potentials. Daily fluctuating temperatures released a fraction of *Bromus carinatus* and *Elymus trachycaulus* seeds from photoinhibition yet did not improve *F. hallii* or *K. macrantha* germinability. Nitrates failed to break seed photoinhibition in all species tested. In the field experiment, mulched *F. hallii* seeds (covered with an erosion control blanket) showed a tenfold increase in germination percentages relative to seeds exposed to direct sunlight, indicating the facilitative effects of mulching on attenuation of the light environment. We conclude that germination photoinhibition as a cause of emergence failures in land reclamation where seed is broadcast or shallow seeded should be recognized and germination photoinhibition included in the decision making process to select revegetation seeding techniques.

1. Introduction

Broadcast seeding is more commonly used than drill seeding for prairie revegetation. Rationale for that cultural decision is based on a balance of economic, aesthetic and logistic (Rowe, 2010), rather than biological factors. Broadcast seeding has well recognized limitations generally attributed to insufficient seed imbibition due to poor seed-soil contact and high desiccation rates on the soil surface; these limitations are compensated for by doubling or tripling seeding rates (Doerr and Redente, 1983; Rowe, 2010). Germination inhibition from exposure to long photoperiods of sunlight of surface lying or lightly covered seeds (Pons, 2000) could be an abiotic cause of unexpected revegetation failures.

Prolonged sunlight exposures can inhibit germination of grass species of several different genera (Hilton, 1984; Ellis et al., 1986; Hou and Simpson, 1991; Andersson et al., 2002; Goggin et al., 2008; Barrero et al., 2012). Photoinhibition was observed in row crop grasses, associated grass weeds (Hilton, 1984; Hou and Simpson, 1991; Goggin et al., 2008; Barrero et al., 2012) and grassland species (Probert et al., 1985; Dobarro et al., 2010). The consequences of photoinhibition are easily recognizable when negatively photoblastic seeds fail to germinate after broadcasting or shallow planting. Thus, photoinhibition and ways to overcome it are of great concern as many grassland reclamation attempts are susceptible to emergence failure.

Seed light responses are tightly controlled by environmental cues such as temperature regime and the soil chemical environment (Hilhorst and Karssen, 2000; Pons, 2000). In positively

* Corresponding author. Department of Renewable Resources, University of Alberta, 751 GSB, Edmonton, AB T6G 2H1, Canada. Tel.: +1 780 492 9539; fax: +1 780 492 4323.
E-mail addresses: mollard@ualberta.ca (F.P.O. Mollard), anne.naeth@ualberta.ca (M.A. Naeth).

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photoblastic seeds of many grassland species, germination is promoted by a combination of fluctuating temperatures and light, signals related to vegetation gaps (Thompson and Grime, 1983; Probert and Smith, 1986). In several species, light stimulation of germination require exposure of seeds to cycles of alternating temperatures (Probert and Smith, 1986; Casal and Sánchez, 1998). Soil nitrates in high concentrations can also break seed dormancy indicating vegetation gaps and a safe site for germination (Pons, 1989; Hilhorst and Karssen, 2000). The interaction between nitrates and light in germination induction has been shown, with positively photoblastic seeds from different habitats requiring a simultaneous combination of both signals to break dormancy (Pons, 1989; Hilhorst and Karssen, 2000; Mollard and Insausti, 2009a). Therefore since seed light responses can be modulated by alternating temperatures and nitrates, these factors may alleviate seeds from photoinhibition.

The inhibitory effects of prolonged photoperiods on germination can be increased under conditions of low water availability as partially hydrated seeds are more sensitive to photoinhibitory effects than fully hydrated ones (Hsiao and Simpson, 1971; Hilton, 1984; Fellner and Sawhney, 2002). Photoinhibition responses can appear in partially hydrated seeds that do not have negative photoblastic behavior in otherwise fully hydrated conditions (Niedzwiedz-Siegen and Lewak, 1992). In this way, seeds covered by light amounts of soil or surface applied mulch may still show photoinhibition if kept under suboptimal hydration in the seedbed.

Broadcast seeding under photoinhibitory conditions may fail to give expected emergence rates according to seeding calculations derived from laboratory germination tests that do not test photoinhibition. Thus revegetation may benefit from practices focused on attenuating irradiations. Under field conditions, photoinhibition may be released with use of surface applied mulch to attenuate light. The aim of this research was to determine to what extent grass seeds of native species used to reclaim grasslands in Canadian prairies are subjected to photoinhibition and to explore different conditions to alleviate it. We addressed the following questions: Are grass seeds commonly used for reclamation in the prairies susceptible to photoinhibition? Can photoinhibitory conditions change ability of seeds to germinate at low water potentials? Can grass seed photoinhibition be relieved by nitrates or daily fluctuating temperature regimes? Can grass seeds be released from photoinhibition through the use of mulch?

2. Methods

2.1. Species used in experiments

Seed photoinhibition was studied in native grass species commonly used for reclamation in western Canada. Most experiments were conducted with *Festuca hallii* (Vasey) Piper or *Koeleria macrantha* Schultes seeds to test for photoinhibition in materials that may show contrasting light sensitivity. *Festuca hallii* has notoriously poor emergence when broadcast seeded but establishes adequate plant stands when seeds are hay transferred (Desserud and Naeth, 2013a, 2013b). *Koeleria macrantha* var. 'ARC Mountain View' is a popular and reliable choice for revegetation with a potentially low sensitivity to photoinhibition due to its relatively good broadcast seeding performance. Research to address photoinhibition in different species was conducted with seeds of *Bromus ciliatus* L., *Bromus carinatus* Hook. & Arn., *Deschampsia caespitosa* (L.) P. Beauv. or *Elymus trachycaulus* (Link) Gould ex Shinners ssp. *trachycaulus* (Syn. = *Agropyron trachycaulum* (Link) Malt.). Seeds (caryopses, 1-seeded florets or seeds) were purchased from seed distributors in Alberta, Saskatchewan or Manitoba. Seeds were stored dry at −20 °C immediately after being obtained to avoid after-ripening as this process can change seed light responses (Mollard and Insausti, 2009b) and experiments were conducted throughout 2012 and 2013.

2.2. First laboratory experiment: photoinhibition at different irradiances

Seeds of *F. hallii* and *K. macrantha* were put into a growth chamber (Conviron, PGR15, Controlled Environments Ltd., Winnipeg Manitoba) at continuous temperatures of 20 °C under white light provided by 32 fluorescent tubes (Sylvania Pentron 4100 K FB39/841/HO/ECO) and twelve 40 W incandescent lamps (Frosted Globe, Globe Electric Company, Montreal, Canada). A light period of 14 h per day was used as representative of the photoperiod during the early growing season in the Canadian prairies (Ripley, 1973). The photosynthetic photon flux density (PPFD) was 678 ± 43 μmol m^{-2} s^{-1}. Light had a red to far red ratio (R/FR) of 1.3 ± 0.1, which is close to that of sunlight (R/FR = 1.1). Germination boxes were transparent polystyrene boxes (11 × 11 × 3.5 cm) containing one layer of absorbent cotton and white tissue paper saturated with distilled water. Positions of germination boxes were rotated within the chamber after each monitoring.

The following treatments were replicated four times, with 30 seeds for each species per replication.

- Continuous light treatment with germination boxes subjected to the above described growth chamber light conditions.
- Light pulses of 1 h per day during the first five days (germination boxes were wrapped during dark periods).
- Darkness.
- 21% full light (147 μmol m^{-2} s^{-1}, R/FR light of 1.14).
- 14% full light (98 μmol m^{-2} s^{-1}, R/FR light of 1.10).
- 5.5% full light (38 μmol m^{-2} s^{-1}, R/FR light of 1.06).

Germination boxes were wrapped with two layers of reflective surface black polyethylene (IFlex Ayr-foil reflective insulation, Soprema North America, USA) in the pulse and darkness treatments. In the 21, 14 and 5.5% full light treatments, germination boxes were wrapped with one, two or three layers of white 92 bright, 75 gm^{-2} printer paper (Aspen 30, Boise Paper Holding, Boise, USA), respectively. Daily light pulses and darkness treatments were used as controls.

Photoinhibition was indicated by a significant reduction in seed germination rate at each monitoring period, or final germination in any of the long photoperiod treatments, relative to the controls. The daily light pulses treatment was used to provide light cues to break dormancy (Mollard and Insausti, 2009a, 2009b, 2011) and to fulfill requirements of short light photoperiods for germination (Casal and Sánchez, 1998). Germination was assessed under very low intensity safe green light (wavelength = 527 ± 0.6 nm) during the shortest time possible and at irradiances below detection limits of the quantum meters. Tests were carried out on seeds of *F. hallii* and *K. macrantha* to justify the use of safe light as recent research indicates seeds may be sensitive to green light (Goggin and Steadman, 2012). There were no differences in germination after ten days between treatments subjected to 5 min of green light and those in total continuous darkness.

The chamber temperature below the continuous light treatment germination boxes was 20.5 ± 1 °C (mean ± SD); measured with a HOBO temperature logger (Onset Computer Corporation, Cape Cod, Massachusetts, USA). Germination was monitored every second day for 20 days, the period which ensured that germination rates were closely related to current seed conditions. Already counted germinated seeds were removed at each monitoring. Those