

Seed Dormancy and Germination in
Solanum nigrum and *S. physalifolium*
as Influenced by Temperature
Conditions

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Front cover: Young plants, berries, flowers and seeds of *Solanum nigrum* (left) and *S. physalifolium* (right).

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Seed Dormancy and Germination in *Solanum nigrum* and *S. physalifolium* as Influenced by Temperature Conditions

Abstract

Solanum nigrum L. (black nightshade) and *Solanum physalifolium* Rusby (hairy nightshade) are two important weeds in many crops. They reduce crop quantity by competition and crop quality by contaminating harvested products.

The timing of different control measures is a key factor in integrated weed management, which must be related with emergence of the weeds. Since emergence timing of the species is controlled by seed dormancy and temperature conditions, the effect of temperature on dormancy and germination has to be well understood.

Experiments were conducted to study seed dormancy, the temperature effect on dormancy, dormancy cycle, germination characteristics, and emergence of the species. In addition, a simulation model was developed to study the effect of temperature on the dynamics of dormancy release and induction under different temperature conditions.

I found differences in primary dormancy among populations of *S. nigrum* collected on two dates and in different locations. Fresh seeds of *S. nigrum* were conditionally dormant and germinated at higher alternating temperatures and in light, while seeds of *S. physalifolium* were deeply dormant. Seed dormancy is reduced during autumn, winter and early spring in seeds buried in the soil. The rate of dormancy release and induction is low at lower temperatures and increases as the temperature rises. High temperatures cause short-lasting breakage of dormancy followed by induction.

Short-lasting dormancy induction in spring is likely to delay emergence of the species. Seedling emergence of both species showed a bi- or three-modal pattern during an extended period in late spring and early summer. This enables the species to survive natural catastrophes or escape weed control operations. This information can be used to maximize the efficacy of weed management strategies by timing weed control tactics to coincide with seedling flushes.

Dormancy is mainly induced during summer due to higher temperatures. This prevents seedlings from emerging too late and being killed by frost in autumn before reproduction.

Keywords: black nightshade, hairy nightshade, dormancy, emergence, germination, modelling, seed, seedling, weed

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Dedication

To my mother, wife and family

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List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Taab, A. & Andersson, L. (2009) Seasonal changes in seed dormancy of *Solanum nigrum* and *Solanum physalifolium*. *Weed Research* 49, 90–97.
- II Taab, A. & Andersson, L. (2009) Seed dormancy dynamics and germination characteristics of *Solanum nigrum*. *Weed Research*. In press.
- III Taab, A. & Andersson, L. (2009) Primary dormancy and seedling emergence of black nightshade (*Solanum nigrum*) and hairy nightshade (*Solanum physalifolium*). *Weed Science*. In press
- IV Taab, A., Eckersten, H. & Andersson, L. (2009) Modelling temperature effect on dormancy dynamics in moist stratified *Solanum nigrum* seeds (*submitted manuscript*).

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Introduction

Knowledge of weed biology helps to optimize weed management strategies and avoid unnecessary weed control input by for example accurate prediction of emergence timing of the weeds. There is an increase in environmental pressure for reduced pesticide inputs. Consequently, there is a greater emphasis both on optimizing the timing of application and rates of the available products, and on finding sustainable non-chemical alternatives. Integration of knowledge of weed emergence and seed dormancy status could be used to improve weed control strategies (Grundy, 2003). It is of vital importance to know how seed dormancy is regulated by temperature and how it affects the conditions for germination and subsequently emergence timing in the field. Emergence timing is mainly regulated by dormancy and soil temperature conditions. The annual dormancy cycle is largely responsible for seedling emergence patterns (Popay *et al.*, 1995), because changes in the level of dormancy determine the range of environmental conditions needed for germination. Few effective herbicides are available for controlling the *Solanum* species and, thus, the need for strategies based on integrated weed management (IWM), in which different control measures are combined, is increasing. One key factor in IWM is the optimal timing of control measures in relation to the emergence of the weeds. Therefore, the focus of this study was on temperature regulation of dormancy, germination and emergence timing of the two *Solanum* weed species.

The species

The section *Solanum*, centering around *S. nigrum*, is one of the largest and most variable species groups of the genus (Edmonds & Chweya 1997). The majority of the diagnostic characters, which have been used by some authors to identify the species belonging to the section *Solanum*, are

extremely variable, while some species within the section are also very variable morphologically (Edmonds, 1986). This variability, associated with many of the dominating characters, has caused the names of some species to be misapplied. Therefore, there is a taxonomic confusion surrounding *S. nigrum* and its component species (Edmonds & Chweya, 1997), presumably because of the historical factors, phenotypic plasticity, genetic variation, the existence of a polyploid series, and the possibilities of interspecific hybridization (Edmonds, 1977). Because of this, there may be mistakes in reported literature on *Solanum* species. For example *S. physalifolium* Rusby var. *nitidibaccatum* (Bitter) Edmonds was identified as a separate species from *S. sarrachoides* Sendtn in 1912 (Edmonds, 1986).

S. nigrum L. (black nightshade) is considered an important weed in many crops (Keeley & Thullen, 1989; Ogg & Rogers, 1989; Holm *et al.* 1991; Defelice, 2003). It is reported as being a weed of over 37 crops in 61 countries around the world. It is a common weed of many fruits, vegetables, other crops, waste areas, and open forest (Holm *et al.* 1991). *S. physalifolium* (hairy nightshade) has also been reported as a weed in vegetables and ornamental plants in Europe (Weber & Gut, 2005). In addition, the two *Solanum* species are alternate hosts of some insects, nematodes, and disease organisms that attack crops (Ogg & Rogers, 1989; Holm *et al.*, 1991).

Further, *Solanum* species are notorious for reducing grain quality, interfering with harvest, and contaminating stored grain. For instance, black nightshade berries rupture during harvest, staining the seed and allowing soil particles and other foreign material to stick to the seed surface, thus reducing the grade and value of the grain. Also, members of the Solanaceae family contain a toxic glycoalkaloid called solanine. The amount of this toxin varies with the species, environment, part of the plant, and stage of growth (Defelice, 2003), genetic races, soil factors, management practice, and climate conditions (Ogg & Rogers, 1989). The highest concentrations of solanine in *S. nigrum* are in the immature fruits (Defelice, 2003). The toxic unripe green berries may inadvertently be picked up and mixed with crops, e.g. peas. The berries are similar in size to soybeans, peas, and other seeds, making them difficult to separate using sieves. Seed staining and berry contamination have resulted in severe dockage for many crops and rejection by processors of peas (*Pisum sativa*) and beans (*Vicia faba*). Nightshade seeds also stick to the surface of crop seeds, allowing their spread to new fields. Seed companies and foundation seed suppliers reject soybean seeds that have been stained by the juice or that contain berries or seeds of black nightshades. The stems, leaves, and berries also form a wet, sticky mass in

harvesting equipment, plugging rotors and screens and, thereby, slowing or stopping harvesting operations. The juice also increases moisture in the stored grain, thereby increasing mold problems. Livestock producers are concerned about poisoning from nightshades in pastures, and the berry juice has stained the wool of sheep grazing in infested areas (Ogg and Rogers, 1989; Defelice, 2003). Therefore, control of *Solanum* species is given high priority in agricultural production. During the last decades the two species have become an increasing problem in field-grown vegetables in southern Sweden (Jönsson, 2002).

Seed dormancy

Dormancy is a seed characteristic that defines the conditions required for its germination, and therefore any factor that widens the range of environmental conditions for germination should be regarded as a dormancy release factor (Finch-Savage & Leubner-Metzger, 2006). A dormant seed does not have the capacity to germinate in a specified period of time under any combination of normal physical environmental factors that are otherwise favorable for its germination (Baskin & Baskin, 2004). Primary dormancy develops in seeds when they are on the mother plant (Hilhorst & Karssen, 1992). In contrast, secondary dormancy can be induced in seeds after dispersal because of environmental factors e.g. temperature (Finch-Savage & Leubner-Metzger, 2006). After prolonged inhibition of germination due to lack of proper conditions for germination (e.g. low temperatures, darkness, and deep burial) (Dyer, 1995; Benvenuti *et al.*, 2001; Brändel & Jensen, 2005), seeds may gradually enter a state of secondary dormancy, which often resembles primary dormancy (Hilhorst & Karssen, 1992). Non-dormant seeds germinate over a wide range of temperatures. Those germinating only under a limited range of environmental conditions are called conditionally dormant, and those germinating at none of the temperatures are dormant (Baskin & Baskin, 1985).

For *S. nigrum*, there are conflicting reports on lack (Keeley & Thullen, 1983; Givelberg *et al.*, 1984; Ogg & Rogers, 1989; Agong, 1993; Defelice, 2003) or presence (Roberts & Lockett, 1978; Bithell *et al.*, 2002; Andersson & Yahya, 2003) of primary dormancy in freshly harvested seeds. However, for *S. physalifolium* freshly harvested seeds appeared to be dormant (Del Monte & Tarquis, 1997; Bithell *et al.*, 2002; Andersson & Yahya, 2003). According to Baskin & Baskin (1998) *S. nigrum* seeds are conditionally dormant and the type of seed dormancy in *S. nigrum* and *S. sarrachoides* is

non-deep physiological depending on conditions required to release dormancy. The latter species is closely related to *S. physalifolium* var. *nitidibaccatum*, which was separated from *S. sarrachoides* in 1912 (Edmonds, 1986).

Ecological implication

The function of seed dormancy is probably adapted to time germination so that environmental risks associated with seedling establishment (e.g., drought and frost) are low. For example, seedlings that emerge late in the season may die in autumn due to low temperatures before reproduction. The variation in seed dormancy is ecologically significant for native plants and has resulted in contrasting ecotypes following many generations of selection (Allen & Meyer, 2002). Seed dispersal occurs in two forms whose evolution is closely linked: dispersal in space and time. Seed dormancy as an important life history trait can cause dispersal in time and increase maternal fitness by risk reduction in a variable environment, avoiding the negative consequences of high density and predicting a favorable time for germination. Seed dormancy of the kind which spreads the germination over more than one season, is favored when there is variation in offspring success between seasons, because it reduces risk by allowing a mother to spread the germination of her offspring over several years (Silvertown & Charlesworth, 2006). For example, seasonal dormancy characteristics of *S. nigrum* seeds enable the species to time germination to appropriate conditions for seedling establishment and reproduction.

Agricultural implication

Dormancy is an attribute of many weed seed populations that usually hampers the task of predicting timing and extent of emergence of weeds. The number of established plants of a weed is strongly related to the portion of the seed bank that has been released from dormancy. In addition, the timing of emergence of the weed in relation to crop emergence also depends largely on the dynamics of dormancy release of the weed population (Benech-Arnold *et al.*, 2000). The more seeds released from dormancy, the more seedlings will emerge. Assessment of the degree of dormancy of the buried seed population at the date of soil cultivation is a base for a good prediction of the number of emerged seedlings after soil cultivation (Vleeshouwers & Kropff, 2000). Knowledge of how seed bank dormancy is regulated by environmental factors may allow us to forecast

which weeds would be problematic in subsequent crops, and the potential seedling density that could be expected. This permit farmers to design better pre-emergence control tactics in order to reduce weed problems during the crop-growing season.

The seedling that emerge before or simultaneous to the crop may have a competitive advantage. For weed species that show seasonal dormancy changes, dormancy is alleviated in the seasons preceding suitable conditions for weed emergence (Batlla & Benech-Arnold, 2007). For example, in *S. nigrum* dormancy is reduced during autumn and winter and seedling may emerge in spring (Roberts & Lockett, 1978).

A good knowledge of seed dormancy and emergence timing enables us to design an efficient weed management system. Stimulating seed germination can lead to rapid depletion of the seed bank if carefully timed to coincide with weed control measures (Dekker, 1999). This can be done for seeds with a reduced level of dormancy that need light for germination. By drilling a stale seedbed, a large number of emerged seedlings can be removed during the final seedbed preparation before sowing the crop. Manipulating the crop-sowing date can be a good measure to control weeds. Sowing with appropriate crop geometry before weeds emerge in the field gives a competitive advantage to the crop over weeds, because the crop will build up its canopy and thereby shade and suppress the weeds early in the season. Mechanical weed-control measures can be used to remove late emerging seedlings in row-sown crops. All these measures that depend on the relation between dormancy and emergence help to reduce herbicide usage in agricultural productions.

Primary dormancy

In general the type and degree of (primary) seed dormancy vary greatly both between and within weed species and may also vary considerably between seeds produced on the same individual plant, depending on their position on the plant, time of maturation and environmental condition during maturation (Håkansson, 2003). Environmental factors during seed maturation, particularly temperature (Fenner, 1991; Roach & Wulff, 1987; Steadman *et al.*, 2004) and photoperiod (Munir *et al.*, 2001) influence seed dormancy status. In general, the lower the temperature during seed development, the higher the level of dormancy (Roach & Wulff 1987). For example, seeds of *Lolium rigidum* (Steadman *et al.*, 2004) and *Goodenia fascicularis* (Hoyle *et al.*, 2008) from plants grown at warm temperatures were less dormant than seeds from a cool environment. In contrast, seeds of

Setaria faberi raised under lower temperatures were less dormant than those that ripened under higher temperatures (Kegode & Pearce, 1998). In particular, the photoperiod during seed maturation might be a reliable indicator of season. Seeds of *Arabidopsis thaliana* matured by parents during short days break dormancy more readily when stratified, simulating spring condition; but seeds matured during long days break dormancy more readily on average when not stratified, simulating autumn conditions (Munir *et al.*, 2001). Variation in dormancy may be influenced by level of abscisic acid during the development of primary dormancy (Hilhorst & Karssen, 1992) or gene expression in the maternal parent (Munir *et al.*, 2001)

Weed seeds collected from different populations that had matured in different environments have been shown to have different levels of dormancy (Andersson & Milberg, 1998; Steadman *et al.*, 2004). Dormancy at maturity varied among seeds collected in different years and from different mother plants in *Silene noctiflora*, *Sinapis arvensis*, *Spergula arvensis*, and *Thlaspi arvense* (Andersson & Milberg, 1998). Seeds collected at different times of year, might adapt to the different ecological conditions under which they are produced (Mennan & Ngouajio, 2006). As described above, conditions in the mother-plant environment (Fenner, 1991) affect dormancy level. Therefore, the level of primary dormancy could vary among populations representing variation in site of collection.

Release and induction of dormancy

The level of primary dormancy may change due to environmental factors after dispersal. Temperature is the most important factor in regulating the changes in dormancy (Bouwmeester, 1990; Bouwmeester & Karssen, 1992, 1993; Baskin & Baskin, 1998; Benech-Arnold *et al.*, 2000). In general, applying a certain temperature regime to dry (after-ripening) or to imbibed seeds (stratification) may release primary dormancy. After-ripening is defined as a period of dry storage during which dormancy progressively decreases. Stratification is incubation of seeds in moist conditions to break dormancy, usually in cold to simulate overwintering (Finkelstein *et al.*, 2008). Stratification may also release secondary dormancy (Hilhorst & Karssen, 1992).

Soil moisture (Bouwmeester, 1990; Bouwmeester & Karssen, 1992), nitrate (Bouwmeester, 1990; Bouwmeester & Karssen, 1992, 1993), light and desiccation (Bouwmeester & Karssen, 1993) are factors considered not to influence the changes in dormancy. However, in some species (e.g.

Polygonum aviculare) fluctuations in soil moisture affect the dormancy level of buried seeds, which could influence the temporal patterns of weed emergence under field conditions (Batlla & Benech-Arnold, 2006). Other authors have stated that desiccation may relieve dormancy, which becomes apparent when the seeds are remoistened (Vleeshouwers, 1997a). Seeds of *Polygonum lapathifolium* subsp. *lapathifolium*, which usually require light stimuli for germination, were able to germinate in darkness, after being subjected to a hydration-dehydration cycle under laboratory conditions (Bouwmeester, 1990).

The processes of release and induction of dormancy may overlap but due to a different temperature optimum the process of dormancy release may predominate at lower, and induction at higher temperatures (Totterdell & Roberts, 1979; Hilhorst *et al.*, 1986). Esashi *et al.*, (1983) hypothesized two counteracting systems for seed dormancy in *Xanthium pennsylvanicum*: one is a dormancy breakage-promoting system, and the other a dormancy breakage-inhibiting system. The primary dormancy of the species seemed to result from a lower activity of the dormancy breakage-promoting system. In general, dormancy levels may cycle between dormancy and non-dormancy or conditional dormancy and non-dormancy depending on the species (Baskin & Baskin, 1998).

Species differ in their seed dormancy response to temperature. In summer annual species dormancy is generally released at lower and induced at higher temperatures (Baskin & Baskin, 1998). In contrast, in winter annual species (e.g. *Apera spica-venti* and *Alopecurus myosuroides*) dormancy is released at high and induced at lower temperatures (Andersson & Åkerblom-Espeby, 2009). Breakage of dormancy has been reported at low temperatures of 0.3 to 5°C for different species (Willemsen, 1975; Roberts & Lockett, 1978; Totterdell & Roberts, 1979; Hilhorst *et al.*, 1986; Mumford, 1988; Vleeshouwers & Bouwmeester, 2001; Andersson and Yahya, 2003; Leon & Owen, 2003; Brändel, 2005; Handley & Davy, 2005; Zhou *et al.*, 2005b). The lower temperature limit for induction has been reported to be higher than for breakage, ranging between 1.5 and 8.9°C for different species (Totterdell & Roberts, 1979; Vleeshouwers & Bouwmeester, 2001). The functional responses to temperature seem also to differ among species. For some species breakage requires periods of slowly increasing or decreasing temperatures, and for others daily temperature fluctuations or chilling are sufficient (Baskin & Baskin, 1998). Kebreab and Murdoch (1999) showed in *Orobanch*e species that the rate of induction of secondary dormancy decreased with increasing temperature up to about

20°C, above which the rate was approximately constant. However, the responses varied among different species.

Increase in stratification temperature was shown to cause an increase in dormancy release in *L. rigidum* (Steadman, 2004). Willemsen (1975), for *Ambrosia artemisiifolia*, reported that stratification at 4°C is most effective, whereas -5°C is least effective and 10°C is intermediate for breaking dormancy. Brändel and Jensen (2005) reported that after-ripening at 37°C and 4% seed moisture content resulted in a considerable loss of primary dormancy in potato (*Solanum tuberosum* L.) seeds after 7 days and complete loss of dormancy after 30 days. They also found that moist chilling for 3 days at 4°C alleviates secondary dormancy in potato seeds.

The rate of induction of secondary dormancy due to high temperatures depends on the temperature experienced by the seed during burial, i.e. the extent to which they have been released from dormancy (Batlla *et al.*, 2003). Noronha *et al.* (1997) concluded that the induction of a high dormancy level, expressed as an increased light requirement for germination, might change dramatically over relatively short-time periods during stratification. They also indicated that these inductions could be reversed while seeds remain under stratification. This suggests that the process of induction and release of dormancy may overlap. Under prolonged winter conditions, seeds may gain the ability to germinate in both light and darkness, but the ability to germinate in darkness can be lost again much sooner than the ability to germinate in light (Milberg & Andersson, 1998).

To predict emergence of weeds under field conditions, the changes in dormancy level need to be predicted on a time scale of days or weeks (Vleeshouwers & Bouwmeester, 2001). Both induction and breakage have to be expressed as functions of temperature, because both processes are temperature dependent. Dynamic modeling is used to evaluate these interactions.

The focus on models with physiologically, rather than empirically, relevant parameters, is critical in making better predictions of seed dormancy loss (Benech-Arnold *et al.*, 2000; Forcella *et al.*, 2000). Empirical models do not explicitly ascribe physical meaning to the parameters, while mechanistic models have a physical interpretation of parameters based on an understanding of the underlying process and the way components of the real system operate. Bouwmeester & Karssen (1992; 1993) reported that processes of breakage of seed dormancy of *Polygonum persicaria* and *Chenopodium album* can be modeled as the function of the cumulative sum of cold soil temperatures, and induction of warm temperatures. Thermal time has also been used to model dormancy changes in *Polygonum aviculare*

(Batlla & Benech-Arnold, 2005), *L. rigidum* (Steadman, 2004), and *Bromus tectorum* (Bauer *et al.*, 1998). A sigmoid relationship was found between temperature and the rate of dormancy loss, suggesting non linear relationship. Thus, thermal time may be useful in explaining the dynamic of dormancy changes, but not necessarily in a linear way. Lack of linearity might also indicate that thermal time is not the sole factor determining the dormancy release in *Aesculus hippocastanum* (Steadman & Pritchard, 2003).

Seasonal dormancy cycle

Seasonal changes in seed dormancy have been shown in several species (Håkansson, 1983; Roberts & Boddrell, 1983; Roberts & Lockett, 1978; Bouwmeester, 1990; Bouwmeester & Karssen, 1992 & 1993; Milberg & Andersson 1997; Vleeshouwers, 1997a; Baskin & Baskin 1998; Vleeshouwers & Kropff, 2000; Vleeshouwers & Bouwmeester, 2001). Seeds may undergo seasonal dormancy cycling if conditions are suboptimal (e.g. unfavorable temperature conditions or lack of adequate light or nitrate), progressively gaining or losing dormancy until they eventually germinate or die (Finkelstein *et al.*, 2008). The dormancy cycle is related to temperature changes (Hilhorst & Karssen, 1992) and associated with changes in the range of environmental conditions in which seeds are able to germinate (Vleeshouwers & Kropff, 2000). In summer annual species, cold stratification during winter weakens dormancy thus enabling seeds to germinate in spring. Conversely, high temperatures during summer induce dormancy, and seeds do not germinate in late summer or early autumn (Baskin and Baskin, 1998). In contrast to summer annuals, dormancy becomes stronger in winter annual species after cold stratification (Milberg & Andersson, 1998). Roberts and Lockett (1978) reported reduction of dormancy during autumn, winter and spring and induction of dormancy during summer in *S. nigrum*. For *S. physalifolium* the pattern of seasonal dormancy has to my knowledge not been previously studied.

Germination

Germination is the initial emergence of the radicle from the seed coat. This process requires that the plant embryo leaves the quiescent state, mobilizes stored nutrients, overcomes the barrier of surrounding tissues, and resumes cell elongation, cell division, and development. Dormancy may result from blocks in any of these processes (Finkelstein *et al.*, 2008).

The non-dormant seeds will only germinate if factors required for germination are present (Hilhorst & Karssen, 1992). Seed germination is influenced by environmental factors including temperature, light, nitrate and desiccation (Bouwmeester & Karssen, 1993). However, Derkx and Karssen (1994) reported that nitrate or sensitivity to nitrate do not contribute to the regulation of dormancy and germination in *A. thaliana*.

Weed seeds usually germinate over a range of temperatures (Penny & Neal, 2003) with a minimum and maximum temperature limit for germination. These limits vary quite widely and are normally distributed in the seed population (Kebreab & Murdoch, 1999), and may change depending on changes in the level of dormancy. Relief of dormancy results in a widening of the range of temperatures over which germination can occur, and induction of dormancy results in a narrowing of this range (Vleeshouwers & Bouwmeester, 2001). Lowering of the minimum temperature (T_b) for germination in *A. hippocastanum* (Steadman and Pritchard, 2003) and *P. aviculare* (Batlla & Benech-Arnold, 2003) was found to be associated with a loss of dormancy. Similarly, Del Monte and Tarquis (1997) stated that lowering of the base temperature for germination in *S. physalifolium* was associated with dormancy release.

Moreover, the breakage of seed dormancy shifts the mean base water potentials needed for germination to more negative values, allowing the seed to germinate at a wider range of water potentials. Factors that govern changes in dormancy of seed populations like chilling and after ripening, and those that terminate it like fluctuating temperatures and gibberellic acid, operate through a reduction of mean base water potentials ($\Psi_b(50)$) (Huarte & Benech-Arnold, 2005). Dormancy releases during dark-stratification also cause a gradual increase in sensitivity to light, resulting in conditionally dormant seeds that can be stimulated to germinate by subsequent exposure to light (Steadman, 2004).

Fluctuating temperatures promote seed germination in comparison with constant temperatures (Huarte & Benech-Arnold, 2005). Fluctuating temperatures, chilling pre-treatment and light were all found to be required for germination of *S. nigrum* seeds (Roberts & Lockett, 1978; Wagenvoort & Van Opstal, 1979; Bithell *et al.*, 2002). Roberts & Lockett (1978) reported that neither buried nor freshly harvested seeds of *S. nigrum* can germinate at constant temperatures in the range of 4–30°C with intermittent exposure to light. In contrast, other authors showed germination of *S. nigrum* seeds at constant temperatures ranging from 10 to 36°C, with the highest germination percentages at temperature of 20 to 30°C (Givelberg *et al.*, 1984; Del Monte & Tarquis, 1997; Larina, 2008). Moreover,

germination was increased at constant temperatures and in light in buried seeds of *S. nigrum* with time (Kremer & Lotz, 1998). A population of *S. physalifolium* seeds germinated in light and at constant temperatures of 25 to 35°C with an optimum of 30°C. Differences also found in base and optimum temperatures for germination among populations of *S. nigrum* could be related to the temperature regime of the original environment. Seeds collected from an area with a longer period of days per year with temperatures below 0°C presented a higher base temperature for germination than seed from a warmer area (Del Monte & Tarqius, 1997).

In other species, like *C. album* buried seeds do not germinate in darkness at constant temperatures, but considerable germination occurs when seeds are incubated at alternating temperatures (Bouwmeester & Karssen, 1993). Non-dormant seeds of *S. sarrachoides* germinated at temperatures in a range of 19–39°C, but optimum germination occurred from 27 to 33°C. Germination speed increased with increasing temperatures within a range of 20 to 34°C and declined at higher temperatures. Seeds of *S. sarrachoides* are not photoblastic and they germinated under a long photoperiod and continuous darkness (Zhou *et al.*, 2005a).

Emergence pattern

The information on emergence characteristics (e.g. light requirement, effects of burial, the number of seedling emerging and their time of emergence) of a species could provide a useful quantitative measure of its relative weediness, as early seedling establishment encourages competition with a crop (Vleeshouwers, 1997b; Vleeshouwers & Kropff, 2000; Grundy *et al.*, 2003; Penny & Neal, 2003).

S. nigrum is known to emerge late in the season compared to other weedy species (Buhler *et al.*, 1997) mainly in late spring (Håkansson, 2003). Seedling emergence in *S. nigrum* began in early May, continued during June and July, tailed off during August and ceased in September, in the U.K. (Roberts & Lockett, 1978). A study by Ogg & Dawson (1984) in the USA showed that *S. nigrum* generally began to emerge during the first 2 weeks of April and emergence generally peaked in mid-April to mid-May and continued until September. Keeley and Thullen (1983) stated that *S. nigrum* seeds begin to emerge in March in California when soil temperature at 5 cm depth reaches 17°C. In New Zealand, Popay *et al.*, (1995) reported emergence of *S. nigrum* in late spring and summer with some emergence continuing into autumn. According to the studies above emergence timing

of seedlings seems to vary in different areas and with populations, this highlights the importance of locally based emergence studies.

Soil tillage during light increases emergence of weeds especially in small-seeded broadleaf species (Buhler, 1997). Soil disturbance was also shown to increase the emergence of *S. nigrum* seedlings (Roberts and Lockett, 1978; Ogg & Dawson, 1984). Soil disturbance can be used to stimulate seedling emergence and consequently reduce the weed seed pool in the field (Popay *et al.*, 1994).

Objectives

Seasonal changes in seed dormancy and emergence timing have been studied in *S. nigrum* (Roberts & Lockett, 1978), however there is no report for *S. physalifolium*. There is also a contradiction among reports, for example, regarding presence (Roberts & Lockett, 1978; Bithell *et al.*, 2002; Andersson & Yahya, 2003) or lack of primary dormancy (Keeley & Thullen, 1983; Givelberg *et al.*, 1984; Ogg & Rogers, 1989; Agong, 1993; Defelice, 2003) in *S. nigrum*. Variations were shown in germination characteristics of seeds from different populations or seed lots (Roberts & Lockett, 1978; Kremer & Lotz, 1998; Bithell *et al.*, 2002). In addition to this, agricultural conditions in north European characterized with long winter and short summer seasons necessitate a more specific study for both species.

The main aim of this study was to increase knowledge of the biology (factor regulating dormancy and emergence) of two *Solanum* weedy species and to improve the efficacy of weed management strategies. It is important to know how seed dormancy is regulated by temperature and how it affects the conditions for germination. What regulates emergence timing in the field? This information can be used to optimally time weed control tactics with seedling emergence of the species. To achieve these goals experiments were conducted and presented in four papers. The objectives of these experiments were:

Paper I

First, to observe how the levels of dormancy changed during the season.

Paper II

Second, to observe how stratification temperatures (temperature under moist conditions) influenced seed dormancy, and temperature requirements for germination in *S. nigrum*.

Paper III

Third, to observe the variation in (primary) dormancy status among populations and the variations in emergence between species and their response to soil disturbance.

Paper IV

And finally, to evaluate how well seed dormancy development could be simulated for various temperature conditions, based on the predictions of breakage and induction of dormancy.

Materials & Methods

Paper I

To observe seasonal changes in dormancy of seeds buried in the soil, seed lots of *S. nigrum* L. ssp. *nigrum* and *S. physalifolium* Rusby var. *nitidibaccatum* (Bitter) Edmonds were buried outdoors in pots in autumn. Once every month, four inner pots per species were exhumed to test seed germination. The germination tests were conducted under three conditions in complete darkness at a temperature regime of 25°C for 16 hours and 15°C for 8 hours (HD; high temperature and darkness), at 25/15°C, with 16/8 hours light/darkness (HL; high temperature and light), and at 18/8°C, with 16/8 hours light/darkness (LL; low temperature and light). In addition, soil temperature was registered using a temperature logger at the same depth as the buried seeds (Figure 1).

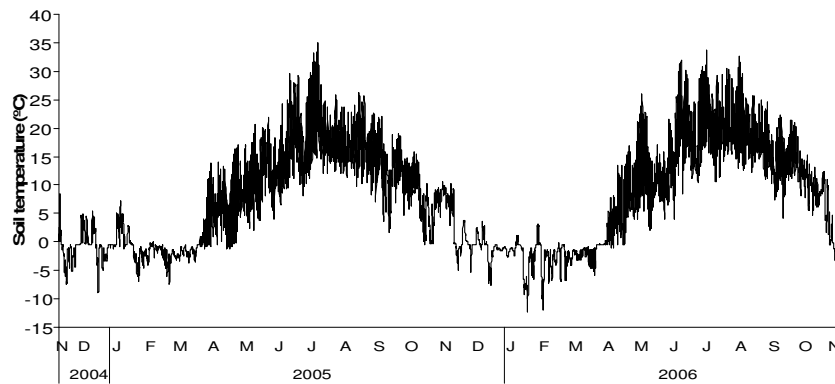


Figure 1. Hourly soil temperature within pots at the buried seed position during the experimental period.

Paper II

To test the effect of temperature on dormancy development, samples of seeds of *S. nigrum* (freshly harvested and dry stored) were buried in Petri dishes and pretreated in complete darkness at $3\pm 1^\circ\text{C}$ for a period of 6 weeks. Thereafter, the Petri dishes were transferred to growth cabinets with constant temperatures of 4.5, 10, 15.2 and 18.6°C and with weekly stepwise increasing temperatures of 4.5, 10, 15.2, 18.6, 25.4, 30.2, 35.2 and 40°C for 8 weeks. Once a week for eight weeks, nine Petri dishes per treatment temperature were used to test seed germination under three conditions with three replicates (at HL, HD, and LL) as in Paper I.

The germination requirement of seeds with three different levels of dormancy (dry stored and stratified freshly harvested seeds) was studied using a table gradient incubator (Ekstam & Bengtsson, 1993). The germination of seeds with three different levels of dormancy was studied at nine constant temperatures of 6, 10, 14, 18, 22, 26, 30, 34 and 38°C in 16/8 hours light/darkness. The effect of alternating temperatures on germination was also tested at eight alternating and increasing temperatures conditions of 21/6, 23.5/8.5, 26/11, 28.5/13.5, 31/16, 33.5/18.5, 36/21, and $38.5/23.5^\circ\text{C}$ with a constant amplitude (15°C) in 16/8 hours light/darkness. In addition, the effect of increasing temperature amplitude on germination was tested at five increasing amplitudes (0, 5, 10, 15 and 20°C) with the same daily mean temperature (25°C) in 12/12 hours light/darkness and temperature regimes of 25, 27.5/22.5, 30/20, 32.5/17.5 and $35/15^\circ\text{C}$.

Paper III

The primary seed dormancy status and emergence pattern of both species were studied. Seed samples of populations of both species collected in the field on two dates (August and September) and their germination was tested under four conditions, three as in Paper I (HL, HD, LL) and one additional test at LD (low temperature and darkness; in complete darkness at 18°C for 16 hours and 8°C for 8 hours). To study the emergence pattern, seed samples of two populations of each species were sown in pots outdoors in autumn during two years under different treatments: no soil disturbance, soil stirring one week after sowing, stirring when the first seedling emerged

in spring, and sowing seeds on the soil surface. The soil temperature was registered using temperature loggers. The soil in the pots was kept moist and watered when needed. In spring, emerged seedlings were recorded and removed every second day until the end of the season when no more seedlings were observed.

Paper IV

A simulation model predicting the development of seed dormancy level as a function of temperature was developed. The model is based on processes for dormancy breakage and induction. These processes may overlap during stratification treatment but due to different optimum temperature conditions breakage may predominate at lower and induction at higher temperatures. The model was calibrated and validated for seeds under stratification in controlled experiments at constant and stepwise rising temperatures. The model predictions of the level of dormancy were tested against observed dormancy level defined by the germination test at HD (Paper II).

Statistical Analyses

The data were analyzed using the GENMOD procedure (SAS Institute Inc., 2001) (Paper II & III). The procedure was used to test the differences among stratification temperatures, germination regimes, duration of stratification, and interactions between those factors. To test the differences among treatments and germination temperatures and interactions separate analysis were done for seeds germinated at constant, alternating and increasing amplitudes (Paper II). The differences in primary dormancy among populations, date of collection and interaction between these factors were also tested (Paper III). The proportion of viable seeds germinating was treated as a categorical variable, assuming binomial distribution, logit link function and type1 option. The Pearson chisquare correction (PSCALE) was applied to correct overdispersion (Paper II). Standard errors of means (SEM) were calculated using the LSmeans statement with pdiff option in the GENMOD procedure to account for the assumed binomial distribution. SEMs were then recalculated using back transformation of estimates from the logit scale to the original (probability) scale by applying the inverse link function (Paper II & III). The differences between species, populations and soil disturbance regimes in total emerged seedlings were tested. A robust method (GEE) was used to compensate for overdispersion (Diggle *et al.*, 2002) (Paper III). To validate the simulation model the best

fit was evaluated in terms of the coefficient of determination (R^2) of a linear regression between observed and simulated values (Pineiro *et al.*, 2008) (Paper IV).

Results and Discussion

In summary, the level of dormancy and conditions needed for germination differed between the species. The level of dormancy also determined the conditions for germination. The dormancy level depended on temperature conditions experienced and dormancy could both be released and induced by temperature. The temperature sum requirements for release and induction of dormancy were modified by a non-linear function of temperature. Seed dormancy in both species showed a seasonal cycle. Dormancy is broken during autumn, winter and early spring. Therefore, seedling emergence of both species takes place during May until July with two or three flushes of seedlings over an extended period. Thereafter, dormancy induction during summer is likely to prevent further seedling emergence.

Seasonal dormancy cycle

Buried seeds of both species followed a seasonal dormancy cycle (Paper I). Dormancy was reduced during autumn, winter and spring and induced during summer (Figure 2). Thus, both species showed characteristics typical for a summer annual species (Baskin & Baskin, 1998; Milberg & Andersson, 1998; Baskin *et al.*, 2001). Induction of secondary dormancy mainly occurred during August and September after seeds had experienced high temperatures in the soil (Paper I). This was followed by a gradual breakage of dormancy and almost 100% germinability in November or December in both species (Figure 2). A similar result has been reported for *S. nigrum* (Roberts & Lockett, 1978) and *S. sarrachoides* (Roberts & Boddrell, 1983). Release and subsequent induction of dormancy was similar to the model prediction, though it was not quantitatively tested (Paper IV). Higher temperatures were also shown to have a prevailing effect on dormancy induction (Paper II & IV). Therefore, dormancy induction during summer

prevents further seed germination, and dormant seeds stay viable in the soil for the coming seasons. Otherwise seeds would germinate and the emerged seedlings would not be able to complete their life cycle because they would freeze in autumn before reproducing.

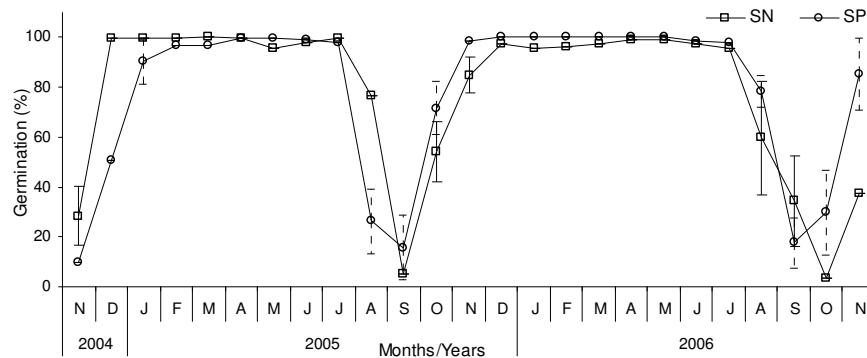


Figure 2. Germination (%) (mean \pm SE, if >5) of *Solanum nigrum* (SN) and *S. physalifolium* (SP) seeds after 14 days at 25/15 °C for 16/8 hour in light/darkness (HL) during two years of burial in the pots outdoors.

Primary dormancy

Large proportions of fresh seeds of *S. nigrum* germinated only at high fluctuating temperatures and in light, but not at high temperatures and in darkness and low temperatures and light (Paper II & III), while seed germination for *S. physalifolium* was zero or very negligible under the same conditions suggesting a deeper level of primary dormancy in fresh seeds of *S. physalifolium* than *S. nigrum* (Paper I & III). Freshly harvested seeds of *S. nigrum* appeared to be conditionally dormant and germinated only at near-optimal conditions for germination, i.e. in light and at high fluctuating temperatures. Therefore, the conflicting conclusions on lack (Keeley & Thullen, 1983; Givelberg *et al.*, 1984; Ogg & Rogers, 1989; Agong, 1993; Defelice, 2003) or presence (Roberts & Lockett, 1978; Bithell *et al.*, 2002; Andersson & Yahya, 2003) of primary dormancy in freshly harvested *S. nigrum* seeds could be due to variation in the state of dormancy among populations or test conditions used by different authors.

The level of dormancy in *S. nigrum* varied among populations and with time of collection (Paper III). This agrees with earlier reports on variation in dormancy, expressed as differences in germination percentages, between *S. nigrum* seed lots harvested in different years (Roberts & Lockett, 1978), sites (Bithell *et al.*, 2002) or from different biotypes (Kremer & Lotz, 1998).

For *S. physalifolium*, only one population showed any signs of germination, suggesting a slightly lower dormancy level than the other populations. This population was from the same site of collection as one of the *S. nigrum* populations, which showed 100 % germination suggesting lowest level of dormancy (Paper III). Environmental factors during seed maturation, particularly temperature, influence seed dormancy status (Fenner, 1991; Roach & Wulff, 1987; Steadman *et al.*, 2004). Consequently, the variation found here in level of dormancy might reflect differences in the growing environment at the site of collection.

Changes in the level of dormancy are associated with changes in the range of conditions for germination (Finch-Savage & Leubner-Metzger, 2006) so that progressively more dormant seeds will germinate in a more restricted set of conditions. In the present study, the three germination regimes represented progressively less restricted conditions for germination (HL>HD>LL) and seed responses in these three regimes can be used to infer the relative dormancy of different seed lots, e.g. freshly harvested (Paper III), following contrasting stratification conditions (Paper II) or burial in the soil (Paper I).

Germination

Results of a germination test at constant temperatures (Paper II) showed that only seeds (of *S. nigrum*) with a reduced level of dormancy, i.e. stratified at 5 and 15°C for 38 days, germinated at constant temperatures of 18 to 34°C with an optimum temperature from 26 to 30°C. Germinability increased substantially at fluctuating temperatures with higher percentages in seeds with lower levels of dormancy, but tended to decrease at higher temperatures. Germinability increased at amplitudes between 5 and 15°C but was reduced at 20°C. For seeds stratified for nine weeks, germinability was lower in seeds stratified at 15 than 5°C, suggesting strengthened dormancy (Paper II). A stronger effect of higher temperature on dormancy induction in addition to induction of dormancy due to prolonged stratification is in line with the model prediction (Paper IV).

Sensitivity to temperature fluctuations might act as a depth sensing mechanism (Thompson & Grime, 1983). Soil temperature usually does not fluctuate much in the deeper soil layers and, in addition, temperature decreases with depth (Thompson & Grime, 1983; Ghera *et al.*, 1992). This characteristic enables the species to time their emergence to the appropriate condition for establishment and reproduction. Response to fluctuating temperatures in addition to regulation of conditions for germination by

changes in dormancy level enables the species to detect the appropriate position and time for germination.

Temperature effect on dormancy

The results of one experiment (Paper II) clearly showed that the rate of dormancy reduction is low at lower temperatures and increases with higher temperatures. However, a high stratification temperature results only in a short-lasting reduction of dormancy, and is subsequently followed by an induction of dormancy. For seeds of *S. nigrum* stratified for eight weeks at 4.5, 10 and 15.2°C, germinability was almost complete throughout the experiment at HL. Substantial dormancy induction was observed after three weeks at 18.6°C at HL. Roberts & Lockett (1978) observed continuous and high germination percentages in light up to 10 or 15 weeks in *S. nigrum* seeds stratified at 15 and 17°C. This could be due to the long period of the germination test (one month or longer). This means that possible induction of dormancy during their experiment might have been reversed again during the germination test. In the present study, germinability at LL was low and did not show a consistent pattern. However, minimum germinability was observed after stratification at 4.5°C, which increased at 10 and 15.2°C at HD. An initial dormancy reduction followed by induction was observed at 15.2 and 18.6°C at HD. This was also confirmed by the stepwise rising temperature treatment at HD. Similarly, a smaller increase of germinability after stratification at 4°C than at 17 and 30°C in *S. nigrum* was reported by Roberts & Lockett (1978).

A similar rapid initial reduction followed by induction of dormancy was observed in seeds of *S. nigrum* and *S. physalifolium* stratified at temperatures of 18, 20, 22, and 24°C (unpublished data). The effect of stratification temperature on seed dormancy of *S. physalifolium* was also studied in a similar experiment to that with *S. nigrum* in Paper II (unpublished data). The results showed a reduction followed by induction of dormancy at all constant temperatures of 4.5, 10, 15.2 and 18.6°C during 8 weeks. Although the pattern was the same at all temperatures, dormancy reduction was higher at higher temperatures, resulting higher germinability. A reduction in dormancy with temperature was also observed at stepwise rising temperatures of 4.5 to 35.2°C followed by a decrease at 40°C. I conclude that reduction and induction of dormancy may occur at all stratification temperatures in *S. physalifolium*. Thus, the two species could differ in their dormancy response to temperature. For example, in *S. nigrum* the rate of dormancy breakage was low at lower temperatures and a pattern of dormancy reduction followed by induction was shown at higher

temperatures, while this pattern was also observed at lower temperatures in *S. physalifolium*. Moreover, freshly harvested seeds of *S. physalifolium*, which were deeply dormant, appeared to need a longer period to release dormancy when buried in the soil than those of *S. nigrum* (Paper I). Buried seeds of *S. nigrum* reached complete germinability after one month of burial, while seeds of *S. physalifolium* reached the same level after three months.

Dormancy level as function of temperature

The development of dormancy levels was successfully predicted as a function of temperature conditions (Paper IV). The model calibration resulted in reasonably good predictions of the observed values for all treatments in which dormancy breakage was observed (Figure 3). The R^2 values ($n=8$) for the 10, 15.2 and 18.6°C treatments were 0.43, 0.36 and 0.40, respectively. The model validation also showed a good prediction of observations from a similar controlled experiment for seeds at weekly stepwise rising temperatures, the R^2 value ($n=8$) was 0.37. Thus, dormancy dynamics of *S. nigrum* seeds under stratification conditions might be explained by temperature conditions, both in terms of current temperature and thermal time.

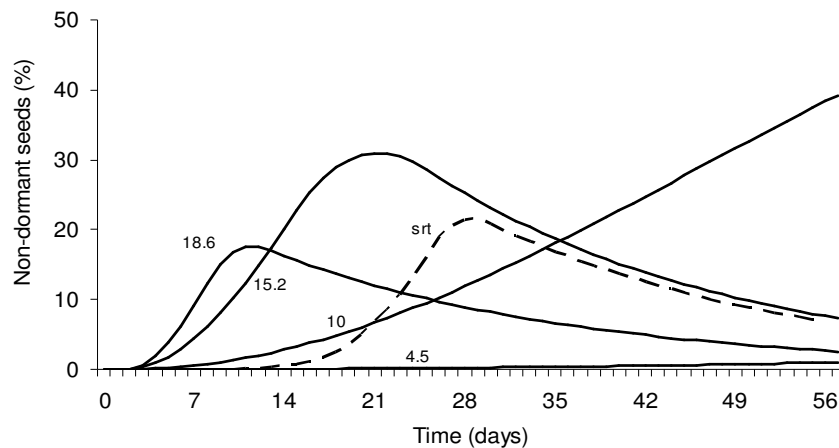


Figure 3. Model simulations of the non-dormant seeds, expressed as a fraction of the total number of seeds, *vs* days since the start of the temperature treatment at constant temperatures of 4.5, 10, 15.2 and 18.6°C and weekly stepwise rising temperatures (srt) from 4.5 to 40°C.

The maximum breakage rate was achieved after 120 day degrees, with a threshold temperature at 0°C (Paper IV). Further increase of the

temperature sum caused a reduction in the breakage rate, which reached zero at 205 day degrees. The corresponding limit for maximum induction rate was 80 day degrees but with a threshold temperature of 5.1°C. After this maximum was reached, the induction rate remained constant and the dominating process. This phenomenon was accentuated by a non-linear response to temperature. Above these threshold temperatures, both the rate of breakage and induction increased with temperature until certain upper thresholds (i.e. 17.5°C for breakage and 20°C for induction), above which the rates became constant (Paper IV). Several studies confirm these results for other species e.g. *A. thaliana* (Cone & Spruit, 1983; Derkx & Karssen, 1993), *Oldenlandia corymbosa* (Corbineau & Come, 1985), and *Sisymbrium officinale* (Hilhorst *et al.*, 1986;), but there are also studies of species such as *P. aviculare* showing the opposite response concerning breakage of dormancy (Batlla & Benech-Arnold, 2003; Batlla *et al.*, 2003; Batlla & Benech-Arnold, 2005). In *Orobanch* species, Kebreab and Murdoch (1999) showed that the rate of induction decreased with temperature for temperatures below 20°C, above which the rate was approximately constant. There are also studies reporting breakage to be independent of temperature up to, for example, 15°C (Totterdell & Roberts, 1979; Bouwmeester & Karssen, 1992; 1993). The reason for these principally different results could be the germination test chosen to study dormancy. For example, in our study germinability was almost complete at HL after stratification at temperatures below 18.6°C (Paper II). This could lead to the wrong conclusion that breakage is independent of temperature up to this limit. However, the test at HD showed that the breakage rate increases with temperature and both processes of breakage and induction are temperature dependent (Paper II).

The present model application (Paper IV) revealed a nonlinear relationship between temperature and rates of breakage and induction of dormancy. The rates were basically proportional to the accumulated temperature sum, but in the calculation of temperature sum high temperatures had a larger impact than low temperatures. Thus, this study negated the use of thermal time as a strict accumulation of heat units for modelling the dormancy status. This non linearity had consequences on how breakage and induction interacted. Breakage dominated at lower temperatures and induction at higher temperatures (20°C), but, with a delay due to the processes responding to the accumulation of temperatures. Due to the non-linear response, induction fairly soon became dominant in, for instance, the 18.6°C treatment. These non-linear responses are in accordance with responses found in another study by Steadman and

Pritchard (2003). The results suggest that both the character of the responses to temperature and the thresholds are species-specific. The model predictions based on breakage followed by induction after prolonged stratification can be used to explain the pattern of the dormancy cycle in the soil.

In the dormancy cycle experiment, the long period of reduced dormancy during spring and early summer was temporarily interrupted by a short period of stronger dormancy (Paper I). This was observed in *S. nigrum* as a lower germination percentage at HD and LL in early May 2005 and at HD in early June 2006. In addition, there was a tendency for a reduced germination when exhumed seeds were tested at HL in 2005. For *S. physalifolium* this was only observed at HD in June 2005. However, the induction process did not continue and seed germinability increased, with increasing soil temperature, up to 100% in early July in both species. To my knowledge, this type of short-term strengthened dormancy, during a period shortly before the soil temperature becomes suitable for germination, has not been previously shown. I suggest that the temporarily increased temperature and/or light requirement might serve to prevent early germination until a lower level of dormancy coincides with high temperature in the field.

Seedling emergence

The short-term induction of dormancy in spring could be a possible reason for late emergence of the species (Paper I) in addition to a high-temperature requirement for germination (Paper II; Del Monte & Tarqius, 1997). It would also explain why the two *Solanum* species are seldom found in crop sequences dominated by spring cereals but constitute large problems in crops like carrots, parsnip and celery. The latter group of crops is sown late, usually in late May to early June in southern Sweden. In addition, these crops are sown with a large row distance, which makes them poor weed competitors, and are often irrigated. This offers good conditions for establishment and growth of late emerging weeds like *S. nigrum* and *S. physalifolium*. Late emergence contributes to the seriousness of the species as a weed of various vegetable and field crops, since it often takes place after early season weed control options have been applied or the efficacy of soil-applied herbicides has been reduced (Roberts & Lockett, 1978). Therefore, late emerging weeds are usually difficult to control (Stoller & Wax, 1973). Thus, the seasonal dormancy pattern plays a major role in regulating the emergence timing and adaptation of the species.

Seedling emergence in populations of both species mainly took place from early May until early July. After this time seedlings rarely emerged (Paper III). This closely resembles the pattern of dormancy induction shown in the dormancy cycle study when dormancy induction after early July prevents further seed germination (Paper I). Emergence timing of both species seems to be mainly regulated by the soil temperature. The emergence of seedling flushes of both species was attributed to a daily mean soil temperature above 13 to 17°C with a ca 10°C fluctuation (Figure 4 & 5). The emergence of *S. nigrum* has also been attributed to a requirement of a fluctuating temperature above 15 to 20°C (Edmonds & Chweya, 1997; Roberts & Lockett, 1978; Keeley & Thullen, 1983; Ogg & Dawson, 1984).

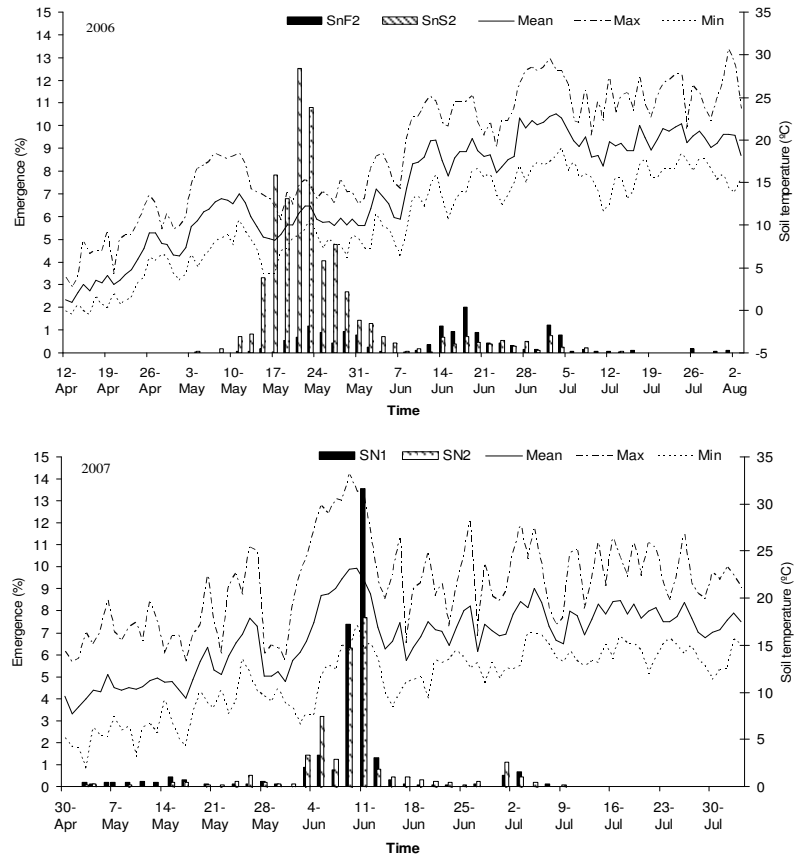


Figure 4. Emergence pattern of *Solanum nigrum* populations (SnF2 & SnS2) in 2006 and (SN1 & SN2) in 2007. Mean, Max, and Min: mean, maximum and minimum soil temperature, respectively, measured at 2 cm depth in pots outdoors.

Different categories were found within seed batches in terms of requirement for emergence (Paper III). This led to an extended bi- or three-modal recruitment pattern in addition to sporadic seedling emergence. A bimodal pattern of emergence has been shown in many weed species (Stoller & Wax, 1973; Ogg & Dawson, 1984; Myers *et al.*, 2005). Genotype, maternal environment, postharvest history, and germination environment, may all contribute to the control of dormancy phenotype and seed germination (Allen & Meyer, 2002).

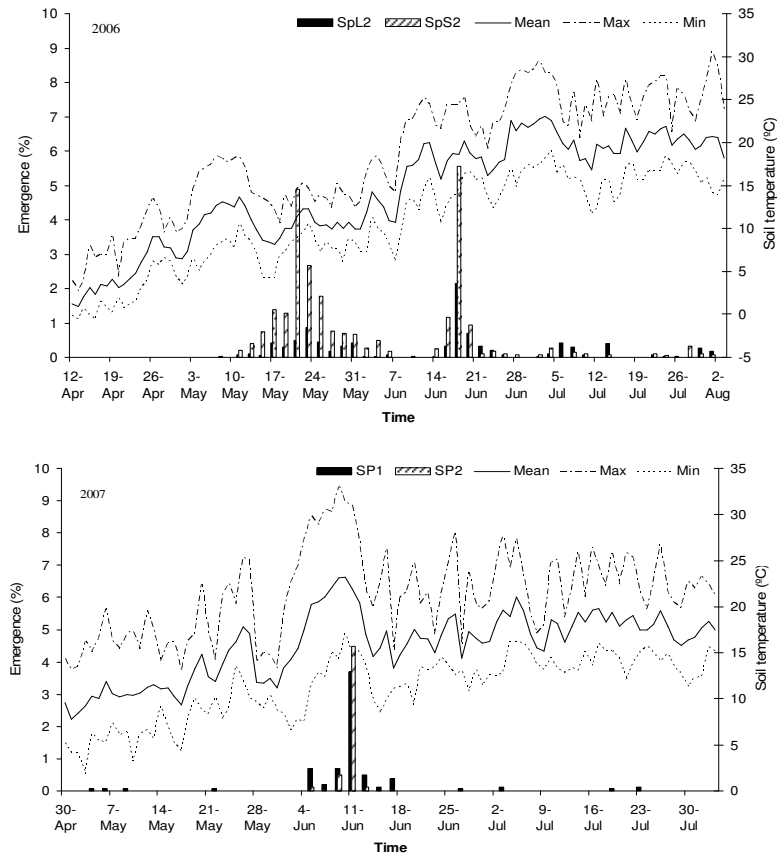


Figure 5. Emergence pattern of *Solanum physalifolium* populations (SpL2 & SpS2) in 2006 and (SP1 & SP2) in 2007. Mean, Max, and Min: mean, maximum and minimum soil temperature, respectively, measured at 2 cm depth in pots outdoors.

The presence of various categories within the seed batches with different requirements for emergence further enhances the problem when trying to

control the two *Solanum* species. This characteristic enables the species to extend their emergence timing since the requirements would not usually be met at the same time. Therefore, in the case of a climatic extreme, for example extreme weather undesirable for seedling survival, at least portions of the seedlings would emerge later on and, thus, enable the plants to complete their life cycle. Therefore, extended emergence helps plants to escape weed control operations. Each weed control operation may target a portion of the seedlings; however, the flushes that emerge later would take advantage of opportunity of space provided in agricultural fields and guarantee the weed infestation in the cropping systems. This needs to be taken into consideration in weed management systems.

In weed management, soil tillage as a control measure can be used to stimulate seed germination or removing emerged seedlings. However, soil disturbance had no significant effect on emergence in any of the species in this study (Paper III). In contrast, others reported an increase of emergence with soil disturbance in *S. nigrum* (Roberts & Lockett, 1978; Ogg & Dawson, 1984). It might be that time of soil disturbance coincided with the time of lower level of dormancy in seeds in the emergence study. Seeds of both species germinated to a large extent in darkness during a large part of the spring and summer season (Paper I). This indicates that they could emerge in the field without need for light and or soil disturbance. Therefore, lack of light requirement for germination was found to be associated with a low level of dormancy so that seeds with a low level of dormancy could germinate in both light and darkness. In contrast, germinability was low in seeds tested at HD while it reached 100% at HL in the stratification experiment (Paper II). According to the model study (Paper IV), the lower the level of dormancy the more likely seeds are to germinate. Since seeds in the dormancy cycle (Paper I) and emergence (Paper III) studies were in soil, while they were only in water in the stratification study (Paper II), there might be other factor(s) in the soil affecting seed germinability of the species.

Further thoughts

I found a contradiction in the rate of dormancy breakage between buried seeds in the soil and in Petri dishes. The rate of dormancy breakage was higher in seeds buried in the soil in the dormancy cycle experiment (Paper I) than in seeds stratified in moist conditions in Petri dishes (Paper II). Applying the model calibrated for seeds in Petri dishes (Paper IV) to the soil temperature, the breakage of dormancy was found to occur earlier in seeds buried in the soil than in Petri dishes, while the required accumulated

temperature sum was achieved later (data not shown). The reason might be that soil temperature usually fluctuates between day and night (Figure 1) in contrast to the constant temperature that we used in the control condition and might have acted to promote dormancy breakage. Moreover, there might be other factors in the soil affecting seed germinability, e.g. nitrogen. Factors like light, fluctuating temperatures, nitrate and desiccation promote germination (Bouwmeester & Karssen, 1993; Dyer, 1995; Benech-Arnold *et al.*, 2000). Germination of *S. nigrum* seeds was also found to increase when potassium nitrate and gibberellic acid were applied (Roberts & Lockett, 1978). Although soil moisture (Bouwmeester, 1990; Bouwmeester & Karssen, 1992), nitrate (Bouwmeester, 1990; Bouwmeester & Karssen, 1992; 1993), light and desiccation (Bouwmeester & Karssen, 1993) do not influence the level of dormancy, they may remove constraints for germination (Benech-Arnold *et al.*, 2000). On the other hand, fluctuation in soil water content may affect the dormancy level of buried seeds as reported for *P. aviculare*. Seed populations subjected to fluctuation in soil water content had a lower level of dormancy and germinated more than seeds subjected to moist soil (Batlla & Benech-Arnold, 2005; 2006). Freezing may cause removal of water from the plant cells as a common adaptive mechanism for cold acclimation (Guy, 1990; Thomashow, 1999). Buried seeds might have experienced freezing and thawing during winter (Figure 1) and therefore, changed in seed water content resembling fluctuation in soil water content. However, to clarify whether nitrogen content in the soil affected germinability of buried seeds or if the soil temperature regime affected their dormancy state further studies are needed.

In previous studies, Kremer and Lotz (1998) reported a reduction in the minimum temperature for germination of *S. nigrum* biotypes with burial time. Del Monte and Tarquis (1997) also reported differences in the base temperature for germination among populations of *S. nigrum*. I therefore, expected a reduction in the minimum temperature for germination when seeds with different levels of dormancy were tested at constant temperature. However, this was not the case (Paper II), although a progressive change in the range of condition for germination was observed in the dormancy cycle study (Paper I). This also demands further detailed study.

Generally, I had expected to see dormancy release in summer annual species at lower temperatures. However, the results showed that lower temperatures have a negligible effect on dormancy release and the rate of dormancy release increases with temperature in *S. nigrum* (Paper II & IV). Therefore, the idea of dormancy release occurring only at lower temperature might not be true for all summer annual species. Dormancy

release is likely to occur at a wide range of temperatures, but the rate could differ with temperature.

Conclusions

- ✓ Seeds of the two *Solanum* species have dormancy, germination and emergence characteristics that make them difficult weed species to control.
- ✓ Differences in primary seed dormancy in populations of *S. nigrum* depended on time of collection. Portions of fresh seeds of *S. nigrum* were conditionally dormant and germinated only under optimal conditions, i.e. light and alternating temperatures, while seeds of *S. physalifolium* were deeply dormant and did not germinate under any conditions.
- ✓ Dormancy can be simultaneously reduced and induced by stratification temperatures. The rate of dormancy release and induction increased with temperature. However, the temperature threshold for breakage was lower than for induction, and consequently induction dominated more rapidly in high compared to low temperature treatments. The model application showed that dormancy dynamics of *S. nigrum* seeds under stratification conditions could be explained by temperature as the single driving variable. However, the results suggest that both the character of the responses to temperature and the thresholds are species-specific.
- ✓ Seeds of *S. nigrum* germinate at constant temperatures providing that the level of dormancy is low. Alternating temperatures with an optimal amplitude further stimulates seed germination.
- ✓ During a large part of the spring and summer season seeds germinate to a large extent in darkness, suggesting no requirement for light or soil disturbance for germination due to low level of dormancy.

- ✓ Seed dormancy in both species shows a seasonal cycle regulated by temperature, so that dormancy is broken during autumn, winter and early spring and induced during summer. In addition, a period of low dormancy in spring is temporarily interrupted by a short-term dormancy induction. This characteristic is likely to delay the peak of emergence in field.

- ✓ Seedling emergence of both species takes place during May until July with two or three main flushes in addition to sporadic seedling appearance. Various categories were found within seed populations in terms of requirements, e.g. temperature probably due to differences in dormancy, for emergence. This enables the species to extend their emergence period and thereby, survive natural catastrophes or weed control operations. This information can be used to maximize the efficacy of weed management strategies by timing weed control tactics with seedling flushes.

Future research

- There might be other factors in the soil affecting seed dormancy or germinability. Differences were found in the rate of dormancy release between seeds stratified in only moist condition and seeds buried in the soil. This could be further investigated to understand the other factor(s) in the soil that may affect seed dormancy/germinability, for example, nitrogen or changes in the seed water content due to freezing and thawing.
- The lower and upper temperature limits for germination are expected to change with a change in the dormancy level. The base temperature for germination of the *Solanum* species is unclear. It could also be studied to see if the base temperature is decreased by a reduction in the dormancy level and to what extent.
- The level of dormancy may oscillate during a transition period of dormancy reduction and induction. During dormancy reduction and induction at a constant temperature, oscillations were observed in germinability. This could further be studied to see if there are short term changes in the dormancy level in addition to the general pattern of reduction and induction of dormancy.
- The environmental conditions during seed maturation may affect the initial level of dormancy. Variations were found in primary dormancy among populations of the species. It is of interest to know if this variation is controlled by genetics or environmental factors.
- There might be some compound in the berries that affects seed dormancy or germinability of the *Solanum* species. A difference in germinability was observed between seeds of the species extracted from the berries and seeds contained in the berries contents (unpublished data). It is also important to check if there is any compound in the berries affecting seed dormancy and germinability.

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