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Role of seed environment and covering structures on large crabgrass germination

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ABSTRACT

The success of large crabgrass (*Digitaria sanguinalis*) growing among summer crops in Argentina, may be partly explained by its escape from weed controls related to the emergence of different seedlings cohorts determined by seed dormancy and germination requirements. The objectives of this work were to evaluate the effect of temperature, red (R):far-red (FR) ratio and the possible role of the caryopses covering structures on the release of seed dormancy in *D. sanguinalis*. Therefore, the effects of moist pre-treatment duration, light and temperature, as well as the caryopsis covering structures, and imbibition with H_2O_2 and the extract of caryopses covers on seed germination, were investigated. Moist pre-treatment at 5 and 20 °C promoted dormancy release and fluctuating temperatures between 20/30 °C and light promoted germination. However, exposure to 30 min of light with a high R:FR ratio reduced germination. Removing or puncturing some of the caryopsis covering structures, as well as imbibition with 2.6 M H_2O_2 enhanced seed germination. Results suggest that the extended seedling emergence throughout the season could be due to the influence of the environmental factors studied here on dormancy release and germination, and that seed covering structures have an important role in seed dormancy imposition for this species.

1. Introduction

Weed population shifts were observed during the last twenty years when conventional tillage systems were changed to permanent no-tillage in the main agricultural region of Argentina. In the absence of tillage, grassy annual populations increased and broad-leaved populations decreased (de la Fuente et al., 2006; Scursoni and Satorre, 2010). However, *Digitaria sanguinalis* (L.) Scop. has maintained or even increased its constancy, becoming an important problematic weed species among local soybean and maize crops, probably because of its extended period of emergence in the field, which allows some seedling cohorts to escape from weed controls (Oreja and de la Fuente, 2005). This summer annual weed grows in both temperate and tropical regions of the world, between 50°N and 40°S (Holm et al., 1977). Its presence produces significant yield losses in different crops (Monks and Schultheis, 1998; Fu and Ashley, 2006; Oreja and González-Andújar, 2007).

Seedling emergence is one of the most critical stages in a weed life cycle, because it determines successful competition and reproduction by the end of the growing season (Forcella et al., 2000). On the other hand, the seedling stage is also the most vulnerable and, consequently, the stage where control measures are most effective. The timing of seedling emergence in the field is determined by previous processes which include seed dormancy, germination and pre-emergence seedling growth (Benech-Arnold et al., 2000; Forcella et al., 2000). Knowledge about how environmental conditions affect seed dormancy and germination would be useful to predict *D. sanguinalis* emergence and, thus, to plan successful weed management strategies.

Temperature is an important factor regulating seed dormancy under field conditions (Batlla and Benech-Arnold, 2010). For example, the seeds of summer annual species generally require exposure to low temperatures during autumn and winter to diminish their dormancy level. This mechanism allows seed germination from spring to early summer and, as a consequence, plant growth occurs during summer and seed dispersion in autumn. This timing of stages ensures the reproductive success of these species in temperate climates (Benech-Arnold et al., 2000; Bewley et al., 2013). Once seeds reach a low dormancy level, many weed seeds require additional factors to terminate dormancy and allow germination, such as light and alternating temperatures (Benech-Arnold et al., 2000). There is evidence indicating that the perception of these signals allows seeds to detect an overlying canopy or excessive burial depth, thus avoiding futile germination (Fenner, 1980; Thompson and Grime, 1983; Batlla et al., 2000). For example, fluctuating temperatures of the upper layers of the soil are reduced by the presence of a crop canopy, thus inhibiting germination of species that require fluctuating temperatures to terminate dormancy (Benech-Arnold et al., 1988; Huarte and Benech-Arnold, 2003). On the

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other hand, the presence of a crop canopy filters sun light reducing the red (R):far-red (FR) ratio of the light reaching the soil surface. This FR enriched canopy-filtered light would reduce the germination of weed seeds located at the surface of species sensitive to environments with low R:FR ratios through the action of phytochrome (Bewley et al., 2013).

Environmental conditions promoting seed dormancy release and germination of *D. sanguinalis* are quite different among published studies (Turner et al., 2012). Successful treatments include exposure to low temperatures, such as 3 °C for 28 days (Toole and Toole, 1941), 4 °C for 2 weeks (Hsu et al., 1985) or 2–4 °C for two months (Delouche, 1956) and moist conditions, and hot temperatures of 50–60 °C and dry conditions (Taylorson and Brown, 1977). According to Toole and Toole (1941), Hsu et al. (1985) and King and Oliver (1994), fluctuating temperatures of 20°/35 °C and 20°/30 °C (18 h/6 h) with light (18 h/6 h) are the best conditions for *D. sanguinalis* seed germination. Zhang et al. (2012) reported that, in addition to fluctuating temperatures of 20°/30 °C (12 h/12 h), germination can also be maximal at constant temperatures of 25 °C and 30 °C (12 h light/12 h darkness). Although most evidence indicates that light promotes seed germination of *D. sanguinalis* seeds, the role of light quality in seed dormancy has not yet been explored for this species.

In most grasses, primary dormancy (innate dormancy of seeds recently dispersed, Benech-Arnold et al., 2000) imposition is related to seed coats. The surrounding tissues can impose dormancy i) preventing water uptake (common in dicotyledonous), gaseous exchange (through seed coats and pericarp tissues surrounding the caryopsis) or embryo expansion (hard tissues of the pericarp and seed coats) or ii) as a source of germination inhibitors (present in different seed outer tissues but mainly in glumes) (Adkins et al., 2002). In *D. sanguinalis*, evidence shows that primary dormancy imposed by the seed coat is not due to permeability barriers to water uptake (Gianfagna and Pridham, 1951; Delouche, 1956; Biswas et al., 1978). Primary dormancy could be due to germination inhibitors in the surrounding structures but the mechanism is still unclear (Gianfagna and Pridham, 1951; Delouche, 1956; Gallart et al., 2008). Among the surrounding structures, the lemma seems to be the most important structure responsible for dormancy imposition (Gallart et al., 2008).

In many grasses, such as barley (Lenoir et al., 1986) and oats (Corbineau et al., 1986), dormancy has been explained by oxygen trapping by phenolic compounds present in the surrounding structures. When in contact with oxygen, these compounds are oxidised, reducing the diffusion of oxygen towards the embryo and thus imposing seed dormancy. The exogenous application of hydrogen peroxide (H_2O_2), a highly oxidative compound, has resulted in a successful technique to promote germination in species showing phenolic compounds, such as sorghum (Benech-Arnold et al., 1992), barley, wheat, rice (Naredo et al., 1998) and *Zinia elegans* (Ogawa and Iwabuchi, 2001). Dormancy imposition in *D. sanguinalis* could possibly be related to the presence of oxidizable compounds in fruit structures, as shown in many other grasses, although this possibility has not been tested yet.

The objectives of this work were to evaluate i) the effect of temperature on primary seed dormancy release, ii) the effect of R:FR ratio on seed germination and iii) the possible role of the surrounding caryopses structures on seed dormancy of local biotypes of *D. sanguinalis*. To achieve these objectives, experiments in germination chambers under different environmental conditions were carried out.

2. Materials and methods

2.1. Seed material

D. sanguinalis dispersal unit is usually called "seed" but it is actually the spikelet composed of the caryopsis enclosed within the lemma and palea, and all these structures are covered by the glumes. Hereafter, spikelets will be referred to as seeds unless otherwise specified. Seeds were collected during the season of natural dispersal: March 2008 (for experiment 1) and March 2009 (for experiments 2, 3, 4, and 5), from 10 plants randomly selected in a field located at Roque Pérez (35°20′S lat, 59°23′W long), Province of Buenos Aires, Argentina. Mature seeds were collected by shaking the panicles into a paper bag. After collection, seed samples were winnowed with a seed blower to eliminate very small seeds and plant residues. Seeds were later stored in paper bags at room temperature (20–25 °C) and relative humidity (<20%) for 40 days approximately, until each experiment was performed, considering that seeds stored under dry conditions for at least 2 months do not have increased germination capacity (Toole and Toole, 1941; Gallart et al., 2009).

2.2. General experimental procedures

Several experiments were carried out in germination chambers at the Faculty of Agronomy of Buenos Aires University, Argentina. Experimental units consisted of 50 seeds per replicate, placed in 9 cm diameter Petri dishes with two paper filters (Double Rings, Argentina). Distilled water (4 mL) was added into each dish at the beginning of the tests, and afterwards dishes were sealed with Parafilm to avoid evaporation. For experiments where seeds underwent moist pre-treatment, seeds were kept in darkness by wrapping the dishes into aluminium foil. Germination (radicle emergence) was recorded at regular intervals in experiments with light until no further seeds germinated, and water was added as required, when germination was checked. For treatments in darkness, germination was recorded 20 days after experiment initiation. At the end of each experiment incubation period, the viability of non-germinated seeds was tested with a 1% tetrazolium (2.3.5-triphenyl-2H-tetrazolium chloride) solution (International Seed Testing Association, ISTA, 1999). Germination percentage of each treatment was calculated based on viable seeds.

2.2.1. Experiment 1: effect of pre-treatment conditions on seed dormancy release and germination

A completely randomised factorial experiment (Exp. 1), with five replicates, was performed. Seeds were pre-treated under moist conditions at three temperatures (5°, 20° and 30 °C) for different periods of time (14, 21 and 28 days). Following pre-treatment, dishes were incubated under three fluctuating temperature regimes (8/16 h: 10°/20 °C, 15°/25 °C and 20°/30 °C) and two light conditions (8 h of darkness and 16 h of light and continuous darkness). For treatments under light, dishes were placed into a germination chamber with six fluorescent tubes providing 40 μmol m^{-2} s^{-1}.

2.2.2. Experiment 2: effect of light quality on germination

A completely randomised factorial experiment, with five replicates was performed. Seeds were pre-treated in darkness at 5 °C under moist conditions for different periods of time (0, 15 and 30 days) and exposed to different light treatments: i) red light for 60 min, ii) far-red light for 30 min, iii) a cycle of red light for 60 min/darkness for 30 min/far-red light for 30 min and iv) always in darkness. After light treatments, seeds were kept in darkness and incubated at 20/30 °C (8/16 h) for 20 days.

Red light (calculated proportion of the phytochrome FR-absorbing form (Pfr) and the phytochrome R-absorbing form (Pr) as [Pfr:Pr]: 87%, 35 μmol m^{-2} s^{-1}) was provided by red fluorescent tubes (Phillips 40/15, Germany). Far-red light (calculated proportion of phytochrome as Pfr [Pfr:Pr]: 2.7%, 42 μmol m^{-2} s^{-1}) was provided by a 150 W incandescent reflector lamp (Phillips R95, Buenos Aires, Argentina) in combination with an 8-cm water filter and an RG9 filter (Schott, Mainz, Germany).

2.2.3. Experiment 3: the role of the caryopsis covers on seed dormancy

An experiment in a completely randomised design with three replicates was performed. The treatments were i) whole seeds, ii) naked caryopses and iii) whole seeds after moist pre-treatment in darkness