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Dormancy, germination and emergence of weed seeds, with emphasis on the influence of light

Results of a literature survey

M.M. Riemens, P.C. Scheepens & R.Y. van der Weide

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Summary

This note reports the results of an inventory study about the influence of the external factors temperature, light, nitrate, gaseous environment of seeds and moisture on the dormancy, germination and emergence of weed seeds. The inventory was made as a guideline for research aiming at the development of weed control methods that make use of these factors to prevent or stimulate germination of weeds in Dutch organic agriculture. Using the available techniques there is still a notable amount of weeds left in the row that has to be removed by hand. Bottlenecks concerning labour are mainly caused by the need to remove these weeds, especially in slowly growing crops. Focus in this study was on the effects of light on the germination and emergence of weeds (seeds) since this factor is relatively easy to alter in the field and is important for germination of seeds for many species.

Several definitions of dormancy are given in literature of which the following definition was found to be the most accurate. Dormancy is defined here as a seed characteristic, the degree of which defines what conditions should be met to make a seed germinate. So, in other words, dormancy is only related to the requirements for germination, not to the question whether or not these requirements are met in the environment. Germination can be regarded as the response of the seed when both internal germination requirements (state of dormancy) and external requirements (environmental conditions) overlap.

Temperature is, as far as we know, the only factor that directly influences the dormancy state of seeds. The influence of other factors such as nitrate and light can, however, not be excluded with certainty yet.
Germination is influenced by factors such as temperature, light, nitrate, gaseous environment of the seed and moisture content.

Light appears to be the factor most suited to influence in the field to enhance weed control.
Several field experiments are mentioned in which light was used to either prevent or stimulate germination of weed seeds.
Results, both in studies aimed at prevention and studies aimed at enhancement of germination, differ in amount of emerging weeds and in emergence of the same weed species.
At this point, knowledge is lacking. The differences found between experiments were ascribed to differences in dormancy state of seeds and environmental conditions such as temperature. However, the mechanism by which temperature in a preceeding season (regulates dormancy state) influences the range of (light) conditions under which germination can take place remains unclear.

In conclusion, photocontrol has possibilities for organic weed control and can be taken into account during the development of innovative weed control methods in organic farming in the Netherlands.

Introduction

Organic farming is regarded as a good answer to the shortcomings of the conventional agricultural practices. Shortcomings may include reduced animal welfare, presence of pesticide-residues in food and environment, the loss of nature and landscape in agricultural areas and the mineral residues in air and water. A small, but growing amount of consumers has little faith in the way and rate the conventional agricultural sector will be able to tackle these shortcomings. Therefore, the Dutch government aspires a market share of 10% of the total agricultural sector in 2010 for organic farming. Achievement of these aspirations not only depends on the demand for organically grown products, but also on the physical and socio-economic infrastructure.

Most organically producing farmers, when interviewed and asked to mention the biggest bottleneck for arable farming will, among a few others, mention weed control. Currently, the amount of labour needed for manual weeding remains high in some crops. In principle there are two ways to decrease the need for manual weed control, one is to develop machines that remove or kill weed plants within the crop rows, and the other to develop or improve preventive weed control measures.
The LNV-weed research programme 'Innovative weed control in favour of sustainable (organic) farming and public space' (397-V) aims at developing new insights to improve existing weed control systems and innovative methods in aid of weed prevention, non-chemical weed control and risk control fitting in the organic farming system.
The preparation of 'false seedbeds' is being developed as a strategy of weed prevention. Weed seeds are stimulated to germinate, and seedlings are subsequently killed. During the definite seedbed preparation, light is prevented to reach the seeds in order to minimise germination simultaneous with the crop seeds. Although the results of this strategy are sometimes very good, at other times there is hardly any effect.
In the present study an analysis was made of the environmental factors that influence dormancy, germination and emergence of weed seeds, and possibilities to improve weed control with false seedbed preparation are discussed.

1. Definitions: dormancy and germination

There is no agreement about the definition of seed dormancy. In many cases viable seeds are called dormant when they are simply not germinating. The causes described for this phenomenon are located both in the seed and in its environment and are related to dormancy as well as germination (Harper, 1959; Vegis, 1964; Baskin *et al.*, 1985). However, according to Vleeshouwers *et al.* (1995) dormancy should be regarded as a seed characteristic, as the degree of which defines what conditions should be met to make a seed germinate. So, in other words, dormancy is only related to the requirements for germination, not to the question whether or not these requirements are met in the environment. Germination can be regarded as the response of the seed when both internal germination requirements (state of dormancy) and external requirements (environmental conditions) overlap (Vleeshouwers *et al.*, 1995) (Fig. 1).
This view is in accordance with the concept of Karssen (1982). He stated that seasonal periodicity in the field-emergence of annuals is the combined result of seasonal periodicity in the field temperature and seasonal periodicity in the width of the temperature range suited for germination. Germination in the field is restricted to the period when field temperature (environmental factor) and the temperature range over which germination is possible (degree of dormancy) overlap. So, dormancy is related to the width of the temperature range over which germination can proceed and not to the question whether or not the current field temperature is in that range. Dormancy varies on a continuos scale, visualized by continuos changes in the range of environmental factors under which germination can take place (Vleeshouwers *et al.*, 1995).

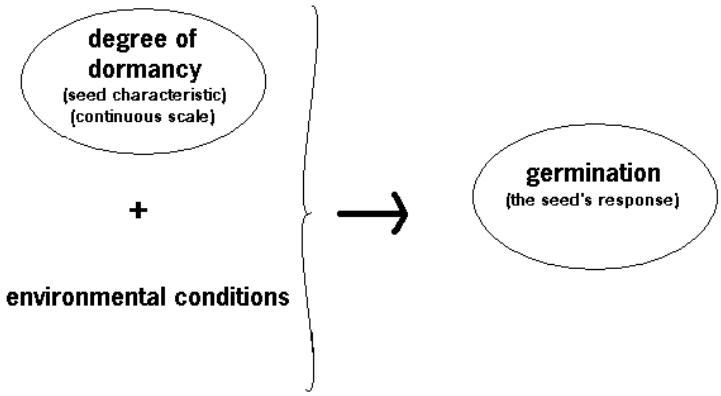

Figure 1. *Interaction of seed and environment in the process of germination. (Redrawn from Vleeshouwers et al. 1995).*

Dormancy itself can be devided into primary and secondary dormancy.
Primary dormancy is the state of freshly shed seeds; these seeds will not germinate under any set of environmental conditions until dormancy is relieved. After the breaking of primary dormancy, the seeds may germinate if conditions are suitable. If the right set of external factors is not present, secondary dormancy may develop. Secondary dormancy can be relieved and re-induced during many successive years (Karssen, 1982) until conditions for germination become favourable. This phenomenon is called dormancy cycling (Egley, 1995) (Fig. 2).
However, it is not completely clear whether secondary dormancy differs from primary dormancy physiologically (Hillhorst, 1998). Due to the above described differentiation between dormancy and germination, it is not possible to directly test the dormancy state of seeds in general. The results of germination tests can only be an approximate representation of the dormancy state of seeds (Vleeshouwers *et al.*, 1995). Nevertheless, differences in sensitivity to nitrate, gibberellines and light have been found for primary and secondary dormant seeds of *Sisymbrium officinale*, indicating a difference between primary and secondary dormancy (Derkx *et al.*, 1993).

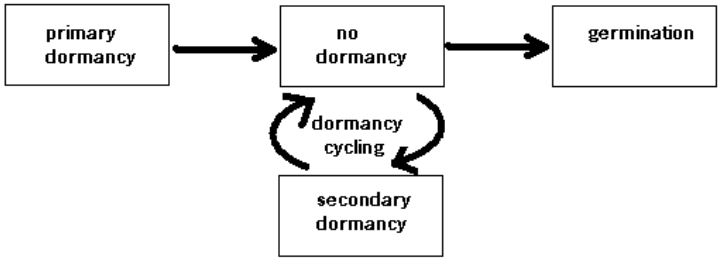

Figure 2. Schematic representation of transitions between dormancy and germination. Redrawn from Hillhorst (1998).

The above described definitions of dormancy and germination will further be used in this report.

2. Factor(s) influencing dormancy (cycling)

Since dormancy is defined as a continuously variable seed condition, the degree of which is defined by the conditions that should be met to make the seed germinate (Vleeshouwers *et al.*, 1995), it is important to know which factors influence dormancy, or in other words influence that degree of conditions.
At this moment, the only known factor that directly influenced that degree is temperature. In this chapter, effects of temperature on the induction and relief of dormancy will be described. Dormancy relieving factors will cause a widening of the range over which germination can occur and dormancy inducing factors will narrow that range.

2.1 Temperature

Bouwmeester and Karssen (1992) buried seeds of *Polygonum persicaria* in the field 10 cm deep. Over a period of 3 years, they exhumed seeds and tested germination over a range of temperatures. Subsequently, they used these data to model the range of temperatures over which germination could proceed. The resulting dormancy pattern regulated by temperature was compared with the temperature fluctuations in the field (Fig. 3). They showed that seasonal changes in dormancy (changes in the temperature range over which exhumed seeds germinate) was regulated by the field temperature. The changes in dormancy did not correlate with changes in soil moisture and soil nitrate content. Therefore, it was concluded that soil moisture and nitrate content do not influence changes in dormancy.

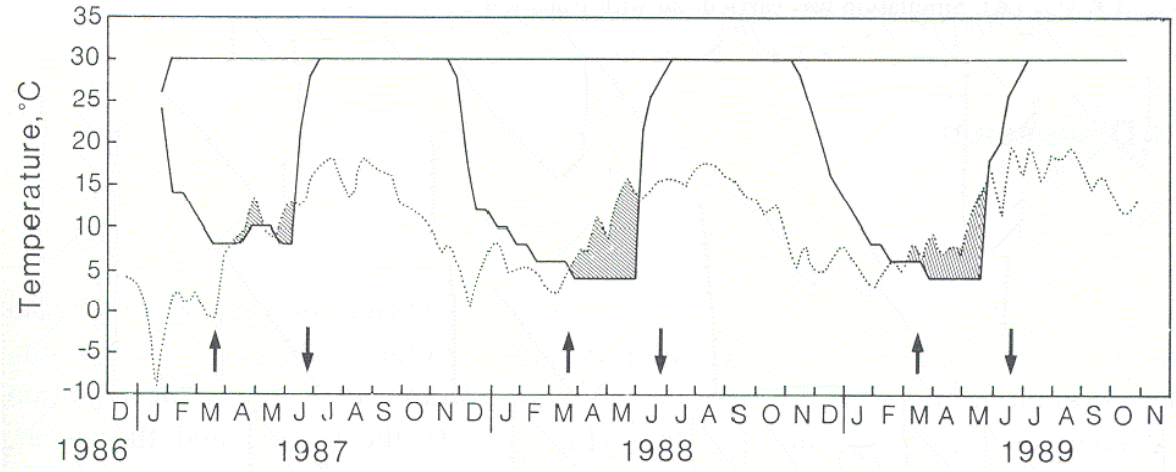

Figure 3. *Simulation of seasonal changes in the range of temperatures over which at least 50% of exhumed Polygonum persicaria seeds germinate. Solid lines represent minimum and maximum temperature required for 50% germination in water, calculated to a descriptive model based on temperature derived parameters. The dotted line indicates the field temperature at 1.50m. Hatched areas indicate overlap of field temperature and germination temperature range. Arrows indicate the time when germination in petridishes outdoors at a height of 1.50 m. actually increased above or decreased below 50%. (Adapted from Bouwmeester et al., 1992).*

Similar effects of temperature on the dormancy of seeds were found for *Chenopodium album* L. (Bouwmeester *et al.*, 1993c), *Spergula arvensis* (Bouwmeester *et al.*, 1993b) and *Sisymbrium officinale* (L.) Scop. (Bouwmeester *et al.*, 1993a).
For other factors than temperature such as nitrate and light, it has never been shown that they influence the range of environmental factors over which germination can occur (Karssen, 1982; Hillhorst *et al.*, 1988; Bouwmeester *et al.*,

1992). They are in many cases indespensible for germination, but only by promoting the germination process itself, not by changing the range of requirements for germination (Derkx *et al.*, 1994).

The principles of temperature perception and long term storage of information on temperature of seeds are still unknown (Hillhorst, 1998).

3. Factors influencing germination

In this chapter factors necessary for the germination of seeds will be discussed. As described in chapter 1, germination is the result of the dormancy state of the seeds (range of environmental conditions at which germination can occur) and the simultaneous occurrence of these environmental conditions. Environmental factors comprise temperature, nutrients (nitrate), light, moisture and gasses (oxygen). The impact of these factors and their relative importance for the germination will be described.

3.1 Light

Seeds of most species seem to germinate better in light than in darkness (Baskin *et al.*, 1988; Pons, 1991). Therefore, light seems to be an important regulator of seed germination in many plants. For some species, the light requirement for germination is fulfilled by very short light exposures; i.e. they have high light sensitivity (Andersson *et al.*, 1997). Light exposures of less than a minute and for some species less than a second of daylight is enough to induce germination in seeds of some species (Milberg *et al.*, 1996). Classification of seeds based on their sensitivity for light is called photoblastism. Three categories are distinguished:

1. Positive photoblastic; seeds only germinate under light.
2. Negative photoblastic; seeds only germinate in the dark, light inhibits germination.
3. Light insensitivity; seeds germinate under light as well as in the dark (Massanori, 2001).

Andersson *et al.* (1997) tested germination of 42 weed species in light of long duration, in darkness and in darkness after a short light exposure (SDLE). They used a photon flux density at seed level of 230 μmol $m^{-2}s^{-1}$(red light = 19 μmol $m^{-2}s^{-1}$ and far-red light =23 μmol $m^{-2}s^{-1}$). Of the 42 species tested, seeds of 26 germinated to significantly higher percentages ($p<0.05$) after a 5-s light exposure than that kept in constant darkness. They used an exposure time of 5 s, which was estimated to correspond to less than 1 s of full daylight (full sun at noon). Of the summer annuals, 76% and of both the winter annuals and unclassified annuals, 65% germinated to higher percentages after the short-light treatment than those kept in the darkness. (See Appendix I for Table 1; an overview of germination percentages of seeds after treatment). The level of light requirement was defined as the proportion of seeds requiring light to germinate, i.e. showing a difference in germination between darkness and short light exposure, or between darkness and full light. In 17 species tested, germination in full light was less than, or not significantly different from, the short light exposure. Thus, in many cases the short light exposure seemed to fulfil the light requirement for germination. In no case did germination in darkness exceed germination in the short- light treatment.

Milberg *et al.* (1996) performed a similar experiment with 44 weed species. They used a photon flux density at seed level of 210 μmol $m^{-2}s^{-1}$ (red light = 18 μmol $m^{-2}s^{-1}$ and far- red light = 23 μmol $m^{-2}s^{-1}$). Of the 44 species germination was stimulated by SDLE in 25, while the other 19 showed no or inconsistent responses. Eight of 11 plant families contained species that responded to SLDE. Light sensitivity was shown equally by summer annual, winter annual and perennial species (See Appendix I for Table 1; an overview of germination percentages of seeds after treatment).

3.1.1 Influence of seed burial on light sensitivity

The light response of seeds can be attributed to a family of chromoproteins called phytochromes. Two stable forms of phytochromes are present in plant tissue: P_r (or P) or the inactive form which absorbs light of 665 nm, and P_{fr}, the active form which absorbs light of 735 nm.
The depth at which a seed is buried can have significant effects on its germination and emergence (Grundy *et al.*, 1998). Seeds are known to undergo important changes in light sensitivity during burial (Scopel *et al.*, 1991). Burial is thought to cause a change in the fluence response (the response to a certain amount of energy delivered in a given time interval) of seeds from low to very low (Appendix II) (Taylorson, 1972), thereby enhancing the sensitivity of these seeds to light.

This enhancement of sensitivity was shown for seeds of *Datura ferox* by Scopel *et al.*, 1991. Seeds were buried at a depth of 7 cm and irradiated with different fluences of R (red light; from 4.8 to $2.9*10^5$ µmol m^{-2}) or FR (far red light; from 3 to $4.4*10^4$ µmol m^{-2}). After irradiation, seeds were buried in the field at 10 cm deep and emerging seedlings were counted two weeks afterwards. High proportions of buried seeds germinated at percentages of less than 0.01% Pfr, whereas non-buried seeds needed Pfr percentages of 1% or more (Figure 4). A similar effect of burial has been found by Bouwmeester *et al.* (1993a) in germination experiments with S*isymbrium officinale* (L.) Scope. Seeds did not germinate in darkness before burial, but germination percentages increased up to 100% after a couple of months of burial.

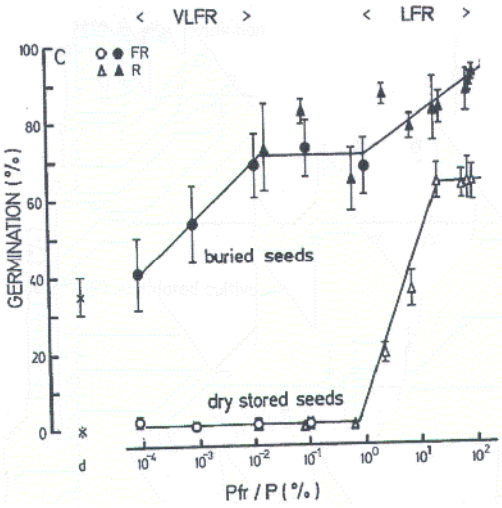

Figure 4. *Rrelationship between germination and the % Pfr established by different fluences of R light (△▲, from 4.8 to $2.9*10^5$ µmol m^2) or FR light (○●, from 3 to 4.4 $*10^4$ µmol m^2) of D. ferox seeds. Germination is expressed as percentage of the number of viable seeds. Viability was >95% (controls) and >90% (exhumed seeds). Crosses indicate the level of dark germination. Adapted from Scopel et al. (1991).*

3.1.2 Influence of soil properties on light-induced germination

The amount of light penetrating the toplayer of the soil is very low. A number of factors affect the transmittance of light through soil; particle size, moisture content, particle colour and presence of organic matter (Tester *et al.*, 1987).

Baumgartner (1953) found that when the diameter of particles of quartz sand is 0.2-0.5 mm, a depth of 1-2 mm was needed to reduce the radiation by 95%, but for very large particles of 4-6 mm in diameter, 10 mm of sand were needed for the same reduction in radiation. Other studies also note a decrease in soil transmittance with decreasing particle size (Bliss *et al.*, 1985). However, there have been no detailed measurements of the penetration of light through soil mixtures of widely different particle sizes, as would often be found in field situations.
Depending on the soil type, moisture content either increases or decreases the light transmittance of the soil. When sand is saturated the transmittance will increase, whereas saturation of clay and loam decreases the transmittance of light. This difference is probably attributed to a reduction in the reflection of light by the soil particles. When the particles are translucent, as in sand, transmission can increase through the particles; but in dark soil, reduced reflection only leads to increased absorption by the particles (Bliss *et al.*, 1985). The darker particles are thought to absorb the light. Another explanation is the increased reflection by particles of the paler coloured soils, whereas the reflection in dark soils is lower (Tester *et al.*, 1987). The role of organic matter has not been investigated yet, but was mentioned by Tester *et al.* (1987) as a factor possibly influencing light transmission.
Based on different studies regarding the penetration of light through soil, it can be concluded that physiologically and significantly amounts of light rarely penetrate more than 4-5 mm through soil, and that only 0.01% light is trans-

mitted through to a depth of 3 mm. Since seeds can germinate from significantly deeper soil layers (up to 8 cm), the sensitivity of the seeds after burial needs to be enhanced to achieve high germination levels (Tester *et al.*, 1987).

It may be an option to cover the machine while disturbing the soil to prevent breaking of dormancy and subsequent germination. The effect of this method, however, will not only depend on weed species and climatic circumstances, but will also depend on the particle size, moisture content and colour of the soil.

3.2 Temperature

Besides the regulation of dormancy (chapter 2) in weed seeds, temperature is also involved in the germination of seeds. It is one of the environmental factors for which a degree of dormancy exists. Several experiments have been performed in which seeds were allowed to germinate at different temperature ranges to determine the temperature germination range (range of temperatures over which seeds are able to germinate). However, since temperature also influences the state of dormancy and the range itself, it is difficult to ascribe temperature effects to either dormancy or germination.
One of these experiments was performed by Benvenuti *et al.* (2001) in which germination of *Rumex obtusifolius* seeds was observed after incubation at several temperatures in both light and dark (Table 1).

Table 1. Effect of incubation temperature on germination of R. obtusifolius *seeds in both light and dark conditions (Benvenuti et al., 2001).*

	Temperature of seed incubation (°C)							
Germination (%)	5	10	15	20	25	30	35	40
Light	0	18	75	88	87	72	23	0
Dark	0	5	51	74	77	65	18	0

Similar experiments have been performed with seeds of *Commelina benghalensis* L (Ferreira *et al.*, 1999) and seeds of *Polygonum persicaria* (Vleeshouwers, 1998). Vleeshouwers (1998) tested the effect of temperature at three different levels of dormancy. These levels were obtained by imbibition of seeds in 10 mM KNO_3 and incubation at 2°C in darkness for 1, 2 and 5 days, respectively (dormancy level 3, 2 and 1). Following the germination of the seeds was tested at a range of temperatures after irradiation of the seed with red light. Dormancy and temperature influenced the final germination percentage of *P. persicaria* seeds (Figure 5) and at all temperatures, final germination percentage is higher at the lowest dormancy level.

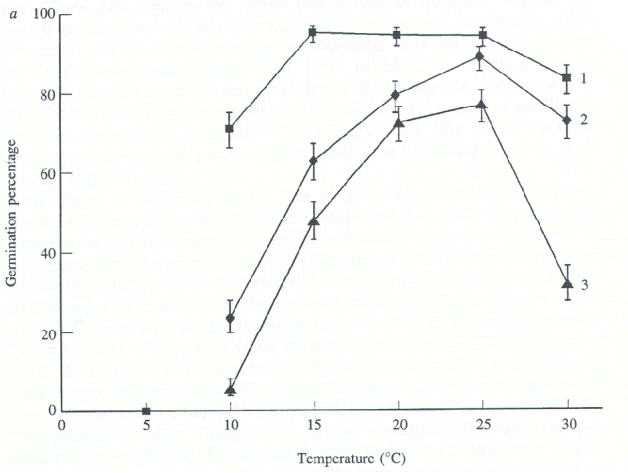

Figure 5. *Final germination percentage of P. persicaria seeds at different levels of dormancy (1,2,3) and different germination temperatures. Vertical bars indicate 95% confidence intervals. Adapted from Vleeshouwers (1998).*

Temperature not only determined the germination percentage but also the germination rate (Figure 6). Low temperatures resulted in a low germination rate whereas high temperatures showed increased germination rate. In contrast, at high dormancy levels (3), germination rate was lower than at low dormancy levels (1).

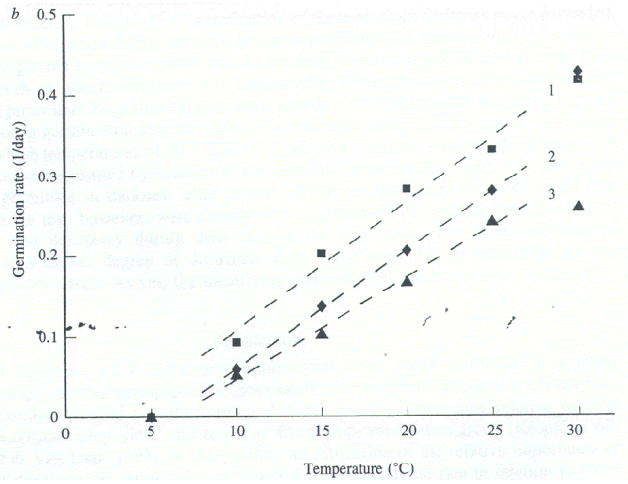

Figure 6. *Germination rate of P. persicaria seeds at different levels of dormancy (1,2,3) and different germination temperatures. Adapted from Vleeshouwers (1998).*

It can be concluded that temperature has an important role in germination of weed seeds, since it both determines the range of temperatures over which germination is possible (dormancy) and is one of the limiting environmental factors during the germination process itself, influencing both germination rate and percentage.

3.3 Nitrate

Nitrate is one of the factors that can stimulate germination of many (weed) seeds. The stimulative actions of light and nitrate often interact in the germination of seeds. For *Sisymbrium officinale* seeds it is known that germination depends on the simultaneous presence of light and nitrate, either exogenously supplied or endogenously present

(Hillhorst *et al.*, 1989). And, as described before, light requirements of seeds change during alterations in dormancy (Taylorson, 1972). In a few studies the importance of nitrate on the germination has been addressed (Bouwmeester, 1990).
Bouwmeester *et al.* (1990) found differences in the effect of nitrate on the germination of *Polygonum persicaria*, *Sisymbrium officinale, Chenopodium album* and *Spergula arvensis* in experiments with seeds buried during three years. They showed a difference between freshly shed and buried *P. persicaria* seeds. Germination of freshly shed seeds was slightly enhanced by applied nitrate whereas germination of seeds buried for a longer period was not. It is hypothesized that this difference is caused by differences in the endogenous nitrate content of freshly shed and buried seeds. Freshly shed seeds of *Polygonum* spp. have a very low nitrate content (approx. 0.2 μmol g^{-1}) and therefore a reaction to exogenous supplied nitrate is to be expected. Seeds of *C. album* and *Sinapsis arvensis* can take up nitrate from the soil during burial. It is well possible that seeds of *P.persicaria* also take up nitrate during the first months of burial, when externally supplied nitrate still stimulates germination. After these first months, the amount of nitrate taken up by the seeds is saturating and externally supplied nitrate will not stimulate germination any longer. The other species, *S. officinale, C. album* and *S. arvensis* probably have higher nitrate requirements for germination.
Seeds of one species can have different nitrogen contents. These differences are probably caused by different nitrate levels in the soil during seed development. The endogenous nitrogen content can be raised by nitrate application to the mother plant (Bouwmeester, 1990).
Similar results were found for *S. officinale* seeds by Derkx *et al.* (1993).
The combination of light and nitrate stimulates the synthesis of gibberellines (GA's) (Hillhorst *et al.* 1988; Derkx *et al.*, 1993) and thereby enhances germination (see also paragraph 4.2).

3.4 Gaseous environment

Most species fail to germinate under reduced oxygen conditions (Corbineau and Côme, 1995). An example is given by Benvenuti *et al.* (1995) who found that lack of oxygen led to a decrease in germination percentage and rate. This decrease could be compensated by daily exchange of the gas surrounding the seed. An explanation for this compensation may be the reduction of the seed's aerobic respiratory activity as a result of oxygen deficiency. This lack of aerobic respiration is probably compensated by an increase of the unaerobic (fermentation) metabolism. This unaerobic metabolism causes an increased accumulation of toxic products in the surrounding of the seed. Regularly changing the gas surrounding the seed will remove (part of) these toxic products and thereby compensate lower germination percentages due to oxygen deficiency (Figure 7). So, oxygen (deficiency) has a dual effect on germination; it inhibits germinaton itself and it stimulates the anearobic reaction that produces germination inhibitors.
Oxygen levels in soil usually do not fall below 19%, although in certain cirumstances it can decrease to 1% or even less in soils that are maintained at field capacity or that are flooded. Values lower as 10% can be found when a crust is formed at the soil surface (Corbineau *et al.*, 1995). Sensitivity of seeds to low oxygen concentrations differs between species.

Carbon dioxide levels are usually not higher than 0.5-1% (Karssen, 1980-1981). CO_2 can have a beneficial effect on germination of seeds, but also a negative effect, depending on species and cirumstances. Knowledge is lacking about the interactions of CO_2 levels and O_2 and ethylene levels in relation to germination of seeds (Corbineau *et al.*, 1995). Factors such as porosity, water content, gas release by living organisms (seeds, (micro)fauna and (micro)flora) and compaction of the soil can play a role in the regulation of seed germination since they determine the rate of soil diffusion (Benvenuti *et al.*, 1995). Therefore, the structure of the soil is of importance in the regulation of the germination of buried seeds not only in relation to light (paragraph 3.1.2) but also in relation to the gaseous environment of the seed.

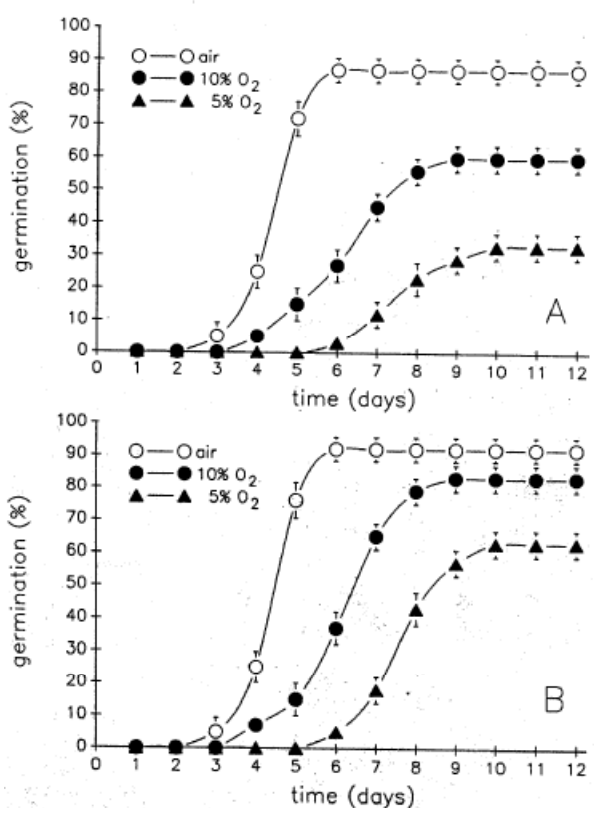

Figure 7. *The effect of oxygen availability on Datura stramonium seed germination without (A) and with (B) gas exchange. Adapted from Benvenuti et al. (1995).*

3.5 Moisture content of seeds

Depending on the weed species, dessication of seeds either improves germination (Karssen et al., 1988) or does not effect germination at all (Griswold, 1936). It has been found for *Chenopodium album*, *Sisymbrium officinale*, *Spergula arvensis* and *Polygonum lapathifolium* that dessication of seeds stimulates germination. This stimulation was proportional with seed moisture content for *C. album*, *S. officinale* and *S. arvensis*, although a larger dessication level of the seed content stimulated germination of *S. officinale* and *S. arvensis* more than germination of *C. album*. This difference between species is due to composition of reserve food in the seed, relative size of the embryo and other seed characteristics differing between the species (Karssen *et al.*, 1988; Bouwmeester, 1990).
The influence of water on the germination of seeds was tested in an incubation experiment with *Origanum vulgare* seeds (Pons, 1991). Seeds were incubated in water or in polyethylene glycol solution (PEG) with an osmotic potential of -1.2 MPa. and irradiated afterwords with R light. Low availability of water (incubation in PEG) appeared to reduce the loss in responsiveness in time and enhance germination.

For the influence of soil moisture content see paragraph 3.1.2.

4. Models describing dormancy patterns and germination

Several dormancy models have been developed; they are either based on an ecophysiological concept (Bouwmeester *et al.*, 1992; Bouwmeester *et al.*, 1993c) on a biochemical concept (Hillhorst, 1998) or quantatively integrate both concepts (Vleeshouwers *et al.*, 2001). Ecophytiological models predict weed seed germination in the field in relation to environmental factors (paragraph 4.1). Biochemical models give a molecular explanation for dormancy (paragraph 4.2). Concepts are not in contradiction with each other, but rather a confirmation or an extension of each other.

4.1 The ecophysiological concept

Temperature has a dual role; on one hand it regulates the seasonal changes in dormancy, but also germination. (Bouwmeester *et al.*, 1993a). However, both processes have quite different temperature requirements.

(1) Temperature influences the induction and relief of dormancy. For instance in summer annuals, dormancy is induced by an increase of the minimum temperature at which seeds can germinate and relieved by a decrease of the minimum temperature at which germination can occur respectively. Winter annuals germinate and emerge in autumn (Baskin *et al.*, 1985).

(2) Temperature influences the period in which germination can occur. Seeds can only germinate when the actual temperature is within a temperature- germination range (range of temperatures over which germination can proceed) (Bouwmeester, 1990).

These effects of temperature can be distinguished and combined with other factors that stimulate germination, such as light. The influence of these factors varies between species (Bouwmeester *et al.*, 1993a). Before seeds are exposed to light, temperature affects the dormancy state of seeds. After irradiation of seeds temperature affects the germination of seeds (Bouwmeester, 1990).

The combined effect of ecophysiological factors is illustrated by the experiments with *Polygonum persicaria* by Bouwmeester *et al.* (1992). They showed that dormancy of *P. persicaria* can be broken at temperatures that will never allow germination of this species. On the other hand, at the end of spring, temperatures favour germination, but also induce dormancy. If, in spring, the light-requiring seeds remain buried in the soil, they will not germinate due to lack of light and current temperatures will cause the induction of dormancy. Tillage practices causing soil disturbances, however, may cause irradiation of the seeds by daylight and subsequent germination of the seeds at these temperatures. In this way, germination and induction of dormancy can occur simultaneously.

Bouwmeester and Karssen (Bouwmeester *et al.*, 1992; Bouwmeester *et al.*, 1993c; Bouwmeester *et al.*, 1993a; Bouwmeester *et al.*, 1993b) developed a descriptive model of the seasonal changes in dormancy of *Polygonum persicaria*, *Chenopodium album*, *Spergula arvensis* and *Sisymbrium officinale*. The basis of their model is the simultaneous occurrence of a dormancy-breaking (cold sum) and a dormancy- inducing factor (heat sum) that lead to the seasonal patterns in dormancy.
The cold sum is calculated as the period spent below a critical temperature; the heat sum as the accumulation of the temperature during burial.
Besides the cold and heat sum, germination of seeds in this model is linked to the presence or absence of nitrate and the temperature during a period prior to exhumation (Bouwmeester *et al.*, 1993a).

4.2 The biochemical concept

In this concept it is hypothesised that properties of cellular membranes are involved in the regulation of dormancy and germination. The reason for this assumption is that membranes appear to be the primary targets for temperature stimulus in living organisms whereas temperature is also the main environmental factor involved in the regulation of dormancy (Hillhorst, 1998). This model is described in Figure 8 for a summer annual weed species.

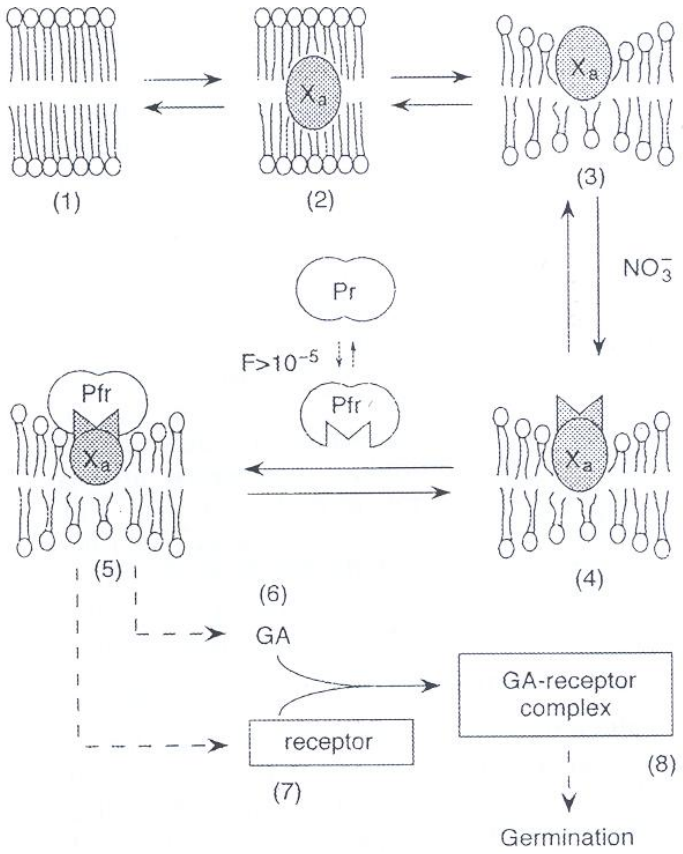

Figure 8. Model for relief and induction of dormancy and stimulation of germination in a summer annual.

Innitially, the represented membrane is the one of a dormant, imbibed seed at low temperatures (1). Breaking of dormancy at low temperatures leads to synthesis of phytochrome receptor X_a (2). Increase of the temperature increases membrane fluidity, which makes movement of the receptor to the membrane surface possible (3). It is now possible for co-factors such as nitrate to activate the receptor (X_a) (4). Irradiation by red light with a fluence (F) higher than 10^{-5} mol m^{-2} transforms Pr into Pfr (Appendix II for backgroundinformation on phytochromes). The activated receptor binds Pfr (5). Pfr is the far-red absorbing form of phytochrome, Pr is the red-absorbing form (Pons, 1991). The receptor-phytochrome complex initiates the biosynthesis of gibberelines (GA) (6) and enhances the sensitivity of receptors to GA (7). Binding of GA to the GA-receptors leads to germination (8). High temperatures cause the degredation of the phytochrome receptor protein (X_a) and induce dormancy (Hillhorst, 1998; Vleeshouwers *et al.*, 2001).

This concept is supported by experiments of Derkx *et al.* (1993). They tested the responses of *S. officinale* seeds buried under natural conditions to different gibberelline concentrations. They presented dose response curves and analysed the parameters R_{min} (minimum germination response in %), R_{max} (maximum germination response in %), $[GA]_{50}$ (dose of gibberellins needed for half-maximum response in mmol m^{-3}). No seasonal changes in R_{max}, the slope of the curves or $[GA]_{50}$ to gibberellins were observed. Only R_{min} fluctuated during the season; it was low in winter, increased in late winter and spring and decreased again in summer.

This seasonal independency on exogenous GA's was explained by an increased capacity to synthesize GA's; addition of tetcyclasi, an inhibitor of GA biosynthesis, reversed the rise in R_{min}. Concentrations of GA's could neutralize the effect of tetcyclasi on $R_{min.}$ Irradiation of the seeds with R (Red light) reduced the requirements for external Gas, since irradiation with R stimulates the internal synthesis of GA's.

4.3 Integration of two concepts

(Vleeshouwers and Bouwmeester, 2001) developed a quantative model describing the integration of both above-described concepts. The model simulates the annual dormancy cycle of seeds of light-requiring species in the seed bank and germination of exhumed seeds after irradiation. Annual changes in temperature are used to explain the annual changes in phytochrome receptor in buried seeds in a seedbank. The model calculates germination percentages of irradiated seeds at different temperatures on the basis of a hypothetical amount of available phytochrome receptor.

5. Field experiments; effects of light on germination and emergence of weeds

Of all factors influencing dormancy and germination described in this report, light is probably the factor that can relatively easy be influenced in field situations, and changes have a potentially large impact on germination of seeds. Temperature and gas content of the soil can not be adjusted or are very difficult to adjust for a longer period of time. Nitrogen level can be regulated by application or reduction of fertilizer, but can be unfavourable for crop growth.
Several field experiments have been conducted to observe the effects of light during different soil tillage practices on the germination and emergence of weeds (Scopel *et al.*, 1994; Jensen, 1995; Botto, 1998; Bleeker *et al.*, 2001). They are described in the next paragraphs.

5.1 Avoidance of germination and emergence

Botto *et al.* (1998) performed cultivations with a moldboard plow on three fields during the day or during the night. The fields had a history of annual crops (2 fields) or permanently covered with an implanted pasture (one field)) in spring, late spring, late summer and late winter. The mold board plow had a working depth of 18-20 cm and a working width of 200 cm. The experiments showed that, depending on the field and season, 50-67% less seedlings emerged when cultivation was performed during the night instead of during daytime. On some fields no differences between cultivation during the night or during daytime were found in certain seasons, probably due to the different histories of the fields. They concluded that the effect of cultivation during the night on the germination response can vary from field to field and from season to season for the same field due to differences in species composition. Seeds of these species may have different seasonal dormancy patterns which are reflected in changes in light sensitivity. Another explanation might be different stress conditions in the different seasons; seeds buried in the upper centimetres of the soil may have experienced water and temperature stress during the experiments in spring and summer which may have inhibited germination or caused the death of seedlings soon after emergence (emergence was 50% less in summer and spring experiments compared to winter experiments) (Botto, 1998) . Similar effects of day- and nighttime treatments were observed by (Scopel *et al.*, 1994) in Oregon, USA; nighttime cultivation reduced the emergence of dicotyledonous weeds and grasses by 50%. (Buhler *et al.*, 1998) in Minnesota, USA found 45% less weeds after tillage with protection from light.

In Europe, similar experiments have been performed in Denmark (Jensen, 1995). They performed daylight harrowings (0-16) at a PAR (photosynthetic active radiation) exceeding 1000 $\mu E\ m^{-2}s^{-1}$ and night- or dark harrowings (0-16) when PAR was below $0.0001 \mu E\ m^{-2}s^{-1}$. Seeds of *Chenopodium album* were sown in the field prior to the experiments. They found that significantly more seeds germinated and emerged after treatments in light than in darkness. It was concluded that 90-95% of the seeds needed a soil disturbance to be able to germinate.

Emergence of weeds in general was reduced by tillage during the night from 80% to 2% in comparison to tillage during daytime in Germany (Hartmann *et al.*, 1990). They performed all soil cultivation activities either in broad daylight or at night at fields in which no crop was growing to avoid competition. Results are shown in Appendix IV. Hartmann *et al.* (1990) recommends to perform tillage practices up to 50 ° geographic latitude between not earlier than 1 hour after sunset and not later than 1 h before sunrise. They advise to perform plowing not at night but around noon to provoke a large flush of emerging weeds in the subsequent weeks to reduce the weed seed bank. Subsequent cultivation practices during the night, such as harrowing and the sowing or planting of the crop, destroy the emerged weeds.

Similar experiments were performed by Ascard (1994). The emergence of weeds after cultivation during the day, night or during the day with covered machinery was compared. They found that night-time harrowing significantly reduced the amount of emergening weeds, but found differences in the amount of reduction between years,

locations, weed species and soil type. Small-seeded species such as *Viola arvensis* and *Stellaria media* were in general more light-dependent than large-seeded species such as *Bilderdykia convolvulus* for their germination (Ascard, 1994).

This variation is in agreement with results of all studies comparing weed emergence after day- and night-time tillage. Part of this variation may be explained by differences in light requirement of seeds in time (e.a. degree of dormancy). As described before, germination is the result of overlap in requirements to relieve dormancy and the actual environmental conditions that permit germination. Changes in the degree in dormancy of seeds between years or different soils, due to different circumstances during the determination of this degree, can cause the differences in environmental requirements for germination and thereby different responses to light.
Hartmann showed that all spectral colours from ultra-violet at 300 nm to near-infra-red at 800 nm are able to cause germination of sensitized lettuce (*Lactuca sativa* L.) seeds. This implies that light of 800 nm is able to form enough active phytochrome Pfr to saturate the VLFR (Appendix II) if seeds are sensitized. This response of the seeds is irreversible, so no addition of FR (around 735 nm) will prevent germination of sensitized seeds after exposure to light, but rather enhance germination (Hartmann and Mollwo, 2000).
Since burial of weed seeds is very common in agricultural land and sensitizes the seeds, a large part of the weed seed bank is highly sensitive and able to germinate at flashes of light ranging from 300 to 800 nm. Therefore, tillage practices performed at night are probably not very effective, since nightly sky- and moonlight is in the order of this range and able to stimulate the germination of highly sensitized seeds via the VLFR.
Another part of the variation may be attributed to differences in environmental cirumstances, not to differences in degree of dormancy.

5.2 Enhancement of germination and emergence

Instead of avoidance of germination and emergence of weeds, one can use factors such as soil disturbance and light to stimulate the emergence and germination prior to crop planting in order to remove as many weeds from the soil seed bank as possible.
To test the strategy of stimulation of weed emergence and germination prior to crop growth, experiments in lettuce have been performed in 1999 and 2000 in the Netherlands on different plots and green bean in 2001 (Bleeker *et al.*, 2001). Several false seedbed preparations were applied and compared to fields in which no false seedbed was prepared and other weed control methods were applied (Table 1 of Appendix III for lettuce control strategies and results 1999 and Table 2 for lettuce strategies and results 2000). Weed pressure could be reduced by 40 to 85% as a result of the false seedbed strategy. And reductions up to 90% could be obtained by covering harrow and hoe, which were used to remove the emerged weeds.

Preparation of a false seedbed in sugarbeet followed by sowing in the dark did not reduce the amount of weeds compared to control treatments (daylight and non- false seedbed treatments) (Zuydam *et al.*, 1995). In their experiments, the number of weeds in both dark and light treatments were very low, which might have been the reason for the absence of differences.

Conclusions

As a part of this programme, the preparation of 'false seedbeds' and covering the soil during seedbed preparation is being evaluated. In the present study an analysis of the dormancy, germination and emergence of weed seeds was made and possibilities to use factors influencing germination as weed control methods are summarised. Focus was on the influence of light since this factor is relatively easy to alter in the field compared to other factors such as soil temperature, moisture content and nitrate.

- Temperature is the only factor known to influence the degree of dormancy directly, it is very well possible that other factors are involved.
- Temperature, light, nitrate, gaseous environment and moisture content are the most important factors that influence germination of seeds.
- Of these factors, light has potentially the most possibilities to influence the germination of weed seeds in the field (Photocontrol) since other factors such as gas content of the soil, are more difficult to alter.
- Photocontrol can be used to either improve (to control emerging weeds prior to crop growth in false seedbeds) or reduce germination and emergence of weed seeds in the field (e.g. coverage of equipment).
- Results from field experiments in which dark tillage is used to reduce emergence of weeds and experiments in which false seedbeds are used to enhance emergence of weeds show different results over the years, soil types and tillage practices. Other environmental conditions and differences in dormancy state probably cause these differences. Nighly sky-and moonlight is probably enough to saturate the VLFR of buried seeds and can cause germination.
- Although the light responses of seeds change continuously with the annual dormancy cycle, the light requirement shown by a large portion of the species tested by Milberg *et al*. (1996) and Andersson *et al*. (1997) implies a great potential for integrating photocontrol of seed germination into weed management programmes.
- For optimal use of photocontrol in a specific situation, one should know the dormancy state of the weed seeds buried in that specific field. (Dormancy determines the range of environmental conditions that should be met to make germination possible, including amount of light). However, knowledge on the influence of seasonal temperature variations (dormancy determining factor) on the range of environmental conditions under which germination can take place is lacking for most weed species.

At this point it is very difficult to experimentally show the difference between widening of the dormancy state of seeds and the enhancement of germination by an environmental factor. One can simply not test the dormancy state of a seed without germination.
Therefore, it is recommended to perform field trials with photocontrol to improve this method experimentally without attempting to unravel the mechanisms by which environmental factors narrow or widen the dormancy state of seeds.

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Appendix I.
Seed germination affected by light

Table 1. Germination percentage of seeds tested in full light, darkness and in darkness after a short duration of light exposure (SDLE). Differences in germination between light-SDLE and SDLE- darkness are given by T1 and T2, respectively. Differences between populations (P) and population-treatment (PxT) interactions are presented for the SDLE-darkness comparison only (Andersson et al., 1997),(Milberg et al., 1996). A represents Andersson result, M Milberg result.

	Germination[a]			Difference[b]			
Species	Light	SDLE	Darkness	T_1	T_2	P	PxT_2
Summer annuals							
Anchus arvensis (A)	58.1	53.7	22.3	***	***	***	*
Avena fatua (A)	3.5	1.3	2.6	d	d	d	d
Bilderdykia convolvulus (A)	64.1	58.0	48.6	ns	ns	***	ns
Bilderdykia convolvulus (M)	94.4	62.3	61.9	ns	ns	***	ns
Chaenorrhinum minus (M)	52.3	56.4	24.6	***	***	***	**
Chamomilla recutita (M)	49.8	0.8	0	x	x	x	x
Chamomilla suaveolens (M)	75.0	4.0	2.1	x	x	x	x
Chenopodium album (A)	99.5	92.3	46.7	**	***	ns	ns
Chenopodium album (M)	75.1	52.4	2.9	***	***	ns	**
Chenopodium polyspermum (M)	75.4	31.4	13.8	***	***	x	x
Chenopodium suecium (A)	97.9	76.7	18.9	*	***	ns	**
Chenopodium suecium (M)	51.9	17.7	1.7	***	***	x	x
Descurainia sophia (A)	6.8	1.4	4.4	d	d	d	d
Euphorbia helioscopia (A)	16.5	29.0	30.7	ns	ns	*	ns
Flaginella uliginosa (M)	97.8	4.3	0.8	***	***	x	***
Fumaria officinalis (A)	14.2	11.6	12.0	ns	ns	*	ns
Galeopsis bifida (M)	45.3	56.0	20.1	***	***	x	**
Galeopsis speciosa (A)	37.5	68.6	26.9	***	***	**	*
Galeopsis speciosa (M)	29.7	46.5	33.8	***	***	***	***
Galeopsis tetrahit (A)	82.7	77.5	70.9	ns	***	***	*
Galeopsis tetrahit (M)	19.1	17.5	2.2	***	***	x	***
Galinsoga ciliata (A)	74.9	7.8	0.9	***	***	ns	ns
Galinsoga ciliata (M)	99.5	1.5	1.9	ns	ns	ns	ns
Matricaria matricarioides (A)	99.7	87.3	11.2	***	***	***	**
Polygonum aviculare (A)	60.5	52.1	32.8	ns	***	***	ns
Polygonum aviculare (M)	69.2	27.8	10.1	***	***	***	ns
Polygonum lapatifolium (A)	76.1	42.8	23.4	***	***	*	ns
Polygonum lapatifolium (M)	74.1	12.3	4.8	**	**	*	**
Sinapsis arvensis (A)	67.1	75.9	57.6	ns	***	***	*
Sinapsis arvensis (M)	28.4	32.8	27.8	**	**	***	***
Sonchus asper (A)	88.7	84.5	79.8	ns	ns	***	ns
Sonchus asper (M)	99.3	25.3	18.3	*	*	***	ns
Sonchus oleraceus (A)	100.0	99.4	74.6	ns	***	ns	ns
Sonchus oleraceus (M)	100.0	50.6	21.2	***	***	***	ns
Spergula arvensis (A)	33.6	35.2	1.8	ns	***	*	ns

Species	Germination[a]			Difference[b]			
	Light	SDLE	Darkness	T_1	T_2	P	PxT_2
Urticura urens (A)	86.3	90.1	23.5	ns	***	***	ns
Urticura urens (M)	87.0	53.4	7.5	***	***	***	ns
Winter annuals							
Buglossoides arvensis (A)	78.9	68.4	63.1	***	ns	***	*
Buglossoides arvensis (M)	87.8	80.4	61.6	***	***	***	*
Capsella bursa-pastoris (A)	34.1	20.9	9.0	***	*	***	ns
Centaurea cyanus (A)	80.9	48.9	43.7	***	ns	***	ns
Erodium cicutarium (A)	37.1	7.4	9.7	***	ns	ns	ns
Erodium cicutarium (M)	15.7	13.1	20.3	ns	ns	***	**
Galium aparine (A)	47.2	32.7	28.9	***	ns	***	ns
Lamium amplexicaule (A)	99.1	94.3	3.2	***	***	**	*
Lamium purpureum (M)	38.3	16.5	17.8	ns	ns	***	ns
Lapsana communis (A)	91.0	53.8	1.2	***	***	ns	ns
Lapsana communis (M)	96.7	7.1	5.3	x	x	x	x
Matricaria chamomilla (A)	98.7	32.3	2.8	***	***	*	ns
Matricaria perforata (A)	99.6	79.9	4.2	***	***	***	ns
Matricaria perforata (M)	99.0	4.4	3.1	***	***	x	***
Myosotis arvensis (A)	36.6	7.9	1.5	***	ns	x	ns
Myosotis arvensis (M)	20.3	3.9	5.6	ns	x	x	x
Papaver argemone (A)	0.7	2.2	0.2	d	d	d	d
Papaver dubium (A)	0.9	2.3	0.5	d	d	d	d
Papaver rhoeas (A)	10.0	11.4	6.2	d	d	d	d
Senecio vulgaris (A)	98.6	93.2	64.7	**	***	***	ns
Senecio vulgaris (M)	92.4	9.5	4.1	ns	ns	**	ns
Silene noctiflora (A)	99.8	99.5	85.7	ns	ns	***	**
Silene noctiflora (M)	100	71.3	18.9	***	***	***	***
Stellaria media (A)	89.3	96.5	33.6	***	***	ns	ns
Stellaria media (M)	45.9	52.4	17.5	***	***	***	**
Thlaspi arvense (A)	41.2	60.8	0.2	***	***	ns	ns
Veronica agrestis (A)	88.5	59.8	6.7	***	***	***	ns
Veronica agrestis (M)	16.3	11.9	9.0	ns	ns	***	ns
Veronica arvensis (A)	75.5	9.9	0	***	**	ns	ns
Veronica arvensis (M)	49.5	0	0	x	x	x	x
Viola arvensis (A)	41.2	71.9	34.1	***	***	***	ns
Unclassified annuals							
Apera spica-venti (M)	40.9	17.8	9.9	**	**	***	***
Berteroa incana (M)	23.3	14.6	14.3	ns	x	x	x
Bromus tectorum (M)	84.3	99.0	100.0	x	x	x	x
Conyza canadensis (M)	18.6	7.8	0.8	***	***	ns	ns
Galium spurium (A)	8.7	47.0	25.7	***	***	***	*
Lactua seriola (M)	988.7	84.2	54.2	***	***	x	***
Lamium hybridum (A)	83.3	57.4	14.0	***	***	***	**
Lamium hybridum (M)	87.2	75.6	65.2	***	***	***	***
Poa annua (M)	90.0	46.7	45.3	ns	ns	***	ns
Perennials							
Bunias orientalis (M)	18.1	17.4	14.0	ns	ns	***	**
Cerastium fontanum (M)	88.0	59.2	16.7	***	***	x	x
Melilotus alba (M)	32.7	24.1	23.6	ns	ns	***	ns

Species	Germination[a]			Difference[b]			
	Light	SDLE	Darkness	T_1	T_2	P	PxT_2
Rumex crispus (M)	46.5	0.5	0	x	x	x	x
Rumex longifolius (M)	98.0	21.5	0.2	***	***	***	x
Rumex obtusifolius (M)	94.5	26.0	0.2	***	***	x	***
Taraxacum officinale group (A)	98.1	97.8	95.3	ns	ns	ns	ns
Taraxacum officinale group (M)	100.0	100.0	65.2	x	x	x	x
Verbascum thapsus (M)	49.9	32.3	0	x	x	x	x

[a] *Values are the means of three populations with two replicates*

[b] **, **, ***= significant differences, or significant interactions (p<0.05, p<0.01 and p<0.001, respectively)*

ns= not significant, d= strong dormancy, x= analysis not possible due to missing value

Appendix II.
Phytochromes

Phytochromes are photoreceptors regulating seed germination responses to light. The two forms are the physiologically active form, Pfr and the inactive form, Pr. Pfr absorps light of 735 nm in the far-red (FR) regions of the light spectrum, Pr absorps light of 665 nm in the red (R) regions of the light spectrum (Massanori, 2001). Light pulses (R) establishing high levels of Pfr in the seed frequently trigger germination (Botto, 1998).
Different responses of phytochromes to light pulses exist:

- Low Fluence Response (LFR): production of Pfr promotes germination, whereas removal of Pfr reverses the response of the seeds. Seeds germinate at relatively high percentages of Pfr. Under the influence of light, Pfr can be transformed into Pr and vice versa. Radiation of the seed with FR will reduce the percentage of Pfr immediately to ≈ 2% and seeds will not germinate any longer. This R/FR reversible response is known as the LFR (Taylorson, 1972) (Botto, 1998).
- Very Low Fluence Response (VLFR): seeds have a very high light sensitivity and germinate at very low (<2%) percentages of Pfr (Mandoli and Briggs, 1981; Kendrick and Cone, 1985). This response is not reversible because the photoequilibrium maintained by far red light or even dim green safe light used in photomorphogenic experiments produces enough Pfr to saturate these responses (Massanori, 2001).
- High Irradiance Responses (HIR): response produced by prolonged high irradiance, which do not show reversibility or reciprocity (Massanori, 2001).

Appendix III.
Results of false seedbed experiments

1999

Hoeing with torsionweeder removed 96% of the weeds. Remaining weeds were situated in the row. Yield and quality of the crop were slightly lower compared to the untreated, these differences were however not significant.

Hoeing with fingerweeder removed 99% of the weeds. Yield and quality of the crop were slightly better compared to hoeing with torsionweeder.

Preparation of a false seedbed with a rotoray harrow and control of weeds by hoeing a day prior to planting resulted in a weed reduction of 74%. By hoeing the plot after planting, a further reduction up to 96% was accomplished. Yield and quality of the crop were good. There was no difference when using a false seedbed 2 weeks prior to planting instead of 4.

Preparation of a false seedbed with a rotoray harrow and control of weeds by a rotoray harrow prior to planting resulted in a weed reduction of 44%. According to the authors, the difference with the previous treatment is ascribed to the working depth of both systems. Rotoray harrowing requires a deeper working depth, which may have caused the transport of seeds from deeper soil layers to the surface, resulting in a higher emergence percentage compared to hoeing.

False seedbed followed by chemical control of weeds prior to planting with glyphosate resulted in reduction of the amount of weeds by 74%. The biomass of the remaining weeds however was higher than the amount of biomass in the untreated plots. Yield was slightly lower than average.

Preparation of a false seedbed with a rotoray harrow and control of weeds by a rotoray harrow prior to planting resulted in a weed reduction of 44%. Coverage of the rotoray harrow with black plastic raised weed reduction to 74%. Yield in this plot was high.
Addition of farred light under the black plastic did not signficicantly alter the germination of weeds.

Table 1. *Weed control strategies and results in lettuce for 1999 (Bleeker et al. (2001)). Other species comprise* Polygonum persicaria, Rorippa sylvestris, Sonchus oleraceus, Senecio vulgaris *and* Stellaria media. *N= number of weeds per m^2.*

	Weed control strategy	Total Weed reduction (%)	*Poa annua* (N)	*Chenopodium album* (N)	*Solanum nigrum* (N)	*Veronica spp* (N)	*Capsella bursa pastoris* (N)	Other species (N)
A	Untreated	0	0.6	2.0	7.5	3.1	3.8	0.5
B	Chemical weed control, 5l. Legurame and 1.5 l. CHIIPC.	59	0.1	0.6	0.8	3.3	0.8	0.8
C	Hoeing with torsionweeder (6 km/h)	96	0	0	0.1	0.4	0.1	0.1
D	Hoeing with fingerweeder (6 km/h)	99	0	0	0.1	0	0	0
E	Hoeing	89	0.1	0.2	0.8	0.3	0.2	0
F	4 weeks false seedbed. Prior to planting: 1-2 cm deep hoeing + harrowing, after planting hoeing.	96	0.1	0.3	0.1	0	0	0.2
G	4 weeks false seedbed. Prior to planting: 3-4 cm deep rotoray harrowing.	44	0.7	1.4	1.5	0.4	0.4	0.9
H	4 weeks false seedbed. Prior to planting: chemical control with 3 l. glyphosate	69	1.5	1.5	1.0	1.4	0.1	0.6
I	4 weeks false seedbed. Prior to planting: 3-4 cm deep rotoray harrowing. Rotor covered with black plastic and two blankets.	74	0.1	1.1	1.0	1.0	0.1	0.9
J	4 weeks false seedbed. Prior to planting: 3-4 cm deep rotoray harrowing. Rotor covered with black plastic and two blankets. Under the plastic two infra red lights (100 watt).	69	0.1	1.0	1.1	0.1	0.4	0.6
K	2 weeks false seedbed. Prior to planting: 1-2 cm deep hoeing + harrowing.	75	0.3	1.4	0.1	2.0	0.1	0.2

2000

Hoeing with torsionweeder resulted in a weed reduction of 96%. Yield and quality were not significantly different from untreated plots.

Hoeing with fingerweeder resulted in a reduction of 99% compared to control and gave good quality and yield.

Hoeing resulted in a weed reduction of 93% with good quality and yield.

Preparation of a false seedbed with a rotoray harrow and control of weeds followed by hoeing a day prior to planting resulted in a weed reduction of 53%. Yield and quality of the crop were slightly lower compared to the untreated control. Coverage of the hoe reduced the amount of weed further, resulting in a final weed reduction of 71%.

Preparation of a false seedbed followed by rotoray harrowing prior to planting resulted in a weed reduction of 60% with yield and quality not being significantly different from control.
Coverage of the rotoray harrow raised the reduction from 60 to 72%. Addition of farred light under the black plastic did not signficicantly alter the germination of weeds.

False seedbed followed by chemical control of weeds prior to planting with glyphosate resulted in reduction of the amount of weeds by 68%. The biomass of the remaining weeds however was higher than the amount of biomass in the untreated plots. Yield was slightly lower than average.

By covering the rotoray harrow during plantbed preparation without false seedbed strategy the amount of weeds could be reduced by 63%.

Table 2. Weed control strategies and results in lettuce for 2000 (Bleeker et al. (2001)).N= number of weeds per m^2.

	Weed control strategy	Total Weed reduction (%)	*Poa annua* (N)	*Chenopodium album* (N)	*Solanum nigrum* (N)	*Veronica spp.* (N)	*Capsella bursa pastoris* (N)	*Sonchus arvensis* (N)
A	Untreated	0	10.9	35.8	10.0	3.8	2.7	3.0
B	Chemical weed control, 5l. Legurame and 1.5 l. CHIIPC.	70	0	18.6	1.4	1.4	0.6	1.2
C	Hoeing with torsionweeder (6 km/h)	96	0.6	1.1	0.3	0	0.1	0.1
D	Hoeing with fingerweeder (6 km/h)	99	0	0.4	0.2	0	0	0
E	Hoeing	93	0.6	2.4	0.9	0.6	0.1	0.1
F	4 weeks false seedbed. Prior to planting: 1-2 cm deep hoeing	53	3.5	19.9	3.5	2.0	1.2	1.3
G	4 weeks false seedbed. Prior to planting: 3-4 cm deep rotoray harrowing.	60	2.2	17.3	2.5	1.6	0.9	0.8
H	4 weeks false seedbed. Prior to planting: 1-2 cm deep hoeing. Hoe covered with black plastic and blankets	71	1.9	13.8	2.0	0.9	0.6	0.6
I	4 weeks false seedbed. Prior to planting: 3-4 cm deep rotoray harrowing. Rotor covered with black plastic and two blankets.	72	2.2	12.3	2.5	1.3	0.4	0.6
J	4 weeks false seedbed. Prior to planting: 3-4 cm deep rotoray harrowing. Rotor covered with black plastic and two blankets. Under the plastic two infra red lights (75 watt).	72	1.6	11.3	2.6	1.0	0.8	0.8
K	4 weeks false seedbed. Prior to planting: chemical control with 3 l. glyphosate	68	2.0	15.0	1.9	1.4	0.8	0.6
L	No false seedbed. Rotor covered during plantbed preparation	63	2.3	17.0	2.3	1.7	1.0	0.8

2001

Preparation of a false seedbed with a rotoray harrow followed by hoeing a day prior to planting resulted in a weed reduction of 85%. Yield and quality of the crop were not significantly different from the untreated control. Coverage with black plastic of the hoe reduced the amount of weed further, resulting in a final weed reduction of 91%. Application of farred light under the black plastic did not significantly influence the amount of weeds.

Preparation of a false seedbed followed by rotoray harrowing prior to planting resulted in a weed reduction of 71% with yield and quality not being significantly different from control. Coverage of the rotoray harrow resulted in a weed reduction of 80%. Application of farred light under the black plastic did not significantly influence the amount of weeds.

False seedbed followed by chemical control of weeds prior to planting with glyphosate resulted in reduction of the amount of weeds by 74%. The biomass of the remaining weeds however was higher than the amount of biomass in the untreated plots. Yield was slightly lower than average.

By covering the rotoray harrow during plantbed preparation without false seedbed strategy the amount of weeds could be reduced by 62%. Yield was equal to untreated plots, quality was higher.

Table 3. Weed control strategies and results in lettuce for 2001 (Bleeker et al. (2001)).N= number of weeds per m^2.

	Weed control strategy	Total weed reduction (%)	*Poa annua* (N)	*Chenopodium album* (N)	*Stellaria media* (N)	*Solanum nigrum* (N)	*Senecio vulgaris* (N)	*Capsella bursa pastoris* (N)	Remaining species (N)
A	untreated	0	1.8	10.8	14.7	5.0	5.2	6.3	1.7
B	Chemical weed control, 5l. Legurame and 1.5 l. ChllPC.	69	0.2	2.8	0.8	0.2	9.5	0.5	0.2
C	4 weeks false seedbed. Prior to planting: 1-2 cm deep hoeing	85	0.3	2.3	0.8	1.0	1.7	0	0.5
D	4 weeks false seedbed. Prior to planting: 3-4 cm deep rotoray harrowing	71	0	3.8	2.2	1.8	2.2	2.0	1.3
E	4 weeks false seedbed. Prior to planting: 1-2 cm deep hoeing. Hoe covered with black plastic and blankets	91	0.8	1.3	1.0	0.3	0.5	0.2	0
F	4 weeks false seedbed. Prior to planting: 3-4 cm deep rotoray harrowing. Rotor covered with black plastic and blankets.	80	0.3	4.7	1.3	0.5	0.8	1.0	0.3
G	4 weeks false seedbed. Prior to planting: 1-2 cm deep hoeing. Hoe covered with black plastic and blankets. Under the plastic three infra red lights (75 watt).	85	0.3	1.7	0.5	0.8	2.0	1.2	0.3
H	4 weeks false seedbed. Prior to planting: chemical control with 3 l. glyphosate	74	0.3	2.7	1.0	2.2	3.7	1.8	0.2
I	4 weeks false seedbed. Prior to planting: 3-4 cm deep rotoray harrowing. Rotor covered with black plastic and blankets.Under the plastic three infra red lights (75 watt).	82	0.5	3.7	1.7	1.0	0.2	0.2	0.8
J	No false seedbed. Rotor covered during plantbed preparation	62	2.0	4.2	5.5	2.0	1.2	1.5	1.2

Appendix IV.

Effect of dark tillage on several weed species

Table 1. Weed coverage after tillage treatments at night or at daytime. 5= more than 75% of the ground covered, 4= 50 to 75%, 3= 25 to 50%, 2= 5%, 1= less than 5%, += neglible and -= species not present. From Hartmann et al. (1990).

	Cover degree after cultivation	
Weed species	During dark	In daylight
Agropyron repens	1	1
Alopecurus myosuroides	1	2
Anagallis arvensis	-	1
Capsella bursa-pastoris	-	+
Chaenarrhinum minus	-	2
Chenopodium album	-	1
Convolvulus arvensis	+	1
Equisetum arvense	+	+
Euphorbia helioscopia	-	+
Fallopia convolvulus	1	1
Galium aparine	1	3
Lamium amplexicaule	+	2
Lamium pupureum	-	+
Lapsana communis	-	+
Lolium perenne	+	_
Matricaria chamomilla	-	2
Plantago intermedia	-	+
Poa annua	+	_
Polygonum aviculare	+	1
Polygonum lapathifolium	+	+
Raphannus raphanistrum	-	+
Sinapsis arvensis	+	+
Sonchus asper	-	+
Sonchus oleraceus	-	+
Stellaria media	+	1
Taraxacum officinale	-	+
Thlaspi arvense	+	2
Tussilago farfara	-	+
Veronica persica	+	3
Veronica polita	+	1