Weed Biology and Management

Weed Biology and Management **14**, 77–87 (2014)

REVIEW ARTICLE

Weed seed germination and the light environment: Implications for weed management

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Light regulates dormancy termination and the subsequent germination in many weed species. Under field conditions, the light environment of the seeds, which is perceived mainly by photoreceptors of the phytochrome family, provides essential information for cueing germination in the proper environmental situation. The light environment's spectral composition and irradiance allow weed seeds to sense their position in the soil profile, the presence of a leaf canopy capturing light and other resources and the occurrence of soil cultivation. From an agronomical point of view, the control of germination by light represents a potentially useful step in the life cycle of weeds for developing effective control practices. The goal of this article is to place current knowledge regarding photoreceptors, physiological and molecular bases of seed responses to light and their ecological implications within the context of weed management in agricultural systems. With that final objective, the authors intend to show how a better understanding of the way in which the light environment regulates dormancy termination and the subsequent germination of weed seeds could be used to develop more accurate control practices and to improve weed management strategies.

Keywords: germination, light environment, phytochrome, weed management, weed seed.

SEEDS AND THE LIGHT ENVIRONMENT

Seedling establishment from seed germination is a mostly risky process. Indeed, the seedling stage is possibly the most vulnerable stage within a plant's life cycle and weed management practices take advantage of this vulnerability, focusing weed control on the seedling stage. Under natural conditions, seedling establishment and subsequent reproductive success can be impaired due to a multiplicity of reasons: untimely emergence, germination at inconvenient depths and emergence under environments where the competitive pressure is too high for surviving or leaving offspring. For this reason, seeds must have effective mechanisms for sensing the environment and detecting propitious conditions for the establishment of the plant and fitness in subsequent life stages. In species from temperate habitats that normally display primary dormancy, this detection is carried out at a seasonal scale through the physiological mechanisms that alleviate or reinforce dormancy, responding to the effect of a trustable environmental signal, like soil temperature (Benech-Arnold *et al.* 2000; Finch-Savage & Leubner-Metzger 2006) (Fig. 1). However, within the season of emergence (i.e when dormancy is at its minimum), the detection of adequate conditions for seedling establishment must be done at a spatial scale or, in other words, in a more immediate way, through mechanisms that respond to other environmental signals, like light (Fig. 1). This and other factors, as for example alternating temperatures, are regarded as terminating dormancy once the seeds in the soil seed bank are sufficiently sensitized to their effect as a result of having

Communicated by T. Yoshioka.

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Received 12 July 2013; accepted 28 February 2014

doi:10.1111/wbm.12039

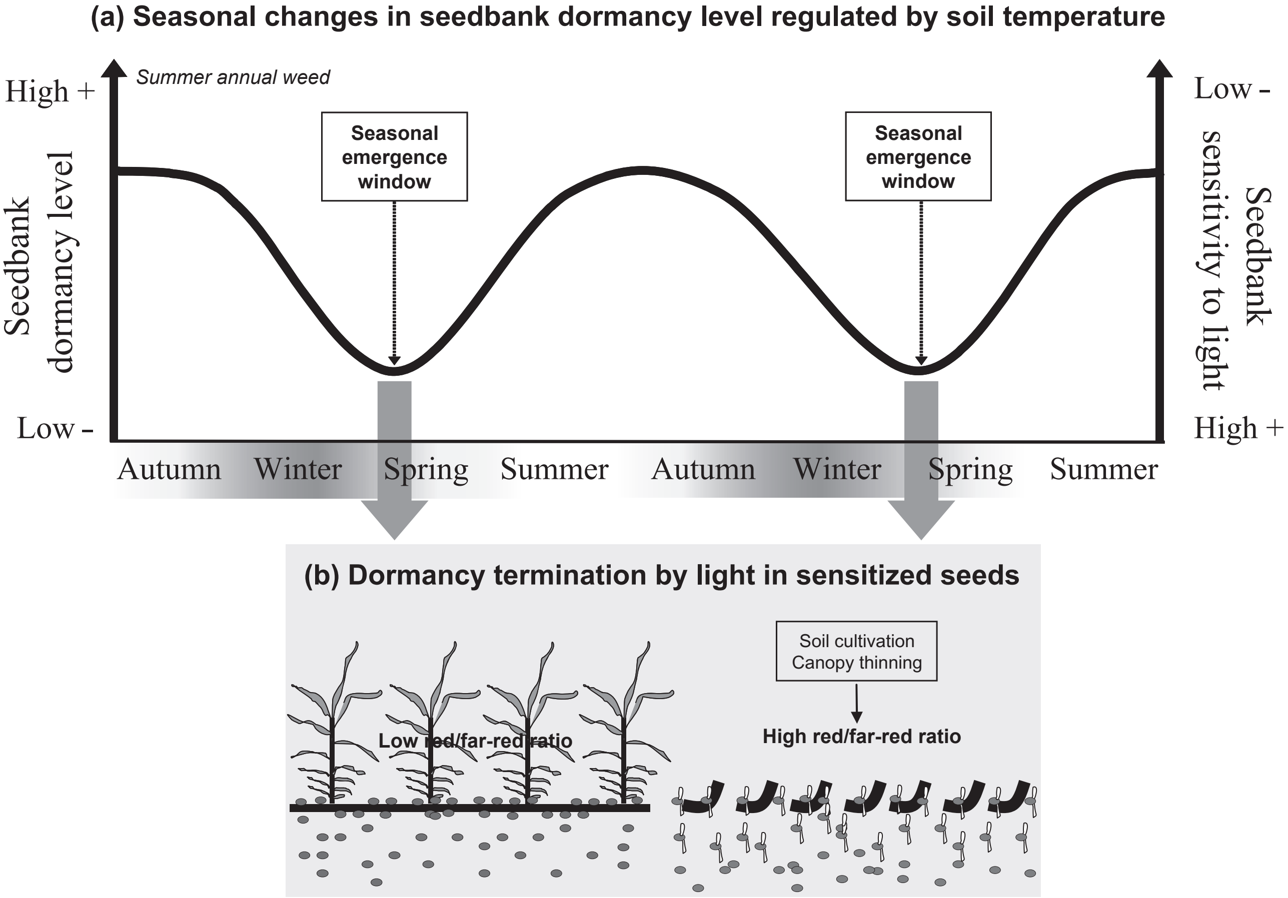

Fig. 1. (a) Schematic representation of the seasonal changes in the seed bank's dormancy level and light sensitivity for a summer annual weed and (b) schematic representation of dormancy termination by light in sensitized seeds (i.e. seeds with a low dormancy level). (After Batlla and Benech-Arnold 2007).

their dormancy lowered (Benech-Arnold *et al.* 2000; Finch-Savage & Leubner-Metzger 2006). For seeds in the soil, these factors represent important signals carrying essential information, cueing germination in the proper environmental situation. Light, in particular, carries such information through its spectral composition and irradiance. Through any or both of these attributes, seeds can sense their position in the soil profile, the presence of a leaf canopy capturing light and other resources that, otherwise, would be captured by the establishing plant and the occurrence of soil cultivation. An understanding of the fundamentals of these processes is essential for the design of weed management and control practices.

Recent reviews on light and seed germination can be found in the literature (Casal & Sánchez 1998; Pons 2000; Mella & Sánchez 2004; Bae & Choi 2008). The aim of the present article is not merely to update the information on photoreceptors, physiological and molecular bases of seed responses to light and their ecological implications but, rather, to place that information within the context of weed management in agricultural systems. With that final objective, the authors intend to propose ways of using that knowledge for developing weed management tools.

PHYTOCHROMES

Phytochromes are a small family of chromoproteins with a molecular mass of 120–130 kDa (Furuya & Song 1994; Casal & Sánchez 1998). Phytochromes display two forms that are photo-interconvertible: the red (R)-absorbing form (maximum absorption at 660 nm; Pr) and the far-red (FR)-absorbing form (maximum absorption at 730 nm; Pfr), which is the active form for germination. However, because there is considerable overlap between the wavelengths that are absorbed by these two forms, light absorbed by phytochromes produces a mixture of Pr and Pfr. At 660 nm, for example, Pr is photoconverted to Pfr, but Pfr also absorbs at this wavelength and hence some Pfr molecules are phototransformed back to Pr. A mixture of ~80% Pfr and 20% Pr is thus established (Pfr/total phytochrome [P] = ~0.8). Even at 730 nm, where Pfr absorbs more strongly, there is some absorption by Pr, yielding a photoequilibria of 0.02 (i.e. 2% Pfr). Small energies are required to carry out these photoconversions: a saturating R dose in lettuce seeds is ~10 Jm^{-2}, an amount given by 0.2 s of direct summer light (Bewley & Black 1994). The absorbance spectra of both forms display a secondary peak in the blue (B) region.

The phytochromes are encoded by a small gene family in most plant species. There are five PHY genes in *Arabidopsis thaliana* L. (*PHYA–PHYE*) (Mathews & Sharrock 1997), three in rice (*PHYA–PHYC*) (Bae & Choi 2008) and five in tomato (*PHYA*, *PHYB1*, *PHYB2*, *PHYE* and *PHYF*) (Pratt *et al.* 1997). The rate of synthesis and destruction is different for different phytochromes, which is important considering that the total amount of phytochromes depends on the balance between these two processes. Phytochrome A (phyA) is synthesized at a high rate but is light-labile, particularly in the Pfr form; for this reason, phyA is the most abundant phytochrome in etiolated seedlings (Clough & Viestra 1997). In contrast, phytochrome B (phyB) and phytochrome C (phyC) are synthesized at lower rates than phyA but are more stable in the Pfr form (Somers *et al.* 1991).

SEED RESPONSES TO LIGHT

Low fluence response

Many seeds germinate when incubated in darkness. This indicates that Pfr is already present in the seeds and/or that germination does not require Pfr. If after imbibition in darkness, a seed lot germinates at a high proportion but this proportion is reduced after exposition to a FR pulse, the dark germination capacity can be ascribed to pre-existent Pfr (Casal & Sánchez 1998). The amount of pre-existent Pfr might be related to the chlorophyll content of extra-embryonic tissues. Indeed, Cresswell and Grime (1981) demonstrated the existence of a negative relationship between germination in the dark and the amount of chlorophyll that was retained in the tissues for prolonged periods during seed maturation. This is because the seeds that retained chlorophyll for longer would have had the most of phyB, which accumulates during the ripening period in seeds, in the Pr form (Shinomura *et al.* 1994).

Light can promote or inhibit germination, depending on its spectral composition and irradiance, the physiological status of the seeds and the conditions of other environmental factors, like temperature and water potential (Bewley & Black 1994; Casal & Sánchez 1998). Seeds that are imbibed and incubated in the darkness could have their dormancy terminated if subjected to a pulse of R; if the effect of R is canceled by a subsequent pulse of FR, then the phenomenon can be considered as a low fluence response (LFR). In this case, the photocontrol of germination displays the classical R–FR reversibility (Borthwick *et al.* 1952). The photoreceptors of this mode of action that have been identified in *Arabidopsis* are phyB and phyE (Hennig *et al.* 2002). It is a characteristic of a LFR that its extent is directly related to the amount of Pfr that is established by the light treatment; the photoconversion of Pr to Pfr lower than the maximum can be caused by a R pulse not providing sufficient light (i.e. low fluence rate or short exposition) or when a R–FR mixture or a wavelength that is different from R is used for the light pulse (Casal & Sánchez 1998). Sometimes, a single R pulse is not enough to terminate dormancy and continuous light or repeated pulses are required (Hsiao & Vidaver 1984; Grubišić & Konjević 1990). This is possibly the case when the amount of time that is required by Pfr to complete the action is prolonged and either Pfr-to-Pr dark reversion is rapid (particularly at high incubation temperatures; Kristie and Fielding 1994) or Pfr destruction is rapid but Pr is available due to *de novo* synthesis.

Very low fluence response

Dormancy alleviation that results from seed burial under particular thermal and moisture conditions or some incubation conditions in controlled environments causes some seeds to display an extreme sensitivity to light. In those cases, the extremely low levels of Pfr that are established by a FR pulse (i.e. 2% Pfr) or by very low fluences of R, like those resulting from millisecond exposures to sunlight, are enough to terminate dormancy. This is known as a "very low fluence response" (VLFR), which in *Arabidopsis* is mediated by phyA (Botto *et al.* 1996; Shinomura *et al.* 1996). This response is saturated with very low levels of Pfr (often <1% of P in the Pfr form) and does not display the classical R light–FR light reversibility (Mandoli & Briggs 1981; Casal *et al.* 1998). Pre-incubated lettuce seeds at low (4°C) or high (28°C) temperatures (VanDerWoude 1985), *Kalanchoë blossfeldiana* Poell. seeds incubated with gibberellic acid (De Petter *et al.* 1985) and buried seeds of *Stellaria media* L. (Taylorson 1972), *Datura ferox* L. (Scopel *et al.* 1991), *Sisymbrium officinale* L. (Derkx & Karssen 1993) and *Polygonum aviculare* L. (Batlla & Benech-Arnold 2005) have been shown to display a

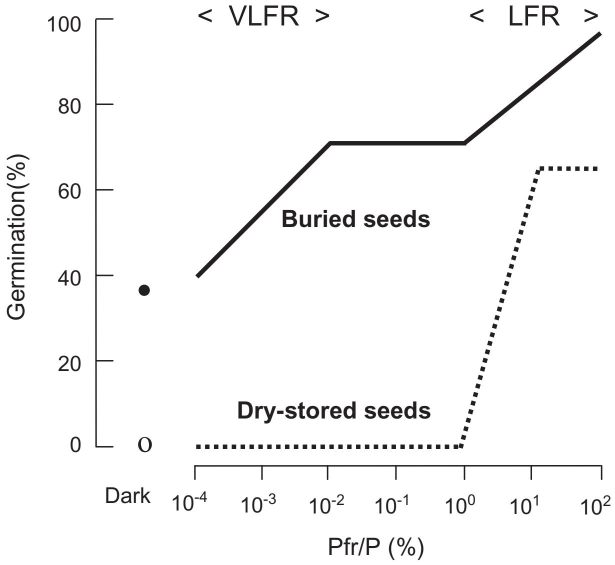

Fig. 2. Schematic representation of the germination response of buried and dry-stored *Datura ferox* seeds in relation to the phytochrome (Pfr)/total phytochrome (P) ratio. The circles indicate the level of dark germination in the buried (●) and the dry-stored (○) seeds. The approximate ranges for the low fluence response (LFR) and the very low fluence response (VLFR) are indicated. (Redrawn from Scopel *et al.* 1991).

VLFR. When a R pulse terminates dormancy but the reversion by a subsequent FR pulse is only partial, the seeds display a VLFR and a LFR. In such cases, plotting germination against the calculated Pfr/P, provided by a series of R–FR mixtures, yields a biphasic curve, with the VLFR (mediated by phyA) at the lowest Pfr/P and the LFR (mediated by phyB and other phytochromes that are different from phyA) above the photoequilibria that are typically imposed by FR (Fig. 2) (Casal & Sánchez 1998).

High irradiance response

The inhibition of germination can be produced by light in the FR or B spectral region (Bewley & Black 1978). When inhibition by FR requires prolonged exposures to continuous light (λmax: 710–720 nm) or very frequent pulses and is irradiance-dependent, it is considered to be an effect that is mediated by the high irradiance response (HIR) mode of action of phytochrome (Hartmann 1966; Mancinelli 1980); in tomato seeds, it has been shown that phyA is the receptor (Shichijo *et al.* 2001). One important characteristic of the HIR is that the effect of continuous light does not obey the law of reciprocity (i.e. equal fluences do not give the same response independently of the use of continuous or pulsed light) (Casal *et al.* 1998). A HIR can both inhibit the germination of dark-germinating seeds and antagonize the termination of dormancy that is initiated by a LFR or a VLFR (De Miguel *et al.* 2000). As an exception to the common inhibitory effect of the HIR, Hennig *et al.* (2002) showed the promotion of *Arabidopsis* germination by continuous FR, which suggests a possible promotive effect of the HIR. Blue light can also inhibit the germination of many species (Gubler *et al.* 2008). Plants possess several classes of photoreceptors that absorb in the B region of the spectrum. Phototropins, cryptochromes and the ZTL/FKF/LPK2 receptors are classified as B light receptors, but it is well known that the R/FR light receptors, phytochromes, also absorb and respond to the B region of the spectrum (Banerjee & Batschauer 2005; Wang 2005).

PHYSIOLOGY OF THE TERMINATION OF DORMANCY IN LIGHT-REQUIRING SEEDS

It is a matter of debate if light really terminates dormancy (i.e. removes the last constraints for seed germination) or if it merely promotes germination (Benech-Arnold *et al.* 2000; Thompson & Ooi 2010; Finch-Savage & Footit 2012). The phytochrome-dependent physiological changes that lead to germination have been studied most extensively in seeds with tissues that surround the embryo and impose a mechanical restraint to its growth. According to Bewley and Black (1994), this is one of the mechanisms for seed coat-imposed dormancy; hence, an environmental factor (i.e. light) whose action ultimately leads to the removal of this restraint can only be regarded as a factor that breaks dormancy. As said before, this dormancy termination effect takes place once the seeds in the soil seed bank are sufficiently sensitized to the effect of "dormancy-terminating" factors as a result of having their dormancy lowered (Benech-Arnold *et al.* 2000; Finch-Savage & Leubner-Metzger 2006) (Fig. 1). This "high sensitivity" to light in a seed population whose dormancy has been relieved means, for example, that low Pfr levels might rapidly trigger the chain of events (to whose component effects the seeds also have been sensitized as a result of dormancy relief) that will lead to dormancy termination.

In seeds with dormancy that is imposed mechanically by the tissues surrounding the embryo, the control of germination lies in the balance between the capacity of the embryo to grow and the constraint imposed by the surrounding tissues (Bewley & Black 1994). Phytochrome is known to control both processes (Casal &

Sánchez 1998): (i) Pfr has been shown to induce germination by promoting embryo growth through a decrease in the osmotic potential and an increase in cell wall extensibility, the latter supported by the accumulation of expansins (Carpita *et al.* 1979; Sánchez & de Miguel 1985; 1992; Mella *et al.* 2004); and (ii) in the seeds of *D. ferox*, Pfr also induces germination by reducing the constraints imposed by the endosperm through the mobilization of cell wall mannans by endo-β-mannanase and β-mannosidase (Sánchez *et al.* 1990; Sánchez & de Miguel 1997).

Since suggested by Derkx and Karssen (1993), it has been clearly demonstrated that the termination of dormancy by light requires giberellin (GA) synthesis: in lettuce seeds, a R pulse causes a significant increase in the active GA_1 and this effect is reversed by FR in a classical LFR mode (Toyomasu *et al.* 1993). Red promotes the expression of the genes encoding GA-3-β-hydroxylases (the last enzymes committed in the conversion of 20C GAs into biologically active GAs) in lettuce and *A. thaliana* (Toyomasu *et al.* 1998; Yamaguchi *et al.* 1998). Although the increase in GA levels affects processes in both the embryo and the endosperm, the available evidence suggests that the synthesis of GA takes place only in the embryo (Mella & Sánchez 2004). The GA that is synthesized in the embryo would migrate to the endosperm cap, where it induces weakening through the promotion of the expression of a number of cell wall hydrolases and related proteins. The effect of GA would be mediated by the down-regulation of the expression of the repressors of GA signaling, such as RGL2 and SPY, that might increase the germination potential of the embryo; GA reaching the endosperm would induce the expression of proteins that are related to weakening through signaling factors (GCR1, SLY and CTS among others) (Peng & Harberd 2002).

ECOLOGICAL SIGNIFICANCE OF SEED RESPONSES TO LIGHT

The timing and place of germination are crucial factors in the survival of the resulting seedling and the possibility of leaving offspring. As the current light environment could provide an indication of the condition to which the seedling would be exposed if germination was induced, light control of seed germination has been suggested as playing an ecological role in different circumstances under field conditions (Pons 2000). Many of these ecological implications are related to the possibility of sensing the place in which germination should take place, so it can be said that phytochrome-sensing systems act as the "eyes" of the seeds that are sensing their surrounding environment in order to decide whether germination should take place or not.

The phytochrome action modes that are described above (LFR, VLR and HIR) are involved in different seed responses to light under natural conditions (Casal & Sánchez 1998; Pons 2000). The promotion of seed germination can be mediated by a LFR and/or VLFR, while the inhibition of seed germination can be mediated by a LFR and/or HIR. Different types of light responses can be found in the seeds composing the seed bank under field situations and these are determined mainly by the position of the seeds, which in turn determines the light climate in the seeds' surroundings (Pons 2000).

Low fluence response

In the case of seeds on the soil surface, for example, a LFR is one of the modes that mediates gap-opening detection under dense canopies. Reductions in the canopy density lead to an increase in the R:FR ratio and consequently raise the Pfr level within the LFR range, promoting germination by the action of phyB (and other phytochromes that are different from phyA) (Benech-Arnold *et al.* 2000). Under natural conditions, this type of response has been associated with the promotion of seed germination by grazing in pastures (Deregibus *et al.* 1994) or flooding events, which are frequent in some herbaceous communities (Insausti *et al.* 1995). On the contrary, the presence of a canopy decreases the R:FR ratio, thus decreasing the Pfr level within the LFR and inhibiting seed germination (Taylorson & Borthwick 1969; Smith 1973; Casal & Sánchez 1998). For example, Huarte and Benech Arnold (2003) showed that the presence of an alfalfa (*Medicago sativa* L.) canopy inhibited the germination of the weed seeds that were located on the soil surface and that this inhibitory effect could be reverted by increasing the R:FR ratio beneath the canopy by filtering the FR component of the canopy-filtered light. This inhibitory response to a FR light-enriched environment allows weed seeds to detect the presence of vegetation that would indicate potential competition and to remain ungerminated until more favorable conditions for seed germination are met. The decrease in R:FR that is required to inhibit seed germination due to the presence of a leaf canopy would depend on the weed species, its dormancy level and other interacting environmental conditions, such as temperature and seed moisture content (Kruk *et al.* 2006).

In the case of buried seeds, the requirement of light for germination prevents the germination of seeds that are buried too deep in the soil for the seedling to reach the soil surface (Fenner & Thompson 2005). This mechanism is most frequent in small seeds, in which the available nutrient reserves for shoot elongation are limited. Thus, only when seeds are brought to the soil surface are the seeds exposed to light and germinate. Although many seeds require light for germination at dispersal, a light requirement for seed germination can be induced upon burial, as observed for many weed species (Wesson & Wareing 1969). This phenomenon can be the consequence of Pfr reversion in the dark, when germination is prevented by unsuitable environmental conditions for a certain time (Pons 2000). The requirement of light for germination allows species to form persistent seed banks under field conditions, a common characteristic of many important weed species. In those species in which light is not required for germination when ripe, the induction of a light requirement upon burial is of great importance for the formation of a persistent seed bank (Pons 1991).

Light can stimulate the germination of seeds that are buried in the top few millimeters of the soil, although the depth to which enough light penetrates to stimulate seed germination varies for different species. For example, Bliss and Smith (1985) showed that *Chenopodium album* is capable of germinating at <2 mm of sand but not at 4 mm, while *Rumex obtusifolius* L. can germinate at 4 mm, but not at 6 mm. The depth to which light penetrates the soil depends on the soil particle size, moisture content and color. Longer wavelengths, especially FR, penetrate deeper than shorter wavelengths (i.e. R light) (Baskin & Baskin 1998).

Very low fluence response

There is enough evidence to show that, during burial, seeds can acquire an extreme sensitivity to light stimuli through another light response: germination in response to milliseconds of light through a VLFR (Fig. 2). The VLFR is mediated by phyA that is synthesized in rehydrated seeds (Shinomura *et al.* 1994). This response allows seeds to be stimulated by the very brief exposition to light that occurs during tillage operations, for example, favoring the appearance of seedlings when the soil has been removed and potential competitors have been eliminated due to tillage operations (Scopel *et al.* 1991). Indeed, experiments have shown that night-time cultivation or daytime cultivation with the soil surface protected from exposure to light resulted in significantly less weed emergence than that observed under daytime cultivation (Hartmann & Nezadal 1990; Scopel *et al.* 1994; Jensen 1995; Buhler *et al.* 1997; Gallagher & Cardina 1998). Probably agricultural production systems in which tillage practices are frequent have favored weed populations with a light requirement for germination; however, the adoption of non-tillage systems in many agricultural regions probably would have changed the composition of the weed communities associated with the crops, favoring those species without a light requirement for germination (Radosevich *et al.* 1997).

Finally, although germination under dense canopy conditions also can be possible eventually through the VLFR (Botto *et al.* 1996), it is not clear whether or not under natural field conditions that this situation is actually important (Casal & Sánchez 1998).

High irradiance response

The experimental results suggest that the inhibition of seed germination under plant canopies by light that is enriched with FR also can be mediated by the HIR. For example, Lytgohe B. and Sánchez R. (1997, unpublished data) showed that the inhibition of ryegrass (*Lolium multiflorum* L.) germination under dense canopies was dependent on the length of the exposure to the FR-enriched light environment, suggesting the participation of a HIR in the observed response. Similarly, *Silene gallica* L. and *Brassica campestris* L. seeds should be exposed for an extended amount of time to a light environment that is subtly enriched with FR due to the presence of an incipient wheat canopy in order to produce an inhibition of seed germination, also suggesting a HIR (Batlla *et al.* 2000). In this latter case, the inhibition of germination occurred ~15 days after crop emergence, when the canopy leaf area index was below one and the R:FR ratio that was recorded under the canopy was well above 0.8. These results show that some weed seeds can be capable of sensing small environmental light quality modifications when under long time exposures. Kruk *et al.* (2006) observed that while the germination of some weed species was inhibited by the presence of the establishing canopy of wheat very early in the crop cycle, the seeds of other species required a denser canopy in order to be able to generate a greater modification of the light environment (i.e. FR enrichment) to inhibit germination.

The germination of seeds in the soil surface also can be inhibited by direct solar radiation (Górski & Górska 1979; Bewley & Black 1994). This inhibitory effect of high irradiances is supposed to be mediated by the HIR and it has been hypothesized that it might provide a mechanism for reducing seedling death due to the extreme high temperatures and dry soil conditions that are likely to occur at the soil surface (Górski & Górska 1979; Pons 2000). This type of response has been reported for many weed species; for example, *C. album* L., *Galium aparine* L., *Amaranthus caudatus* L. and

Amaranthus quitensis H.B.K. (Bliss & Smith 1985; Batlla *et al.* 2000).

DORMANCY AND CHANGES IN THE SEED BANK'S LIGHT RESPONSES

The buried seeds of many weed species exhibit cyclic changes in their dormancy status under field situations. Those changes are regulated mainly by seasonal variations in the soil temperature (Benech-Arnold *et al.* 2000; Batlla & Benech-Arnold 2010). For example, in the case of the seed banks of summer annual weed species, low winter temperatures alleviate dormancy, while conversely, high summer temperatures reinforce dormancy, determining the existence of an annual cyclic dormancy pattern (Baskin & Baskin 1998; Allen *et al.* 2007; Batlla & Benech-Arnold 2010) (Fig. 1). This seasonal dormancy pattern determines that summer annual weed seed banks usually present their emergence "window" during spring, the season in which the seeds present their lower dormancy level. Several winter annual weed species show the reverse dormancy pattern: high temperatures during summer result in dormancy relief, while low temperatures during winter can induce secondary dormancy. In many weed species, these dormancy cycles that are displayed by the seed population are related to changes in their sensitivity to light (Taylorson 1972; Froud-Williams *et al.* 1984; Gallagher & Cardina 1998; Benech-Arnold *et al.* 2000) (Fig. 1). For example, Derkx and Karssen (1993; 1994) observed that the buried seeds of *S. officinale* and *A. thaliana* showed an increase in light sensitivity during dormancy loss, while a decrease in seed light sensitivity was observed during secondary dormancy induction. A similar increase in seed sensitivity to light also was observed during dormancy loss in the summer annual weed, *P. aviculare* (Batlla & Benech-Arnold 2005). This increase in seed sensitivity to light was denoted by the acquisition of different phytochrome action modes by an increasing fraction of the seed population: first, the seeds acquired a LFR, then a VLFR and finally a fraction of the seed population acquired the capacity to germinate in darkness. These results show that while seed populations with an intermediate dormancy level are characterized mainly by showing responses to light in the LFR mode, seeds that show a low dormancy level can show VLFRs. This is the previously mentioned case of *D. ferox*, in which the seeds that were buried in the soil acquired an extreme sensitivity to light, showing a VLFR, while the dry-stored seeds only responded in the LFR range (Fig. 2) (Scopel *et al.* 1991). As specified above, the acquisition of this VLFR mechanism by seeds is considered to be important for the production of weed seedlings because a significant proportion of seeds can be induced to germinate through extremely short exposures to light as, for example, those that could take place during tillage operations (Scopel *et al.* 1994; Jensen 1995; Botto *et al.* 1998; Casal & Sánchez 1998; Ballaré & Casal 2000). Therefore, the proportion of the seed bank that would germinate as a consequence of soil disturbance would depend mainly on the dormancy level of the seed population at the moment of carrying out the tillage, or specifically, on the fact that an important fraction of the seed population has acquired an extreme sensitivity to light (i.e. presents VLFRs) (Batlla & Benech-Arnold 2007).

Although as pointed out above, the soil temperature is considered to be the main factor governing seasonal changes in dormancy in the field, there is evidence showing that the soil moisture conditions also could affect the dormancy status of buried seeds and consequently their sensitivity to light stimuli (Karssen 1982; Benech-Arnold *et al.* 2000; Batlla & Benech-Arnold 2006). For example, Batlla *et al.* (2007), working with *P. aviculare* seeds, showed that while changes in soil moisture conditions did not affect the acquisition of a LFR during dormancy release, the seeds that were exposed to drier soils showed a lower fraction of the population presenting a VLFR. Additionally, the reported results showed that the exposition of the seeds to fluctuations in soil moisture content significantly increased the capacity of the seeds to germinate in the dark. Based on the fact that marked changes in soil moisture content only take place in the upper centimeters of the soil profile, the authors proposed that this loss of the light requirement for germination as a result of exposing the seeds to soil moisture fluctuations could represent a depth detection mechanism in addition to that previously ascribed to the requirement of light.

PREDICTING LIGHT RESPONSES AND DERIVING MANAGEMENT PRACTICES ON THE BASIS OF THE PREDICTED RESPONSE

The success of chemical and mechanical weed control is based on reaching a high proportion of the weed population in the seedling stage because at this stage plants present a high vulnerability to control methods (Benech-Arnold & Sánchez 1995; Ghersa *et al.* 2000). The possibility of predicting the time at which seeds present the maximum sensitivity to light would allow the planning of tillage operations to provoke the emergence of a high proportion of the seed bank and consequently to improve the efficiency of the subsequently applied control methods (e.g. stale and false seedbed approach) (Bond & Grundy 2001; Grundy 2003; Juroszek & Gerhards 2004).

Batlla and Benech-Arnold (2005) developed a model to predict changes in the light sensitivity of a *P. aviculare* seedbank population as a consequence of stratification at low temperatures (Fig. 3). More specifically, the model is able to predict how different fractions of the seed bank successively acquire a LFR, VLFR and the possibility of germinating in the dark during dormancy loss. The model uses a stratification thermal time index (S_{tt}) to relate the observed changes in the seeds' sensitivity to light to the stratification temperature. This index was based on the accumulation of stratification degree day units below a threshold temperature for dormancy release to occur (17°C for *P. aviculare*). Thus, the seed bank's sensitivity to light would increase in accordance with the accumulation of stratification degree day units during winter (Fig. 3a). The model could be used under field conditions to sum up the degree day units that are accumulated, based on the soil temperature data, and to calculate the proportion of the seed bank presenting a LFR, VLFR and germinating in the dark (Fig. 3b). Based on this model, tillage operations could be planned when the seed bank potentially would produce the emergence of a high fraction of the *P. aviculare* seed population (for example, September 13 in Fig. 3c), which could be subsequently controlled by applying mechanical or chemical control methods. Alternatively, tillage operations could be carried out when the seedbank population has a low sensitivity to light (for example, July 23 in Fig. 3c), thus diminishing the potential emergence of weeds from the seed bank prior to crop planting and consequently reducing herbicide applications and weed infestations (Batlla & Benech-Arnold 2007).

Understanding weed seed responses to modifications in the light environment below a crop canopy should allow us to improve weed management strategies by manipulating crop canopy attributes (Dyer 1995; Ghersa *et al.* 1997; Radosevich *et al.* 1997; Kruk *et al.* 2006). For example, changing the plant architecture, crop-sowing densities, crop plant spacing and the use of

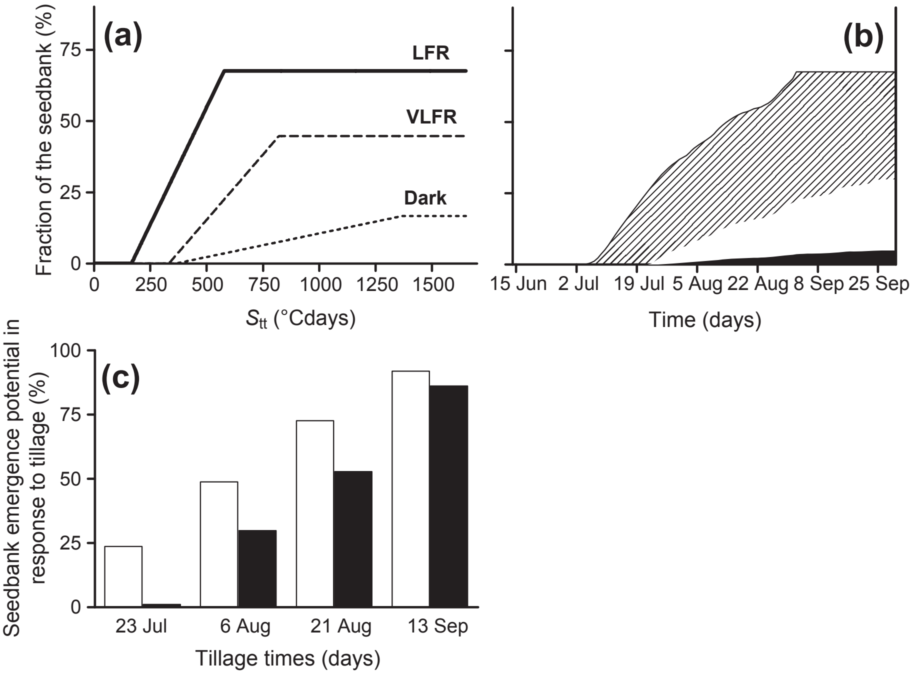

Fig. 3. Expected changes in the fraction of a *Polygonum aviculare* seedbank population showing a low fluence reponse (LFR), very low fluence response (VLFR) and germinating in the dark in relation to (a) the accumulation of stratification thermal time units (S_{tt}) and (b) time in days: (▨), LFR; (□), VLFR; (■), dark. (c) Simulated changes in the emergence potential in response to tillage operations in a *P. aviculare* seed bank during 1999 and 2000 in relation to different tillage times, calculated based on the proportion of the seed bank showing a VLFR: (□), 1999; (■), 2000. Panels (a) and (b) were redrawn from Batlla and Benech-Arnold (2005) and Batlla and Benech-Arnold (2007), respectively. The simulations were done using the year 1999 (panel c) and 2000 (panels b and c) with a soil temperature at a 5 cm depth and the equations were published in Batlla and Benech-Arnold (2005).

cover crops and inter-crops could have a high potential for improving weed management by preventing dormancy termination by light in weed seeds that are located at the soil surface. Reported results showing that subtle changes in the light environment, such as those resulting from the presence of an incipient canopy, can inhibit germination in numerous weed species suggest that minor changes in the sowing date also can be effective in suppressing the germination of weeds that are located at the soil surface. The strength of the regulation of weed emergence by the presence of a crop canopy will depend on the overlap between the "emergence window" of the weed and the density of the crop canopy that is modifying the environmental signals that affect seed germination, such as light and alternating temperatures (Kruk *et al.* 2006). The possibility of predicting changes in seed sensitivity to light for seeds that are located at the soil surface would allow for the planning of sowing dates in order to overlap the time period's, during which seeds are sensitive to light stimuli with a below-canopy light environment that is sufficiently enriched with FR as to inhibit seed germination. The application of this strategy would be useful under the no-tillage cropping system, in which a high proportion of the seed bank is located at the soil surface.

CONCLUDING REMARKS

In the future, there will be increasing pressure to reduce pesticide inputs in agricultural systems due to environmental reasons (Mortensen *et al.* 2000) and this will require weed scientists to focus their research on the development of more sustainable weed control strategies. The possibility of developing such control strategies inevitably will require a better knowledge of weed biology and ecology and how the different environmental factors affect weed behavior under real-field scenarios. In this article, it was shown how a better understanding of the way in which the light environment regulates dormancy termination and the subsequent germination of weed seed banks could be used to develop more accurate weed control methods and to improve weed management strategies in order to meet these challenges.

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