SEED DORMANCY AND GERMINATION IN AN ECOLOGICAL CONTEXT

COMPARATIVE STUDIES OF ANNUAL WEEDS

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Linköping Studies in Science and Technology
Dissertation No. 1088

Seed dormancy and germination in an ecological context

comparative studies of annual weeds

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ISBN 978-91-85715-29-9
ISSN 0345-7524

Front cover: Seeds of five *Papaver*, six Asteraceae and four *Lamium* taxa, and flowers of *Papaver argemone*, *Guizotia scabra* and *Lamium confertum*.

Printed by LiU-Tryck
Linköping, Sweden, 2007

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I Karlsson LM & Milberg P (2007) A comparative study of germination ecology of four *Papaver* taxa. Annals of Botany, in press.

II Karlsson LM & Milberg P. Seed dormancy pattern and germination preferences of the South African annual *Papaver aculeatum*. Acceptance in South African Journal of Botany pending minor revision.

III Karlsson LM & Milberg P. Variation within species and inter-species comparison of seed dormancy and germination of four weedy annual *Lamium* species. Submitted manuscript.

IV Karlsson LM, Tamado T & Milberg P. Inter-species comparison of seed dormancy and germination of six annual Asteraceae weeds in an ecological context. Submitted manuscript.

Publication information, updated 24th September 2007

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IV Karlsson LM, Tamado T & Milberg P (in press) Inter-species comparison of seed dormancy and germination of six annual Asteraceae weeds in an ecological context. Seed Science Research, in press.

Note

This version of the thesis does not include the papers, and differs from the original by the figure numbers being changed according to the published version of Paper IV.

Abstract

Germination ecology studies, *i.e.* studies of interactions between characteristics of the seeds and environmental circumstances, provide understanding of spatial and temporal patterns of emergence of wild species, as weeds in the field. A large number of species have seed dormancy, *i.e.* seeds respond to circumstances not directly evoking germination. Thus, germination may occur only if specific environmental events have occurred in the seeds' past life story, and/or if a suitable time period has passed since ripening on mother plants. In this thesis, three characteristics, *i.e.* dormancy pattern, germination preferences and dormancy strength, hypothesised as mutually independent seed characteristics, are used to describe dormancy and germination in an ecological context. This conceptual model may be used for descriptions of differences between species, to understand emergence patterns in the field from controlled germination tests, and probably for increasing the understanding of evolution of ecological important properties of seed dormancy and germination.

Fifteen annual weedy taxa were investigated: two groups of temperate climate weeds, *Lamium* and *Papaver*, and one group of tropical weeds, co-occurring Asteraceae species of different genera. Intra-species variations in germination occurred for all species, but species-specific germination responses within all groups were revealed in analyses. All species showed some kind of species-specific dormancy pattern that was expressed as increased germination in response to one or more environmental factors not required for the actual germination.

For *Lamium* and *Papaver*, the general dormancy pattern was genus-specific. Germination preferences varied slightly within genus. Dormancy strength was to some extent species-specific, but highly variable. The species belonging to Asteraceae showed differences in dormancy pattern. It is shown how such differences can be visualized and compared by plotting response time and achieved germination in two-dimensional graphs, giving species-specific patterns.

Dormancy pattern and germination preferences explained how *Papaver* can perform as winter annuals in warmer climates, but substantially as summer annuals in colder climates. Hence, there is no need to infer local adaptations to explain the differing phenology of germination. For *Lamium*, the results indicate a local adaptation of increasing dormancy strength: in the relatively cold climate in Sweden, a strong dormancy restricted part of each cohort from germinating during autumn, thus preventing from winter mortality. For the Asteraceae, five of six species clearly responded to cold pre-treatment, which is noteworthy considering the small seasonal temperature differences in the study area and in the areas of origin of the species. The six Asteraceae achieved similar emergence timing in the field by responding to different environmental factors.

Together, the results from the fifteen species studied indicate that dormancy pattern is an evolutionary conservative characteristic, dormancy strength is relatively easily changed, and germination preference is intermediate.

Key words Asteraceae, *Bidens*, Compositae, deadnettle, *Galinsoga*, germination timing, *Guizotia*, evolution, Labiatae, Lamiaceae, *Lamium*, morphophysiological dormancy, Papaveraceae, *Papaver*, *Parthenium*, physiological dormancy, poppy, summer annual, *Tagetes*, *Verbesina*, winter annual.

Frövila och groning i ett ekologiskt sammanhang – jämförande studier av annuella ogräs

SAMMANFATTNING

Studier av groningsekologi, det vill säga studier av interaktioner mellan fröns inneboende karaktärer och miljömässiga omständigheter, ger förståelse av temporala och spatiala groningsmönster för vilda växter. Många arter har frövila: fröna reagerar på omständigheter som inte direkt har med groningsbetingelser att göra, och förändrar på så sätt sin benägenhet att gro. Detta leder till att groning endast sker om fröna först har utsatts för specifika miljömässiga händelser och/eller att tillräckligt lång tid har gått sedan de mognade på moderplantan. I den här avhandlingen används tre karaktärer: frövilemönster, groningspreferenser och frövilestyrka, för att beskriva frövila och groning i ett ekologiskt sammanhang. De tre karaktärerna anses, hypotetiskt, vara oberoende av varandra. En sådan konceptuell modell kan användas för att beskriva skillnader mellan arter, för att förstå uppkomstmönster i fält från resultat av experimentella studier, och troligen för att öka förståelsen av evolutionen av ekologiskt viktiga egenskaper som rör frövila och groning.

Femton ettåriga ogräsarter studerades: två grupper från tempererade klimat, *Lamium* (plistersläktet) och *Papaver* (vallmosläktet), och en grupp tropiska Asteraceae (familjen korgblommiga växter) från olika släkten. Skillnader i groning mellan olika populationer förkom inom alla arter, men alla hade artspecifika generella miljöresponser. Alla arter hade någon form av artspecifik frövila, vilket visade sig som ökad groningsbenägenhet efter en tid i miljöer där groning inte skedde; arterna reagerade på en eller flera sådana miljöer.

För *Lamium* och *Papaver* var det generella frövilemönstret släktspecifikt, medan groningspreferenserna skilde mellan arterna inom släktena. Frövilestyrkan var till viss del artspecifik, men varierade mycket mellan olika populationer. Arterna av Asteraceae hade olika frövilemönster, dock grodde de samtidigt i fält i ett varmt klimat med torrperioder. I avhandlingen visas hur skillnader i frövilemönster kan visualiseras i två-dimensionella grafer, så att man erhåller artspecifika mönster.

Frövilemönstret och groningspreferensen förklarar hur *Papaver* kan uppträda som vinterannueller i varmare klimat, men i stor omfattning som sommarannueller i kallare klimat, utan lokala anpassningar. Arterna ökar sin benägenhet att gro efter en varm period, men själva groningen skjuts upp till våren i kallare klimat eftersom hösten ofta inte gynnar groning. För *Lamium* indikerar resultaten att det förekommer en lokal anpassning, i form av ökad frövilestyrka, till det svenska klimatet. Visserligen ökar benägenheten att gro efter en varm sommarperiod, men en stark frövila gör ändå att en påtaglig andel av varje kohort inte gror på hösten, och därmed undviker dödlighet under vintern. För Asteraceae var det fem av sex studerade arter som tydligt ökade sin benägenhet att gro efter att ha utsatts för en kall period, vilket är något förvånande med tanke på att arterna idag huvudsakligen förekommer i trakter utan speciellt stora temperaturväxlingar mellan årstiderna.

Sammantaget tyder resultaten för de studerade femton arterna på att frövilemönstret är en evolutionärt konservativ karaktär, men att frövilestyrkan relativt lätt kan förändras som respons på miljöomständigheter, vilket kan ge lokala anpassningar. Groningspreferenserna förefaller vara mer konservativa än frövilestyrkan, men ge större möjlighet till evolutionär förändring än frövilemönstret.

Seed dormancy and germination in an ecological context – comparative studies of annual weeds

Laila M. Karlsson

"Convince me that you have a seed there, and I am prepared to expect wonders"
Henry D. Thoreau, 1817-1862.

"...den försummade åkern blir icke äng, utan ogräs, förbannelsens örter"
[*"...neglected arable land becomes not meadow, but weeds, the herbs of nuisance"*]
August Strindberg, 1849-1912.

1. INTRODUCTION

1.1. WEEDS AND GERMINATION ECOLOGY

Since Henry D. Thoreau observed and investigated seed dispersal and germination in the field and indoors in the mid 19th century, convincing himself that a seed is the only possible origin of a new individual plant springing from the soil (Thoreau 1993, posthumous published manuscript), and August Strindberg referred to weeds both as concrete indicators of bad agricultural management and as metaphor for phenomena he considered wretched (Strindberg 1910), a lot of scientific work has been done on seed germination and on weedy plant species. The underlying reasons for these studies may have been fascination *sensu* Thoreau and disapproval *sensu* Strindberg, respectively. Merging the interests of these two gentlemen gives a background to the subject "germination ecology of weedy species".

What is, strictly speaking, a weed? In fact, there is not one single official definition of the term "weed" available. In a broad sense, all plants that occur in areas where they are unwanted by man are weeds. In that meaning, it is impossible to define a species as being a weed: for example, crops can be weeds by occurring in fields they are not sown in. However, intuitively the term "weedy species" is seldom a problem, referring to species that commonly perform as weeds in an area. But of course, weeds of one part of the world can then be integrated parts of the natural flora, or ornamental plants, in another. In this thesis, the term "weed" is used, *sensu*

Buckman (1855), for species being regarded as weeds in the areas referring to, and, when applicable, where they were collected.

Weeds will always be present – at least to some extent – within agriculture. There are a number of reasons for that: management with herbicides and/or mechanical treatments do not target all individual weeds (*e.g.* not the ones that germinate after management), species can develop resistance to herbicides (*e.g.* Main *et al.* 2004, Scarabel *et al.* 2004, Wakelin & Preston 2006, Yu *et al.* 2007), and the use of reduced herbicide doses, in order to increase cost-efficiency and/or decrease herbicide runoff, may increase the amount of weeds if not managed properly (*e.g.* Blackshaw *et al.* 2006). Within organic farming, herbicides are not used and the amount of weeds, compared to conventional farming, increases in the above ground flora (*e.g.* Hyvönen *et al.* 2003) as well as in the soil seed bank (*e.g.* Albrecht 2005). To allow sound predictions of weed emergence in response to local weather and soil management, knowledge about germination ecology is needed (Batlla & Benech-Arnold 2005, Colbach *et al.* 2006, Rhaman *et al.* 2006).

Germination ecology deals with understanding of how the interaction between environments and seeds result in spatial and temporal patterns of germination and emergence. The study of germination ecology of weeds is not different from studies of germination ecology of other plant species. It deals with the understanding of what kinds of environmental circumstances that influence germination and germination timing, and of to what extent germination timing may lead to successful establishment. Understanding of germination ecology also includes understanding of how seeds respond to circumstances not directly evoking germination. One could expect well-timed emergence patterns from weeds, especially from annual weeds, which have, in addition to the challenge of all annual species (*i.e.* flowering and seed set must succeed during the season following germination; there is no second chance), to be successful also in the meaning of not being out-competed, killed or removed in the interaction with crops and with field management. Thus, it is, for practical and theoretical reasons, of interest to understand germination ecology of weeds.

1.2. GERMINATION

When investigating seed germination, the first question is "what is the study object?". The proper definition of a seed is "the discrete body from which a new plant develops" (Allaby 1998). There are a number of cases where the structure which is dispersed, and from which a new plant seems to develop, that is more than a seed, *e.g.* a stone, a nut, a caryopsis or an achene. That is, a seed may be naturally delivered in some package. In this thesis, studies done and referred to use the dispersal unit of the species in question for experiments and investigations. That object is here referred to as a "seed" throughout.

A step towards understanding of emergence patterns in the field is to understand during which current environmental circumstances germination occur: seeds of different species have various basic requirements. The presence of water is a universal requirement, but some species are capable of germinating also at relatively low soil water content (Flores & Briones 2001), and the germination rate may be influenced by water pressure (Bradford 1990). In addition, several species have seed coats with some kind of construction that must open before imbibition, *i.e.* uptake of water, is possible (*e.g.* Baskin *et al.* 2000), and further other species have seeds that are provided with enough water for germination from the mother plant (*e.g.* Kioko *et al.* 2006).

A suitable temperature should be present for germination to occur; what is suitable varies between species, even when co-occurring (*e.g.* Kos & Poschlod 2007). The temperature range accepted for a species to germinate is not rigid but increase and decrease depending on other environmental circumstances and on the life story of the seeds (*e.g.* Baskin *et al.* 2003). There are examples of species that have bimodal germination responses to temperature scales: *Arctotheca calendula* had peaks of germination at 10 and 30°C (Chaharsoghi & Jacobs 1998). The amplitude of daily temperature fluctuations is, for some species, *per se* an important cue for germination (*e.g.* Schütz 1999). Further, species may differ substantially in germination rate, even when accepting the same lowest temperature for germination (Trudgill *et al.* 2000). Models of hydrothermal time may be useful for predicting germination rate given any specific combination of temperature and moister condition within ranges acceptable for the species (*e.g.* Grundy *et al.* 2000), but the model requires previous investigations of optimal and lower and higher threshold temperatures of the species/seed batch under consideration.

It is common with a light requirement for germination (*e.g.* Milberg *et al.* 2000), which is interpreted as a way for seeds to detect whether they are located at a soil's surface, and not buried. Some light-requiring species respond with germination after a very short (seconds) light exposure, while other require longer times to respond (Milberg *et al.* 1996). On the other hand, continuous light during 24 h day^{-1} prevents germination for *Lamium amplexicaule* (Jones & Bailey 1956). The quality of light, for example if sunlight is filtered through leaves or not (*e.g.* Fenner 1980a) or if seeds are provided with white, red or far-red light (*e.g.* Thanos *et al.* 1995), influences germination for a number of species. Total exposure to light, over several days, has been reported to influence the extent of germination for *Betula papyrifera* (Bevington 1986). There are also species for which continuous darkness and light during daytime promotes and restricts germination, respectively; for example *Glaucium flavum* (Thanos *et al.* 1989). Such a response is interpreted as an adaptation to environments where soil surfaces frequently and unpredictably dry out; germination beneath the surface is then a way for a newly germinated seedling to be protected from drought.

Further, species may have demand for a special chemical composition in the surroundings, as such resulting from fire (*e.g.* Keeley & Keely 1987); a specific molecule occurring in smoke has been identified to promote germination for different species (Flematti *et al.* 2004). There are also species that respond positively to smoke even if they also germinate without smoke during other circumstances (*e.g.* Adkins & Peters 2001). Occurrence of nutrients, for example nitrate, in the substrate may increase germination and/or germination rate (*e.g.* Pons 1989), but has not, to my knowledge, been reported as an obligatory requirement. The composition of the substrate can also be negative for germination: increasing soil/sand fraction as well as contamination with motor oil decreased the germinated fraction of lettuce (Banks & Schultz 2005). Without doubt, substrate composition may influence germination. However, with the exceptions of fire related substance(s) for a number of species adapted to fire-prone environments (*e.g.* Keeley & Keely 1987 [America], Browns *et al.* 2003 [Africa], Tierney 2006 [Australia]) and chemicals indicting the presence of a host for some parasitic species (*e.g.* Vallance 1950), a specific chemical composition seems not to be a requirement for germination.

A number of species with fleshy fruits are known not to germinate before the fleshy part is removed from the stone (*e.g.* Mayer & Poljakoff-Mayber 1989), which can be done by gut passage in animals, by decomposition in soil or by peeling (*e.g.* Meyer & Witmer 1998). This should not be misinterpreted as implying that consumption of seeds by animals could be a general requirement for germination, even though species with fleshy fruits are well suited to dispersal by for example birds. Instead, seeds without fleshy parts usually show reduced germination after gut passage, as *Papaver argemone* and *Papaver dubium* when fed to cows (Mayer *et al.* 2000); probably a result of mortality, as for twenty grassland-species after simulated sheep ingestion (Peco *et al.* 2006) or for *Juncus subulatus* when fed to ducks (Espinar *et al.* 2006). Further, seed-eating birds, rodents and other animals do the same as humans: they usually remove or crush the structure protecting the plant embryo and endosperm when consuming a seed, thus completely killing it.

The effect of one factor influencing germination may be affected by another (*e.g.* Vincent & Roberts 1977, Bare *et al.* 1978, Baskin & Baskin 1981a, Baskin & Baskin 1981b, Hartmann *et al.* 1997, Milberg & Andersson 1997, Sharif-Zadeh & Murdoch 2001, Baskin *et al.* 2003, Rivas-Arancibia *et al.* 2006). Thus, germination requirements are not a fixed package where a specific amount of different factors in a specific combination always give germination for a species. Instead, the outcome depends on how the effects of the involved factors are affected by each other, and of the interaction with the inherent and obtained characteristics of the seeds.

Natural variation, within species, of seeds' eagerness to germinate has a number of sources, for example heteromorphic seeds are frequently reported as having different eagerness to germinate (*e.g.* Brändel 2004). The source(s) of variation in nature can often not be controlled. For example, seeds' eagerness to

germinate differed depending on site of maturation when mother plants were grown in two different uncontrolled environments (Gutterman 1996), but the environmental circumstances causing the differences could be several different factors or combinations of factors. Andersson & Milberg (1998) reported large, frequently 50 percent units, differences in germination of fresh seeds between individual mother plants, populations, and year of collection for three common annual weeds from southern Sweden; suggesting a random pattern of variation. When mother plants were grown in one environment and seeds were tested for germination, the eagerness to germinate differed between genotypes, but also due to placement of seeds within one single growth chamber (Simons & Johnston 2006). A germination test of *circa* 8500 seeds of *Conyza canadensis*, evenly distributed in 99 Petri dishes, revealed substantial differences between dishes (Fig. 1). The seeds were collected from one population at one occasion, and well mixed. Germination tests were performed at one occasion in one incubator, and dishes were randomly re-arranged daily. Thus, there will always be variations present within species in nature; variations that not obviously can be deduced from detectable inherent or environmental factors.

Germination can be, and is often, studied physiologically and molecularly (*e.g.* Benech-Arnold *et al.* 2003, Downie *et al.* 2003, Perez-Flores *et al.* 2003, Bove *et al.* 2005, Boudet *et al.* 2006, Traverso *et al.* 2007). The knowledge gained from such studies can explain the mechanisms leading to germination, both in terms of bio-molecular activities and proteomics and in terms of visible changes of structures within the seed. However, when studying germination in an ecological context, knowledge of mechanisms within seeds is seldom the major subject; the influence of different environmental factors may as well increase, out-level or reverse differences in eagerness to germinate between genotypes. For example, Donohue *et al.* (2005), using a large number of homozygote genotypes originating from two individuals of *Arabidopsis thaliana*, whose seeds performed different in laboratory germination tests (Munir *et al.* 2001), detected difference in performance between genotypes. However, they also showed that the site seeds were sown at was the outstandingly most important factor for explaining fractions of germinated seeds as well as germination timing. The importance of including phenology to understand and foresee field performance of genetically homogeneous crops has been emphasized by, for example, Miflin (2000), Araus *et al.* (2003), Habash (2003) and Slafer (2003). Donohue (2005) pointed out the importance of the interaction between ecology and genetics for understanding of all aspects of seed germination.

Species in the wild are subjected to natural selection, not to deliberate selection by man or to gene modification. Thus, even though man sometimes "selects" weeds by, unintentionally, favouring types tolerant to the weed control methods used, weeds in the field are genetically diverse. Seeds in the field are also subjected to a heterogeneous environment, which man rarely has recorded in detail;

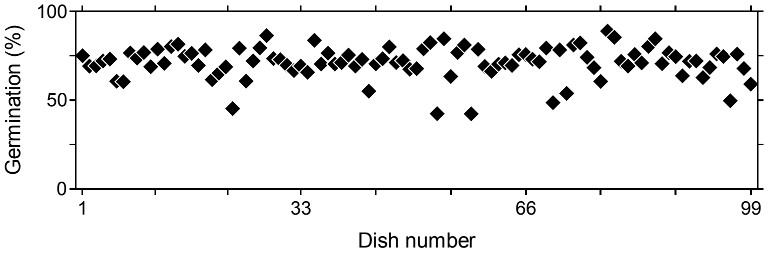

Figure 1. Germination of *Conyza canadensis*. Circa 8500 seeds, from one seed batch, were incubated at 25/15°C day/night in continuous darkness for 14 days. Seeds had first been dry stored for about one year. The seeds were evenly distributed into 99 Petri dishes that were re-arranged daily. Unpublished results.

especially not during the entire period that may have influenced seeds until any specific point in time. Further, the knowledge about the complex interaction of combinations of environmental events on seeds is very limited. Therefore, to understand the general germination pattern of wild species or ecotypes in an ecological context, the study object must be the phenotype, including naturally occurring variations.

1.3. GERMINATION TIMING

Germination timing is a critical factor in the life cycle of plants that propagate sexually (Harper & White 1974), that is, seeds should avoid germination on occasions when it would be hard or impossible to develop further. To stay un-germinated after dispersal is a strategy that is possible for orthodox seeds, *i.e.* such seeds that can be dried and stand for a period, which may be hundreds of years for a number of species (Ødum 1965), in environments where they cannot germinate. On the contrary, there are seeds that have a more or less continuous growing activity between ripening and germination, and that do not survive drying out: recalcitrant seeds (*e.g.* Daws *et al.* 2004). Such species depend on dispersal at a point in time when the environment will not be dry before germination, which is possible in stable environments such as rain forests; one example is *Minquartia guainensis*, one of the most common tree species in central Amazon (Ferraz & Camargo 2005). Thus, germination timing, in another meaning than dispersal in a suitable environment, is only possible to achieve for orthodox seeds. The remaining of this thesis deals with orthodox seeds.

Germination timing includes more aspects than the possibility for the seed to germinate, or not, during momentarily occurring circumstances. For example, in areas with temperate climates, spring and autumn may offer the same environment regarding temperature, light and humidity. For several species, germination in one of these occasions would be lethal, and strategies to avoid such bad timing have consequently been favoured during evolution.

Germination requirements can sometimes, *per se*, lead to proper germination timing. One example is *Conyza canadensis*, originating from North America (Noyes 2000) and spread over the major part of the northern hemisphere (Hultén *et al.* 1986). It is known as a winter annual for example at 40°N (Regehr & Bazzaz 1979 [Illinois], Thébaud *et al.* 1996 [France]), but in areas with shorter summers, and cold winters, as at 58°N in Sweden, it performs mainly as a summer annual (personal observation). Such an emergence phenology, changing over the warm-cold environment gradient, can be achieved by germination requirements.

Conyza canadensis germinates only at sufficiently high temperatures, preferably over 10°C daily average (Shontz & Oosting 1970, Hayashi 1979, Trudgill *et al.* 2000, Karlsson & Milberg ms 1). Therefore, the circumstances present when seeds are ripe and are dispersed in autumn in the colder parts of the world do not allow germination. On the contrary, *Conyza bonariensis*, originating from South America (Noyes 2000) and occurring in tropical to warm temperate regions around the world (Tutin *et al.* 1976, Wilson *et al.* 1995, Bromilov 2001), germinates readily at 10°C daily average (Karlsson & Milberg ms 1). The two species are reported as co-occurring in USA (Andersen 1993), Mexico (Vibrans 1998), France (Thébaud & Abbot 1995), South Africa (Bromilov 2001) and Australia (Wilson *et al.* 1995).

In a relatively warm climate, both *Conyza canadensis* and *Conyza bonariensis* can germinate and establish during autumn, over-winter as seedlings, and grow and set seeds the following summer (Fig. 2). In a colder climate, only *Conyza bonariensis* germinates at the relatively low temperature in autumn (Fig. 2). Such seedlings seriously risk winter mortality, if at all able to over-winter in cold climate: autumn temperature is low, time may not allow establishment, and the winter survival of at least *Conyza canadensis* at 40-50°N is favoured if seedlings have achieved a sufficient size in autumn (Regehr & Bazzaz 1979 [Illinois], Buhler & Owen 1997 [Minnesota, Iowa]). If *Conyza bonariensis* is transferred to a cold climate as seeds during winter or spring, it will germinate and set seeds once, but then again germinate in autumn. On the contrary, *Conyza canadensis*, because of its germination requirement, does not germinate at the low autumn temperatures in the colder climate, but over-winter as seeds (Fig. 2); germination, growing and seed set then occur as one continuum during summer. This results in relatively late seed dispersal, which *per se* minimizes the possibility of facing warm days during autumn, further minimizing the possibility of autumn germination and the following high risk for seedlings being killed during winter. Thus, germination requirements, without local adaptations, can explain why the introduced *Conyza canadensis* is well established in Norway, but *Conyza bonariensis* only occurs as an occasional species in that relatively cold climate (Lid & Lid 2005).

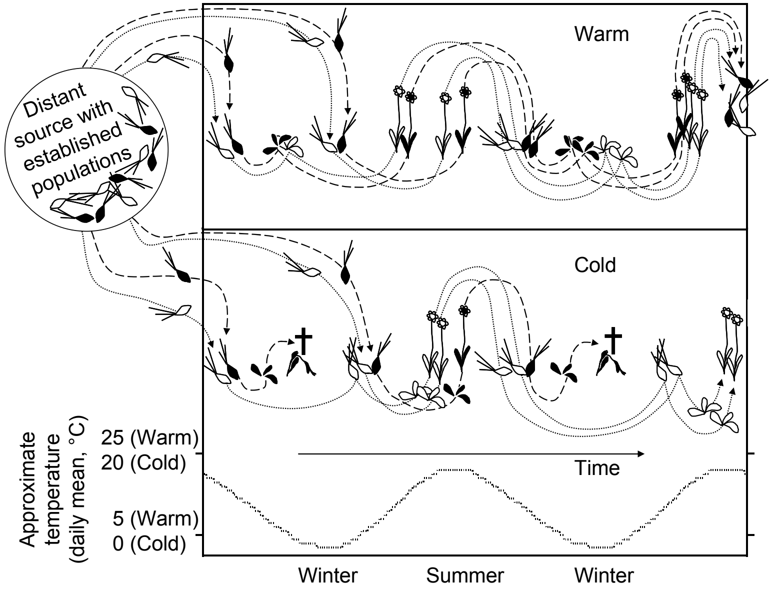

Figure 2. Germination timing of the annuals *Conyza bonariensis* and *Conyza canadensis* in two different climates. *Conyza canadensis* (white), that does not germinate when the daily mean temperature is lower than about 10°C, can get suitable germination timing as winter and summer annual in warmer (*e.g.* France) and colder (*e.g.* Sweden) climates, respectively, because of germination requirements and without specific local adaptations. *Conyza bonariensis* (black), which germinates readily at 10°C, is restricted to occur in warmer climates because of the broad temperature range accepted for germination. Interpreted from Karlsson & Milberg (ms 1).

Another example of germination preferences being the main source for proper germination timing is *Viburnum tinus* (Karlsson *et al.* 2005), a shrub occurring in the Mediterranean region. This perennial species has relatively dry fruits, which remain on plants when ripe, and are dispersed by birds. Therefore, seeds may be dispersed any time of the year. Germination is inhibited when temperature is as high as 25/15°C day/night, occurs slowly but as one continuum at 20/10°C (Fig. 3), more slowly at 15/5°C than at 20/10°C, and very slowly, if at all, at 5°C. When subjected to annual changing temperatures, root protrusion occurs during autumn, root growth continues during the following winter, and shoot emergence occurs during the following spring, regardless of whether the seeds are dispersed in summer or winter (Fig. 3). Together, the temperature preferences for germination and the slow development process result in proper germination timing, independent of time of dispersal, in the Mediterranean climate, where the warm and dry summers are unsuitable for seedling establishment (Karlsson *et al.* 2005).

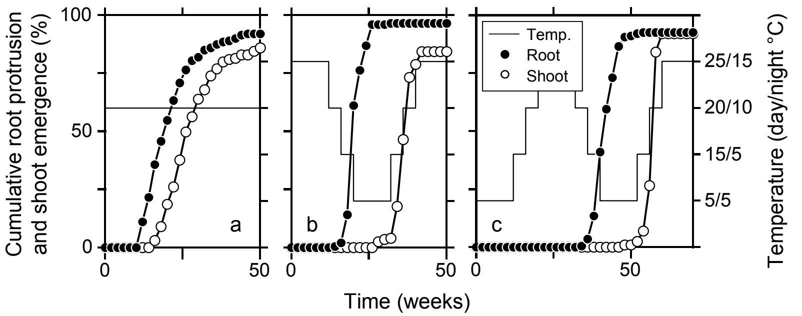

Figure 3. Germination timing of the perennial *Viburnum tinus*. The process of root protrusion and shoot emergence is relatively slow but occurs as one continuum at a suitable temperature regime, such as 20/10°C day/night (a). Germination is inhibited when temperature is as high as 25/15°C, occurs more slowly at 15/5°C than at 20/10°C, and very slowly, if at all, at 5°C. When subjected to annual changing temperatures (b, c), root protrusion occurs during autumn, root growth continues during the following winter, and shoot emergence occurs during the following spring, regardless of whether seeds are dispersed in summer (b) or winter (c). Redrawn after Karlsson *et al.* 2005.

1.4. Seed dormancy

Far from all species rely on only germination requirements to achieve proper germination timing. A large number of species have seeds which germinate only if specific environmental events have occurred in their past life story, and/or if a suitable time period has passed since ripening on mother plants (Figs 4, 5). That is, they do not always germinate when placed in the appropriate environmental conditions where the species is known to germinate. This characteristic is often referred to as "seed dormancy". Unfortunately, "seed dormancy" is a term used in different ways by seed scientists. There is no consensus whether the term principally refer to: i) all viable seeds that do not germinate, ii) seeds that do not germinate when provided with such environmental circumstances that are known to make the species germinate, iii) lack of readily germination because of seed/embryo morphology and/or ungermination even if suitable germination conditions prevail, or iv) seeds that do not germinate because of absence of some specific environmental circumstances (often in combination with iii).

Whatever definition of seed dormancy is used, the phenomenon of seeds that remain ungerminated even when subjected to such environmental circumstances

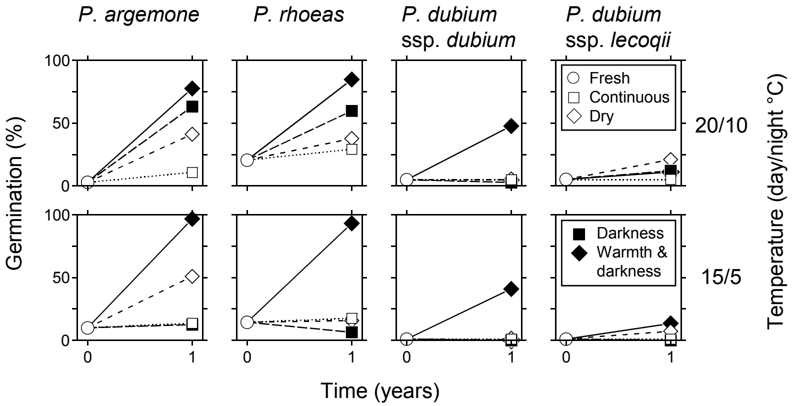

Figure 4. Germination responses of four annual *Papaver* taxa. Seed were tested for germination (*i.e.* incubated for 45 days with light during daytime) at two different temperature regimes (15/5 and 20/10°C day/night) when fresh and after *circa* one year subjected to three different pre-treatments: dry storage ("dry"), incubation in darkness at the same temperature regime as the following test ("darkness") or incubated in darkness at 25/15°C ("warmth & darkness"). Seeds were also incubated continuously with light during daytime at 15/5 and 20/10°C during the entire period ("continuous"). Each data point shows average of four seed batches of each taxon. Unpublished results.

that are suitable for germination for the specific species is important for the understanding of germination ecology. That phenomenon is in this thesis referred to as "seed dormancy". In this sense, seed dormancy is a characteristic of seeds, not involving seed morphology or mechanisms. As agreed with by most scientists, seed dormancy in this meaning can be reduced (or for a number of species also induced) by environmental events, which are usually not suitable for germination, and/or by time (Harper 1957, 1977, Nikolaeva 1977, Foley 2001, Baskin & Baskin 2004). A distinct example of seed dormancy reduction is when a short period of heat reduces dormancy markedly, as for *Geranium bicknelli, Geranium bohemicum* and *Geranium lanuginosum* that do not germinate before they had been subjected to a short period at 50-100°C in a humid environment (Granström & Schimmel 1993); these species are known to germinate after fires.

Seed dormancy is often influenced by yearly recurrent circumstances. An example is four weedy *Papaver* taxa (Fig. 4). These taxa germinate very little when fresh, regardless of test environment (Karlsson & Milberg 2003). After incubation in a warm and dark environment, *Papaver rhoeas* and *Papaver argemone* germinate to 80-100% at suitable temperature regimes, *Papaver dubium* ssp. *dubium* to about 50% and *Papaver dubium* ssp. *lecoqii* to 10% at the same circumstances (Fig. 4). Another

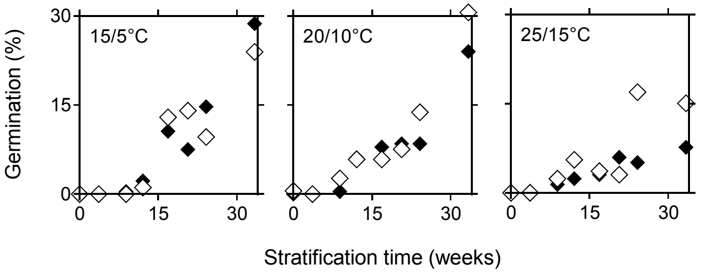

Figure 5. Germination responses of *Galeopsis speciosa*. Seeds were tested for germination (*i.e.* incubated for 21 days) with light during daytime (open symbols) or in continuous darkness (filled symbols) at three different temperature regimes (15/5, 20/10 and 25/15°C day/night). Germination tests were performed with fresh seeds and after periods of cold stratification in continuous darkness. No, or nearly no, germination occurred during incubation at the three test temperatures during the entire period, nor if stratified in warmth before test (data not shown). Each data point shows average of two populations. Redrawn after Karlsson *et al.* 2006.

example is *Galeopsis speciosa* for which cold stratification, but not warm stratification or dry periods, reduces dormancy (Karlsson *et al.* 2006). This feature allows seeds to germinate at a specific time of the year but not at another, even when subjected to exactly the same circumstances at both occasions.

When seeds are transferred from burial to a soil's surface, a flush of germination can occur, which is common within agriculture where soil cultivation leads to more germination than in soil not disturbed by man (*e.g.* Roberts 1984). In nature, transference results from soil movement by freezing and thawing or by burrowing animals. The effect of transference from darkness to light is illustrated by *Papaver argemone* and *Papaver rhoeas*, which not germinate much at 20/10°C when incubated with light during daytime for one year, but when incubated at 20/10°C in darkness for one year (where no germination occurred) before being transferred to light during daytime, at the same temperature, substantial germination occur (Fig. 4).

One explanation for germination when seeds are transferred from burial to surface is that seed dormancy is, at least for some species, more efficiently reduced in darkness than in light, which can be observed as an increased sensitivity to light after a period in darkness (Scopel *et al.* 1991), even though that is not a universal truth. *Drosera anglica* reduces dormancy during cold stratification, but more efficiently when daylight is present all time than in continuous darkness before transference to light (Baskin *et al.* 2001). For *Galeopsis speciosa*, cold stratification in darkness reduces dormancy (Karlsson *et al.* 2006) but the germination response is not correlated to the presence of light but to suitable temperature (Fig. 5). Another explanation is, of course, that non-dormant seeds, of species with a light requirement for germination, have been buried and germinate when they are provided with daylight (Thompson *et al.* 2003), or that there is a combination of dormancy and germination requirements, not necessarily involving light condition for changes in dormancy.

Given all environmental and inherent sources that influence germination, one can ask whether it is at all possible to separate seed dormancy from germination requirements. In this thesis, germination requirements allude to environmental circumstances that have to be there for the seed to germinate. Thus, if it is enough with water and a suitable temperature for germination that is the requirement, even if an infinite number of other environmental factors may influence germination. Seed dormancy reduction is regarded as a response to an event (or events) that pass by, *i.e.* something that usually is not still present when germination occurs. Such changes in dormancy are manifested as increase in germination and/or widening of environmental range accepted for germination after the event has passed, compared with the germination performance before onset of the event. The "event" is often a period of cold incubation (Fig. 5), warm incubation, or dryness (Fig. 4), and the period of the event being present is often an important factor for the response (Fig. 5).

When studying seed dormancy of species or other groups from an ecological perspective, it is desirable to distinguish groups with different responses to similar environmental circumstances, and to identify groups with similar responses. Preferably, comparisons should not be based on discrete sorting but use characteristics that can be measured on continuous scales, to be useful even when responses are relatively similar. There have been a number of suggestions of sorting systems for seed dormancy (Crocker 1916, Harper 1957, 1977, Nikolaeva 1977, Lang 1987, Baskin & Baskin 2004), that, despite using more or less different definitions of seed dormancy, all sorted species or seeds into discrete groups, separating them partly according to seed morphology but not necessarily paying attention to similar or different responses to environmental factors.

In this thesis, three characteristics, which I hypothesise as mutually independent seed characteristics, are used to describe dormancy and germination in an ecological context. Thus, I do not assume that species that perform ecologically equally necessarily have the same morphology and/or mechanisms directing dormancy and germination, nor do I assume that species with similar or same morphology and/or mechanisms necessarily performs ecologically equal. The characteristics are (i) dormancy pattern - described by the kinds of environmental events that reduce and, if applicable, induce dormancy, (ii) germination preference - described by the kinds of environments that are (or became during dormancy reduction) suitable for germination and (iii) dormancy strength - described by how much effort that is needed to reduce dormancy. Further, to be ecologically meaningful, seed dormancy should be regarded as a continuous property of a seed batch (even though it is not known whether or not it is a continuum or an on-off property for an individual seed). Dormancy strength, referring to the general pattern of a species, is described as strong-weak, and the extent of dormancy present at any specific moment is referred to as "degree of dormancy". Following this definition, species/batches with considerable germination when fresh can also show a dormancy pattern by responding to pre-treatment with increased (decreased) germination and/or a widening (tightening) range of germination environments acceptable for germination.

Using the characteristics described above for description of dormancy and germination performances, there is a difference in dormancy pattern between the two examples *Papaver* (Fig. 4) and *Galeopsis speciosa* (Fig. 5); degree of dormancy decrease during warm and cold periods, respectively. The temperature ranges suitable for germination is similar for the species, while the four *Papaver* but not *Galeopsis speciosa* is strongly favoured by light for germination (Karlsson & Milberg 2003, Karlsson *et al.* 2006), thus, also general germination preferences differ. There are differences in dormancy strength between the four *Papaver*: *Papaver dubium* ssp. *lecoqii* has the strongest and *Papaver dubium* ssp. *dubium* the second strongest dormancy (Karlsson & Milberg 2003). When fresh, there is no obvious difference between dormancy strength of *Papaver argemone* and *Papaver rhoeas*; they have both lower degree of dormancy than the two *Papaver dubium* subspecies, even though all four *Papaver* germinate relatively little when fresh (Karlsson & Milberg 2003). Based on these characteristics, the four *Papaver* (Fig. 4) and *Galeopsis speciosa* (Fig. 5) should restrict germination when fresh, and be well suited for germination in autumn and spring the year after dispersal, respectively; *Papaver* only when being on the soil surface, and *Galeopsis speciosa* also when buried.

1.5. COMPARISONS

Virtually all studies of germination ecology include some kind of comparison. Comparisons are done between fresh seeds and seed subjected to different pre-treatments, between seeds subjected to different germination test environments, and between species, populations and other types of groups.

Comparisons may be done to understand differences and similarities in causes for germination for co-occurring species (Grime *et al.* 1981, Washitani & Masuda 1990, Thanos *et al.* 1995, Milberg & Andersson 1997, Brändel 2006, Pezzani & Montaña 2006), to compare germination responses of native species with co-occurring weeds (Pérez-Fernández *et al.* 2000, Willis *et al.* 2003), to compare closely related species with different extents of invisibility (Mandák 2003), to evaluate possible local adaptations (Probert *et al.* 1985, Skordilis & Thanos 1995, Keller & Kollman 1999, El-Keblawy & Al-Ansari 2000, Grundy *et al.* 2003, Bischoff *et al.* 2006), for finding an environment suitable for a number of specific species for cultivation (Bare *et al.* 1978), to investigate germination of species with bimodal emergence patterns (Baskin *et al.* 2004, Mennan & Nguajio 2006), to explain distribution ranges (Brändle *et al.* 2003), to evaluate adaptations, selections and evolution (Shontz & Shontz 1972, Baskin *et al.* 1993, Walck *et al.* 2002, Adams *et al.* 2005), or to investigate the effect of a specific environmental factor on a number of species (Thompson & Grime 1983, Milberg *et al.* 1996). Comparisons are also done between species regarding yearly emergence patterns in the field within an area (Brenchley & Warington 1930, Popay 1976, Marks 1983, Roberts 1986) or regarding emergence over long periods, 10-20 years (Chancellor 1986, Schwerzel & Mabasa 1986). A large number of studies aiming at understanding and describing seed dormancy and germination have been done through comparisons of germination responses between fresh seeds and seeds subjected to possible dormancy affecting environments (*e.g.* Baskin & Baskin 1981b, 1984a, 1984b 1990, Baskin *et al.* 2002, 2004).

Regardless for the reason for the comparisons, to draw sound conclusions about possible consistent differences or similarities in the extent of germination from statistical analyses it is necessary to include variation, because within a seed batch there will always be variation (Fig. 1). Despite all inherent and achieved sources of variation to seeds eagerness to germinate, there are often general species-specific responses, as observed by Roberts (1986). For example, *Portulaca olaracea* collected in United Arab Emirates, Egypt and Canada had similar general responses to temperature and light conditions, even though there were significant differences in germination between seed batches when four Petri dishes, each with 25 seeds, of each were used as replicates (El-Keblawy & Al-Ansari 2000). Thus, even though local differences occur (Probert *et al.* 1985, Skordilis & Thanos 1995, Meyer & Allen 1999, Ramakrishnan *et al.* 2004), it may be possible to describe and compare general responses to prevalent environmental circumstances. Also when such large differences within species as in *Pinus brutia* occur (Skordilis & Thanos 1995), the dormancy pattern and germination requirement, according to the definition above, seem to be similar, even though dormancy strength differs substantially.

1.6. AIM

The aim of this thesis was, besides investigating dormancy, if any, and germination preferences of fifteen annual weeds, to contribute to the general understanding of patterns and variation of germination ecology by focusing on descriptions of species-specific characteristics, and on inter-species comparisons with respect to responses to past environmental events and present environments.

2. METHODS

Fifteen annual weedy taxa, constituting three groups, were used in experiments: 1) four *Papaver* species, one of them represented by two subspecies, 2) four *Lamium* species and 3) six co-occurring Asteraceae species of different genera (Table 1). Hereafter, all taxa, including subspecies, are referred to as "species".

Seeds were collected when ripe, *i.e.* only seeds that fell off a plant directly at harvest or during one night after collection were used. Sites for collection of replicating batches were in similar environments. Experiments commenced about ten days after collection. At the start of experiments, all species, except *Papaver aculeatum*, were sown in pots outdoors in the environment for collection.

Germination tests were done, with seed placed on moist substrate allowing full imbibiton, in temperature controlled environments (0 or 5°C constantly, 15/5, 20/10, 25/15 or 30/20°C day/night) with light during daytime. Two principally different methods were used. *Papaver* was subjected to three different artificial annual changing climates for up to 2.5 years, where cumulative germination was observed. For this thesis, the *Papaver* collected in Sweden were also subjected to a change from continuous darkness to light after one and one and a half years in cycles. *Lamium* and Asteraceae were subjected to three different pre-treatments (cold and warm stratification, and dry storage) followed by germination tests at four temperature regimes with either light during daytime or in continuous darkness. *Papaver aculeatum* was also subjected to warm and cold stratification before germination tests, and to combinations of warm and cold stratification before tests. All experimental setups included treatments with both light during daytime and continuous darkness.

Table 1. Sites for collection and number of replicating seed batches of fifteen annual weedy taxa investigated regarding seed dormancy and germination.

Family	Site	Taxa	Batches	Paper*
Papaveraceae	Sweden	*Papaver argemone* L.	4	I
		Papaver dubium ssp. *dubium* L.	4	I
		Papaver dubium ssp. *lecoqii* (Lamotte) Syme.	4	I
		Papaver rhoeas L.	4	I
	South Africa	*Papaver aculeatum* Thunb.	2	II
Lamiaceae	Sweden	*Lamium amplexicaule* L.	5	III
		Lamium confertum Fr.	5	III
		Lamium hybridum Vill.	5	III
		Lamium purpureum L.	4	III
Asteraceae	Ethiopia	*Bidens pilosa* L.	2	IV
		Galinsoga parviflora Cav.	2	IV
		Guizotia scabra (Vis.) Chiov.	2	IV
		Parthenium hysterophorus L.	2	IV
		Tagetes minuta L.	2	IV
		Verbesina encelioides (Cav.) A.Gray	2	IV

* I Karlsson & Milberg (2007)
II Karlsson & Milberg (ms 2)
III Karlsson & Milberg (ms 3)
IV Karlsson *et al.* (ms)

Intra-species variation was reported as absolute results for seed batches, and for Asteraceae also indirectly through principal component analysis (PCA). Analyses of variance (ANOVA) were performed on inter-species differences for all groups (except *Papaver aculeatum* for which the experiment did not coincide with the other *Papaver*). In ANOVA, each seed batch was considered one replicate, *i.e.* even though 2-5 Petri dishes were used for each batch and treatment, dishes were not considered replicates. For Asteraceae, differences between species were illustrated by, through a logistic function (Paper IV), measuring and plotting overall final response and response time to pre-treatments.

Details about material, methods and results are given in the relevant papers (Table 1). References to figures in included papers are done by referring to figure number, in each paper, and paper number, *i.e.* "Fig. X[Y]" where Y is paper number.

3. RESULTS

3.1. GENERAL

All species investigated readily imbibed water and germinated to some extent when fresh, and germination of all species was promoted by light during daytime compared with continuous darkness. All species showed some kind of dormancy pattern that was expressed as increased germination in response to one or more environmental factors not required for the actual germination. Intra-species variations in germination occurred for all species, not seldom reaching a difference of 25-50 percent units at one single occasion (*e.g.* Figs 6, 3[I], 3[II], 3[III]). Species-specific germination responses within all groups were revealed by ANOVA: the factor "species" and interactions including "species" were significant explanatory factors in analyses (Papers I, III, IV).

3.2. PAPAVER

There was a general difference between the *Papaver* collected in Sweden (Table 1) and *Papaver aculeatum*, with the latter germinating more and/or quicker both when fresh and when subjected to annual cycles (*cf.* Figs 1[I], 3[I] and Figs 1[II], 3[II]). Among the species collected in Sweden, *Papaver rhoeas* germinated most and quickest (Figs 1[I], 3[I]).

The species differed in germination response to temperatures. *Papaver aculeatum* and *Papaver argemone* did not germinate at 30/20°C (Figs 1[I], 3[I], 1[II], 2[II], 3[II]). *Papaver rhoeas* and *Papaver dubium* ssp. *lecoqii* germinated at 30/20°C when incubated for long time (Fig. 1[I]), but not in annual cycles (Fig. 3[I]). *Papaver dubium* ssp. *dubium* germinated at 30/20°C both when subjected to continuous incubation at that temperature and in annual cycles (Figs 1[I], 3[I]). At 5°C, *Papaver argemone* germinated more than the other species collected in Sweden (Figs 1[I], 2[I]); *Papaver aculeatum* was not tested at 5°C.

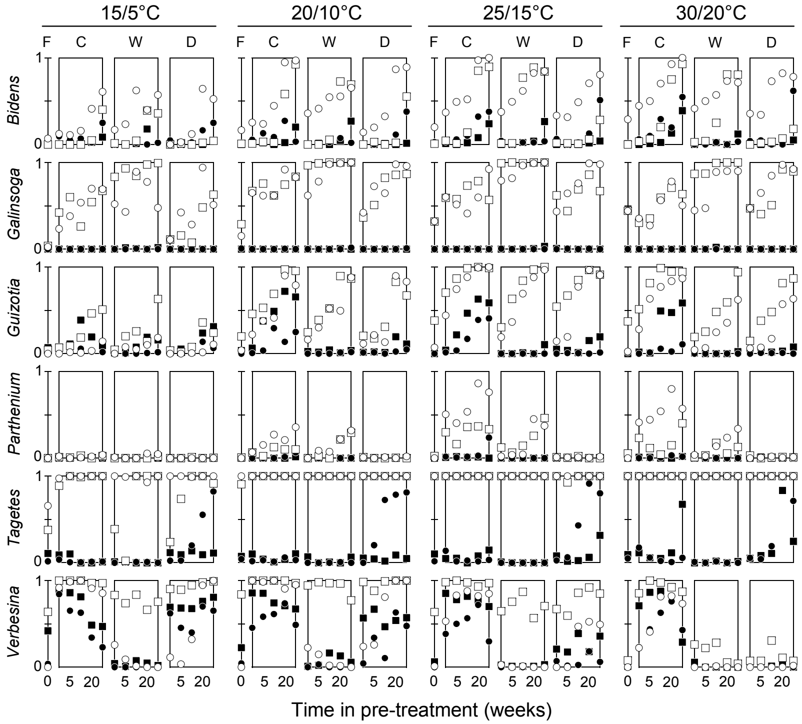

Figure 6. Germination of *Bidens pilosa*, *Galinsoga parviflora*, *Guizotia scabra*, *Parthenium hysterophorus*, *Tagetes minuta* and *Verbesina encelioides* when incubated at 15/5-30/20°C day/night with light during daytime (open symbols) or in continuous darkness (filled symbols) when fresh (F) and after 2.5, 5, 10, 20 or 30 weeks subjected to three different pre-treatments: cold stratification (C), warm stratification (W) or dry storage (D). Seeds were collected at two sites (symbolized with circles and quadrates) circa five kilometres apart in eastern Ethiopia. The y-axes show germination (fraction).

The general response pattern to annual changing climates was similar for the studied *Papaver* (Figs 3[I], 3[II]). Germination occurred in both autumn and spring for all species, with most germination in the warmest climate (Figs 3[I], 3[II]). Germination timing changed with climate: the warmer the climate the larger the fraction of yearly germination that occurred in autumn (Figs 3[I], 3[II]).

When seeds were transferred from darkness to light, substantial germination occurred in both autumn and spring in both the intermediate and the warm climates for *Papaver argemone* and *Papaver rhoeas* (Fig. 7). *Papaver dubium* ssp. *dubium* germinated to circa 60% during autumn in the warm climate, but otherwise little,

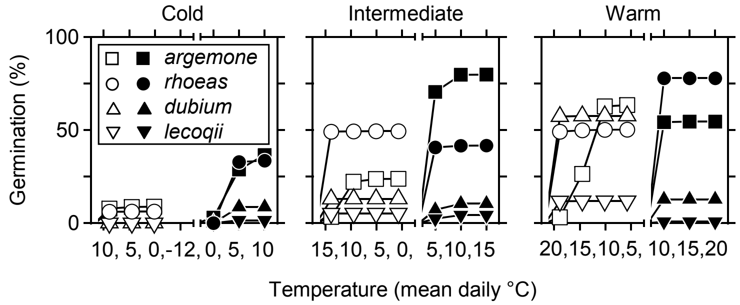

Figure 7. Germination of four *Papaver* species during autumn (open symbols) and spring (filled symbols). Seed were first subjected to one or one and a half year incubation in continuous darkness in three different artificial annual temperature cycles, imitating cold, intermediate and warm climates, before being transferred to light, while continuing in temperature cycles, after summer and winter, respectively. Data points show cumulative germination (% of ungerminated seeds after the period in darkness) for 30 day periods. Data for each species is average of four seed batches.

as did *Papaver dubium* ssp. *lecoqii* (Fig. 7). For *Papaver aculeatum*, which was subjected to continuously warm or cold stratification and to combinations of warm and cold stratification before germination tests, germination increased and decreased when warm and cold stratification, respectively, was the last treatment before test (Figs 1[II], 2[II]).

3.3. LAMIUM

The four *Lamium* species responded in the same general way to test temperatures and pre-treatments (Fig. 4[III]). Germination was favoured by the higher temperatures, 20/10 - 30/20°C, and warm stratification led to increased germination in light, while cold stratification did not increase germination (Fig. 4[III]). Dry storage generally increased germination more and quicker than warm stratification, and, after dry storage, germination occurred also in darkness (Fig. 4[III]). Germination at 15/5°C occurred only after dry storage (Fig. 3[III]).

Despite large intra-species differences under specific test occasions (Figs 2[III], 3[III]), species-specific responses of both extent of germination over time and differences between germination fresh seeds and seeds after pre-treatments were revealed by ANOVA (Paper III). *Lamium hybridum* generally germinated the most and *Lamium amplexicaule* the least (Figs 2[III], 3[III]). *Lamium purpureum* responded faster and to a higher extent to warm stratification than did the other investigated *Lamium* (Fig. 3[III]).

When *Lamium* was sown in pots outdoors, there was emergence in all the included autumns (Fig. 1[III]). Emergence in spring occurred after a winter when seeds had been dry and frozen, but not after a winter when they had been covered with snow (Fig. 1[III]). Plants that emerged in autumn had a low possibility to survive winter, excepting *Lamium purpureum* for which winter survival was relatively good (data not shown).

3.4. ASTERACEAE

Temperature preferences for germination, extent of germination and responses to pre-treatment varied between species (Fig. 2[IV]). *Bidens pilosa* and *Galinsoga parviflora* germinated most at the three highest temperatures tested, *Guizotia scabra* and *Parthenium hysterophorus* at 25/15°C, *Verbesina encelioides* at the two lowest temperatures and *Tagetes minuta* had no clear temperature preference within the studied range (Fig. 4[IV]).

Most species responded, with increased germination, to two or three pre-treatments (Fig. 2[IV]). *Guizotia scabra*, *Parthenium hysterophorus* and *Verbesina encelioides* responded faster and to a higher extent to cold stratification than to other pre-treatments, that either gave a less pronounced response or no response (Fig. 4[IV]). *Galinsoga parviflora* responded faster and to a higher extent to warm stratification than to the other pre-treatments, *Bidens pilosa* responded fastest to warm stratification but to the highest extent to cold stratification, and *Tagetes minuta* showed response a only to dry storage (Fig. 4[IV]). *Galinsoga parviflora* and *Verbesina encelioides* had the overall fastest responses, and *Bidens pilosa* and *Parthenium hysterophorus* the slowest (Fig. 4[IV]).

After sowing outdoors in eastern Ethiopia in November, following little precipitation at the time of sowing, there was a dry period of about three months (Fig. 5[IV]). Most emergences occurred in the middle of February, *i.e.* following the first precipitation (Fig. 5[IV]). Only *Guizotia scabra* did not respond with substantial emergence to the first precipitation, but had, as had *Bidens pilosa* and *Parthenium hysterophorus*, an emergence peak during intense rains in late March and early April (Fig. 5[IV]). *Guizotia scabra* and *Bidens pilosa* were the only species that emerged during May or later (Fig. 5[IV]).

4. DISCUSSION

4.1. EXPERIMENTAL METHODS

All experimental setups included germination tests in light during daytime and in continuous darkness. Such tests resolve whether germination is promoted by light or darkness, or if there is no difference correlated with the presence of light. More subtle responses, as responses to short light exposure or to specific light qualities, can not be interpreted from such results. Temperatures used for germination tests had a daily fluctuation of ten degrees, which is an intermediate daily fluctuation occurring in nature. By using a broad range of naturally occurring temperatures, and involving the response to light, I regard the environments used as meaningful for ecological studies, allowing general responses to environmental events prevailing in nature to be investigated.

For the *Papaver*, cumulative germination was studied during annual changing circumstances. This experimental setup allows comparisons between climates, and it can be adjusted to fit an infinite number of climates. I think this method is the closest available for direct investigations of germination ecology during controlled environmental circumstances. With this method, the relative distribution between winter and summer annual behaviour can be observed (Figs 3[I], 3[II]). For the species collected in Sweden (Table 1), seeds which ripened in both summer and in autumn were included. All seeds batches were subjected to artificial dispersal in both summer and autumn, in three different artificial environments (Figs 3[I]). Thus, the experimental method offers a straight-forward way to evaluate if there are specific adaptations between co-occurring winter and summer annual individuals of a species.

For *Lamium*, Asteraceae and for some experiments with *Papaver aculeatum,* the experimental setup was more conventional, using pre-treatment environments as possible dormancy affecting environments and test of germination after various time periods. The pre-treatments used were cold stratification, warm stratification and dry storage, thus involving three clearly different environments, allowing detection of possible principally different ecological performances among the investigated species. This method has the advantage of requiring a shorter time period for testing the responses to different environments compared with annual cycles imitating yearly changes. Also, this method clearly reveals specific responses to certain treatments, not involving the interactions of environmental factors that arise in annually changing treatments. If there is enough time and space available, both experimental methods could be used, allowing direct knowledge about germination timing as well as about environmental reasons for dormancy changes, as for *Papaver aculeatum* (Paper II).

The methods used for seed collection and experiment ensured that there were probably not larger differences within species than can always be expected within a relatively small area: the sites used for seed collection, of each species, were similar places and located within the same agricultural area. However, *Papaver aculeatum* was collected from two sites about 850 km apart north-south, and the differences observed may be a result of local adaptations. All seeds were tested for germination when fresh and further experiments commenced at the same time, thus allowing interpretations of germination performance at the time for dispersal as well as after subjection to environmental circumstances after dispersal.

4.2. VARIATIONS WITHIN SPECIES

On several occasions there were larger differences in cumulative germination within rather than between the *Papaver* species collected in Sweden (Figs 1[I], 3[I]). As

revealed by ANOVA, part of the intra-species variation depended on the collection date or starting point in the annual temperature changing cycles (Paper I), but there were also substantial differences between seed batches collected on the same day and subjected to the same treatment (Figs 1[I], 3[I]. Especially, large differences were found in *Papaver dubium* ssp. *lecoqii*: of four seed batches only one germinated to a substantial extent under any conditions tested (Figs 1[I], 3[I]). Pronounced differences occurred also within *Papaver dubium* ssp. *dubium* (Fig. 3[I]).

The two seed batches of *Papaver aculeatum* germinated to a relatively similar extent when fresh (Fig. 1[II]). However, when stratified in coldness, the seed batch collected in the environment with coldest winters of the two sites used (Fouriesbourg) decreased germination, *i.e.* increased degree of dormancy, more pronounced than the other (Roundvlei) seed batch (Fig. 1[II]). That difference between batches was apparent also when subjected to annual cycles (Fig. 3[II]).

For all *Lamium* species there were large, frequently 25-50 percent units, differences between seed batches of the same species that were treated in the same way (Fig. 3[III]). Substantial intra-species differences of *Lamium amplexicaule* and *Lamium purpureum* batches collected in different years were also observed by Roberts & Boddrell (1983), *e.g.* 40-70 percent units differences in distribution of yearly emergence between spring and autumn emergence (June and July excluded) between batches of the same species. Also, there were up to 20, 40 and 50 percent units difference between populations of *Lamium amplexicaule*, *Lamium purpureum* and *Lamium hybridum*, respectively, in laboratory tests (Milberg *et al.* 1996, Milberg & Andersson 1998).

The *Lamium* seed batches used here originated from plants within the same area, and the ones from 2005 had grown on the same site. The relatively small differences present in the growing environment for the various seed batches are then such differences that will always occur in nature and will influence the characteristics of seeds. An inspection of Fig. 1[III] and Fig. 3[III] suggests that late-ripened parts (downwards triangles) of the cohorts of *Lamium amplexicaule*, *Lamium confertum* and *Lamium hybridum* had weaker dormancy, and therefore germinated more easily, than the early parts (upwards triangles). Because only one seed batch from each collection occasion and species was included in this part of the study, the basis for general conclusions is too limited. However, the results imply that a substantial part of the variation depends on time for dispersal and/or age of the mother plant; thus, such variations and differences will occur within every cohort.

The Asteraceae seed batches were collected at the most adjacent sites used in these studies. Also, the same two sites were used for all species, and seeds were collected during two consecutive days. The sites did not apparently differ, and they were located within the same agricultural area and at the same altitude. Despite these similar preconditions, there were large differences between populations of each species, with no consistent pattern of difference between the two sites among the species (Fig. 6). As is not rare within Asteraceae, *Bidens pilosa* has germination differences between dimorphological seeds (Forsyth & Brown 1982) and between seeds with central or peripheral position on the flower head (Rocha 1996); these two aspects overlap, *i.e.* the different morphology types mainly occur at different positions. For *Galinsoga parviflora*, fresh ray-seeds are more eager to germinate than disc-seeds (Rai & Tripathi 1987, Espinosa-García *et al.* 2003).

In this study, seeds were not sorted with respect to morphology or position on the flower head but it was observed that there were sometimes (*Bidens pilosa*, *Galinsoga parviflora*, *Guizotia scabra* and *Verbesina encelioides*) transition stages between two clearly different morphologies. By using an even mix of seeds ripened at a specific moment, ignoring variation within flower heads, the results (Fig. 6) describe the natural variation within species from a limited geographical area at one point in time. Thus, one can assume that the variations within an entire cohort or between years are larger. In the PCA, *Bidens pilosa* and *Verbesina encelioides* showed the largest differences encountered along the information-rich PC1 (Fig. 3[IV]). The differences between the two batches of each of these two species were mainly results of the amount of germination (Fig. 6). However, for both species, the pair of batches responded in the same general way to pre-treatments and test environments, and the time to reach the final response level was quite similar for each pair of batches (Fig. 6, Paper IV).

4.3. DESCRIBING AND COMPARING DORMANCY AND GERMINATION

4.3.1. PURPOSE

As mentioned in the introduction, there are numerous reasons for studying, describing and comparing species or ecotypes regarding their seed dormancy and germination performance. In all cases, there is a need to decide what characteristic(s) should be studied and used for descriptions and comparisons. In this thesis, the subject was comparisons of seed dormancy and germination in an ecological context. As, for example, Murdoch & Ellis (2000) point out: seed dormancy cannot be studied directly, only indirectly through germination. According to the seed dormancy definition used here "the phenomenon of seeds remaining ungerminated even when subjected to such environmental circumstances that are suitable for germination for the specific species", not all ungerminated seeds are dormant, and thus, dormancy is not measurable. On the contrary, germination is measurable, and can be statistically analyzed. However, in addition to statistical analyses, for interpreting dormancy and germination performances and comparing species, ecotypes or other groups, some kind of description of general responses that express changes in dormancy is desirable.

4.3.2. STATISTICS

An important point to consider in germination studies is replication. Sometimes, a number of seeds from the same seed batch distributed into a few units (*e.g.* Petri dishes, pots, plots with bare soil) are considered one replicate per unit in analyses and evaluations of differences between species or ecotypes (*e.g.* El-Keblawy & Al-Ansari 2000, Mandák *et al.* 2003, Rivas-Arancibia *et al.* 2006). This kind of replication is, of course, based on variation within the batch, *i.e.* that population at that sampling occasion; not of variation within the species or the ecotype studied. Therefore, this method, *i.e.* to *de facto* not include replication of the studied groups, does not allow evaluation of differences between the species or ecotypes included in the study, only between the actual batches, regardless whether they belong to, for example, the same population or to different species.

Variations within seed batches can be considerable (Fig. 1), even though probably generally much smaller than overall variations within species (Figs 6, 3[III]), and is a feature of the study object. In Figure 8, the results from Figure 1 were randomly distributed into groups of three Petri dishes and each such group of three dishes was compared with each other group by t-test. That resulted in 528 comparisons, with 5.5% of these having a p-value less than 0.05, close to the statistically expected 5.0% type one errors while using p=0.05 as the limit for significance (*e.g.* Zar 1999), *i.e.* they would have been reported as statistically significant differences; thus, there is a built-in risk with focusing too much on p-values. When differences are small, even though statistically significant, it is preferable to discuss whether the difference may have any ecological importance rather than to regard it as a fundamental difference between the investigated objects. For ecological interpretations, the goal is rather to compare general responses than absolute germination.

One way used to cover local occurring variation is to sample seeds from different occasions and from different sites within the study area, and mix all the seeds (*e.g.* Grundy *et al.* 2000, Ferriol *et al.* 2006). If such a merged seed batch is then divided into units that are subjected to the same germination test, these units show a high extent of similarity (Grundy *et al.* 2000) and the result could be assumed to be a good description of the average performance of the species, but would obscure the local variation between sites and collection occasions (*cf. Lamium* Fig. 3[III]). However, for comparing species or ecotypes statistically, it is necessary to include the extent of variation within the species, or ecotypes, studied.

When replicates of the study object are used, *i.e.* several batches from different populations and/or points in time are used in similar experiments, they are rarely considered replicates in analyses but are reported as parallel results (*e.g.* Brenchley & Warington 1930, Baskin & Baskin 1990, Campell & van Staden 1994), but there are exceptions: for example Milberg *et al.* (1996) and Pezzani & Montana (2006) used batches from different populations as replicates in ANOVA, and HA

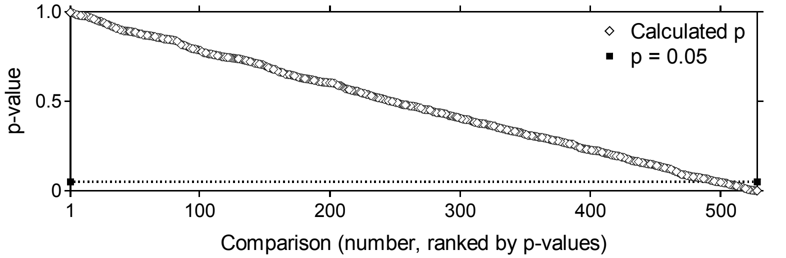

Figure 8. Statistical probability (p) of observed differences comprising the null-hypothesis "there is no difference between compared groups" from pair-wise comparisons (t-tests) of 33 groups of germination results of *Conyza canadensis* (Fig. 1). Each group, which was randomly composed, consisted of results from three Petri dishes treated as replicates; each dish contained *circa* 75-100 seeds. Of 528 pair-wise comparisons, 29 (5.5%) had a p-value lower than 0.05. Unpublished results.

Roberts often merged emergence data, per species, from several batches and years of experiment to visualize and discuss emergence timing in the field (*e.g.* Roberts & Feast 1970 [20 annual weeds], Roberts & Boddrell 1984a [four *Papaver* species], Roberts 1986 [70 species]).

In the studies reported here seed batches, *i.e.* seeds from one population collected at one occasion, are in all cases the unit treated as replicates in analyses. Thus, even though 100-200 seeds, distributed into 2-5 dishes, of each batch were used for each test occasion, the numbers of replicates in ANOVAs are equal to the number of batches collected (Table 1). This method involves intra-batch variation (from test occasions and test environments) as well as intra-species variation (*i.e.* replicates in analyses), and because a large number of results from different treatments and points in time are involved in the first and second order interactions, the risk of drawing conclusions that are strongly depending on one randomly occurring extreme value (Fig. 1) is limited. Further, ANOVAs allow detection of species-specific responses through interaction factors including "species". Despite the variations occurring within species (Figs 6, 1[I], 3[I], 3[III]), in all ANOVAs the factor "species" and interactions including "species" were large, and statistically significant, explanatory factors (Papers I, III, IV). For Asteraceae, the two seed batches of each species grouped well together in PCA (Fig. 3[IV]). Thus, I conclude that it is relevant to evaluate and discuss the differences between the here studied species on a general level, instead of focusing on possible statistically significant differences in fraction of germination at any single moment. To describe performances in an ecological meaningful way, I think absolute results and statistical tools need complimenting to be useful for interpreting germination ecology.

4.3.3. SEED DORMANCY DESCRIPTION

To understand and interpret germination ecology, it is necessary to study ecological meaningful features. It is plausible that there are species-specific responses to environments, and that we can compare and to some extent "sort" species according to responses. For example, HA Roberts' impression was that the emergence patterns he found were generally consistent both for seeds collected different years, often from different sites, and for seeds that had been present in soil for different periods (Roberts 1986). In the present studies, the impression of species-specific general responses are supported by ANOVAs (Papers I, III, IV) and PCA (Fig. 3[IV]).

One way to report results from studies of differences and/or variations is to list the obtained data (*e.g.* Roberts & Chancellor 1979, Grime *et al.* 1981, Roberts & Boddrell 1983, Roberts & Boddrell 1984a, Roberts & Boddrell 1984b). In that way, the readers get direct access to the actual results, which may be very useful, but also difficult to interpret; thus, the mentioned authors also provided different syntheses. Another way is to plot data (Figs 6, 3[I], 3[II], 3[III]) and thus give an impression of differences and/or variations, but also this becomes difficult to interpret if it is a large data set (Fig. 6). Another possibility is to plot Richard's diagrams, that may be useful to visualize responses to two tested factors, and the interaction of these (*e.g.* Murdoch 1998), but, in my opinion, the diagrams tend to be difficult to interpret when more factors are involved (*e.g.* Vincent & Roberts 1977).

In order to structure descriptions and comparisons of germination and seed dormancy, there have been several attempts to construct a dormancy classification system that could be used generally. Crocker (1916) wrote a paper about seed dormancy, and already at that time, there were different definitions used for "seed dormancy". Crocker (1916) used what he called a "dominantly mechanistic interpretation" when discussing both natural occurring and artificial ways for seeds to remain ungerminated and to germinate. Harper (1957, 1977) used a system where seeds could be placed in different groups depending on the circumstances instantaneously preventing germination; Nikolaeva (1977) based her sorting system on embryo/seed morphology followed by descriptions of environments breaking dormancy; Lang (1987) regarded the within-organism location of physiological factors preventing germination or the presence of an unsuitable environment as the most important sorting factors (not only for seed dormancy but for all kinds of non-growing), and Baskin & Baskin (2004), basing their system on Nikolaeva's, first sorted according to morphology and then into subgroups that could include both species that respond to warm and species that respond to cold stratification. Unfortunately, none of these systems uses characteristics that can be measured or estimated on a continuous scale, which could allow comparisons even when responses are relatively similar.

The seed dormancy classification system by Baskin & Baskin (2004) is proposed as suitable for general use within seed science, including ecology.

However, it seems not always possible to use it for ecological interpretations and I will shortly discuss and exemplify three main points I regard as problematic for operational use within germination ecology studies.

The first point is the discrete sorting itself. Discrete groups require limits, and clear limits between performances in nature are hard or impossible to detect, probably because clear limits usually not exist. One example of the difficulties with sorting into discrete groups was mentioned by Sautu *et al.* (2006). The authors had a number of species that took about 30 days to germinate; this time period is the limit between dormant and non-dormant in the classification system suggested by Baskin & Baskin (2004). Sautu *et al.* (2006) solved their problem by using the median time to final germination as limit to determine if dormancy occurred or not, but in some cases they regarded the "right tail of the germination curve could be an indication of dormancy". Thus, a partly subjective method, in combination with regarding median germination before or after 30 days as the dividing characteristic, had to be used to place species on either side of an important limit. An alternative method is suggested by Baskin & Baskin (2006), where the fraction of seeds that germinated within 30 days when fresh was considered non-dormant (or morphological dormant) and the rest dormant (or morphophysiological dormant). Following this, *Lamium hybridum* should be regarded as partly non-dormant (the germinated seeds) and partly non-deep physiological dormant, and *Papaver aculeatum* as to a partly morphological dormant (the germinated seeds) and partly non-deep morphophysiological dormant. This latter phenomenon is mentioned as a rare case of one species having seeds of two different classes referring to *Papaver rhoeas* (Baskin & Baskin 2006). If using the system this way, I think it becomes similar to Harper's system (1957, 1977); *i.e.* rather describing circumstances that prevent germination for individual seeds at any single moment than describing species/populations according to general responses, which is desirable for ecological interpretations.

The second point is the use of seed/embryo morphology as a basal sorting characteristic. Intuitively, the *Lamium hybridum* (having non-deep physiological dormancy according to my interpretation of Baskin & Baskin 2004) seed batches that germinated to a high extent when fresh (Fig. 2[III]) and *Papaver aculeatum* (having non-deep simple morphophysiological dormancy according to my interpretation of Baskin & Baskin 2004) that germinated to a high extent when fresh (Fig. 1[II]) are ecologically relatively similar soon after dispersal, even though the two species differ in seed/embryo morphology, with *Papaver aculeatum* having relatively small embryos (*cf. Lamium amplexicaule* and *Papaver dubium* in Martin 1946). For ecological interpretations I find it difficult to regard the performance of *Papaver aculeatum* as different from species with fully developed embryos that germinate to a high extent when fresh. When Thompson *et al.* (2003), using data from the literature, investigated whether seed dormancy is related to persistence in soil they excluded the category "morphological dormancy" because there were too few species with sufficient information available. One may ask if morphological dormancy should not be regarded as equal to non-dormancy when interpreting performance in nature: except the difference in embryo morphology there is no difference – both groups should germinate within four weeks in suitable environments (Baskin & Baskin 2004). The embryo growth is a visible process, but also species with fully developed embryos have a time lag between full imbibition and root protrusion, even though the mechanisms active during this period are not easily observed. Thus, in both cases the study objects are seeds in which processes leading to germination are ongoing. Analogous, the difference between physiological dormancy and morphophysiological dormancy is the morphology rather than the ecological performance (Baskin & Baskin 2004). The problem with using morphology for sorting of seed dormancy was indirectly underlined by Vleeshowers *et al.* (1995); they aimed at integrating physiology and ecology with respect to seed dormancy, but decided to simply exclude, before beginning their reasoning, all such species that have relatively small embryos.

The third point is that species that respond in the opposite way to cold, or warm, stratification are in some cases grouped together. From an ecological perspective, the response to certain environmental events is important, in fact critical, for evaluating responses of species. One example is the Asteraceae investigated here that have, as virtually all Asteraceae, non-deep physiological dormancy (Baskin & Baskin 2004). Because that classification includes species that respond to cold stratification as well as species that respond to warm stratification, it could not be used for detection or evaluation of such differences to pre-treatment as shown in Figure 2[IV], even thought there is a sub-sorting suggested (Baskin & Baskin 2004), aiming to sort according to changes in germination environment preferences during dormancy reduction.

A comparison from an ecological perspective can be exemplified from the differences and similarities between *Galeopsis speciosa* (Karlsson *et al.* 2006) and the *Lamium* and *Papaver* collected in Sweden (Table 1) studied here. The annual Lamiaceae *Galeopsis speciosa* (Fig. 5) and *Lamium* (Fig. 4[III]) studied, both occurring as agricultural weeds in Sweden, have nearly identical seed and embryo morphology (Martin 1946) but decrease dormancy during opposite conditions; *Galeopsis speciosa* during cold periods (Karlsson *et al.* 2006) and the four *Lamium* species during warm or dry periods (Fig. 4[III]). On the contrary, the annual *Papaver*, which also occurs as agricultural weeds in Sweden, has seed and embryo morphology ("underdeveloped embryo", Baskin & Baskin 2004) very different from Lamiaceae (Martin 1946). Despite morphological differences between Lamiaceae and Papaveraceae, the studied *Lamium* and *Papaver* collected in Sweden responded in a similar way to environmental events: dormancy was reduced during a warm period, which resulted in similar emergence pattern in the field; germination both spring and autumn but mostly in autumn (Figs 5[I], 1[III]). In contrast, *Galeopsis speciosa*, which reduced dormancy during cold periods (Fig. 5), emerged exclusively in springs when sown outdoors at the same site (Karlsson *et al.* 2006). The four *Lamium* differed both from *Galeopsis speciosa* and from the four *Papaver* by preferring the higher temperatures tested for germination, and *Galeopsis speciosa* differed from *Lamium* and *Papaver* by being apparently independent of light conditions for germination (Fig. 5). Thus, in an ecological perspective, *Lamium* and *Papaver* in this example are more similar than *Lamium* and *Galeopsis speciosa* regarding dormancy and response to light for germination, while *Papaver* and *Galeopsis speciosa* are more similar to each other than to *Lamium* regarding temperature range accepted for germination.

In the Baskin & Baskin (2004) system it is mentioned that a sorting of kinds of dormancy should be done regardless of evolutionary position; which is indeed most reasonable. Papaveraceae is phylogenetically distant from, and belongs to evolutionarily older groups than, Lamiaceae (APG II 2003). Thus, using responses, not morphology, for comparison does not, in this case, intimate influence from evolutionary position. On the contrary, the use of relative embryo size as a fundamental reason to put species together (Crocker 1916, Harper 1957, 1977, Nikolaeva 1977, Baskin & Baskin 2004) probably results in correlation with evolution; the ancestral relative embryo size was small, so the only direction for possible changes was increasing relative embryo size (Verdú 2006).

When studying seed dormancy and germination, different scientists have different aspects of seed and germination science in mind, and characteristics used for both main sorting and sub-sorting between groups within one scientific field do not always make sense in another. Finch-Savage & Leubner Metzger (2006), who use the classification by Baskin & Baskin (2004), find out that they, for proper studies of physiology, need to regard non-deep physiological dormancy as being composed of different factors. They base their investigations on placement of dormancy-regulating factors in the seed, and regard the status of the seed as a result of the balance between different such factors. I would guess that this is a phenomenon occurring frequently in seeds, not necessarily correlated to dormancy classification. Further, for studying differences in germination ecology between closely related species, groups within species and/or species with similar emergence patterns in the field, dormancy classification systems are often not used (*e.g.* Keller & Kollman 1999, Copete *et al.* 2005, Bischoff *et al.* 2006), probably mostly because the subtle differences occurring are not possible to handle by discrete sorting, even though a comparison of performances is desirable. Therefore, I think the demand for one single system for general use (*e.g.* Thompson *et al.* 2003, Baskin & Baskin 2004) is a goal that is hard to reach, and not of the highest priority. Most importantly, we need to measure and compare characteristics relevant for the scientific field in question.

I decided to use, as mentioned in the introduction, three characteristics, hypothesised to be mutually independent seed characteristics, to describe dormancy and germination in an ecological context: (i) dormancy pattern - described by the kinds of environmental events that reduce and, if applicable, induce dormancy, (ii) germination preference - described by the kinds of environments that are (or became during dormancy reduction) suitable for germination and (iii) dormancy strength - described by how much effort that is needed to reduce dormancy. Thus, seed morphology and mechanisms involved in dormancy and germination are not considered. This response-based conceptual model may be used for descriptions of performance differences between species and to understand emergence patterns in the field from environmentally controlled germination tests. It may also be a possible way for increasing the understanding of which kinds of characters that easily and hardly change, respectively, and in which way performances are adjusted during evolution in different environments, regarding ecological important response patterns of seed dormancy and germination.

4.3.4. PICTURING GENERAL RESPONSES

When investigating seed dormancy, the common method is to test the germination response over time, in different test environments and with different pre-treatments. Such results give an impression of how much and how fast a response occurs, if any, to a pre-treatment, and under what circumstances that response is observable. I regard both the extent of the final response (the increase or decrease in germination that can be obtained following a specific pre-treatment) and the rate of the response (the length of time it takes to reach the final increase or decrease in response to a specific pre-treatment) as important parameters for evaluating the effect of different pre-treatments. The two factors "final response" and "response time" can be measured by fitting a logistic function to germination results from tests over time (Equation 1[IV]) and using its third derivative (Equation 2[IV]) to calculate the time needed to achieve the final response (Fig. 1[IV]).

This method for measuring time should not be confused with time measurements of cumulative germination in response to a treatment (*e.g.* Grundy *et al.* 2000, Köchy & Tielbörger 2007), frequently reported as T_{50}, the time it takes to reach half of the final germination achieved at any specific test occasion. The method used here (Fig. 1[IV]) is based on independent points, where each point represents one test occasion where seeds have had the possibility to germinate during four weeks. Thus, it is a way to focus on the response to another environment (*i.e.* the pre-treatment) than the environment where germination actually occurs, and to measure the time it takes to reach the plateau of germination for any specific combination of pre-treatment and test environment. Using only specific data points from experiments for such an attempt may result in vague statements like: "the response time is more than 190 days" without indications of when the response reaches its plateau (*e.g.* Tarasoff *et al.* 2007). Another method for measuring response time, through independent points, was used by Kettenring *et al.*

(2006), who fitted a logistic function to data and calculated the time to reach 50% germination. That method has severe drawbacks: because data is not cumulative, the point for 50% germination may occur already at the first test occasions, thus not allowing calculation of response time in such cases, further, a slow response after the measured point is not separated from a quick response after that point, and cases that do not reach 50% are excluded from the calculation. The method used here includes calculation of the time to achieve a major response (Fig. 1[IV]), defined as the point where *f*(*t*) (Equation 1[IV]) begins to flatten toward its upper asymptote, *i.e.* when major change is fulfilled. This can be done regardless of the extent of both initial germination and later responses, thus, achieved germination does not limit the calculation of response time as long there the results are not exactly the same on each test occasion.

Following the calculations of final response and response time, an average and standard deviation (SD) per species were calculated. For the response time, both average and SD were weighted in relation to the magnitude of response (Equations 3[IV], 4[IV]). This was done so that the time to change from, for example, 1% when fresh to 10% final germination was regarded as less important than an analogous change from 1% to 100%. By this method, the dormancy pattern, which is now measured on continuous scales, can be plotted and visualized (Fig. 4[IV]). The dispersal bars shown are not intended as tools for statistical comparisons, but as a way to illustrate the variation in data, that include a number of test environments (Fig. 2[IV]). The resulting pictures (Fig. 4[IV]) show overall responses, compared to fresh seeds, to the tested pre-treatments, allowing visual comparisons of how the species responded to different environmental events, and how efficient dormancy reduction in different environment was for any specific species.

To increase the possibility of finding patterns and to achieve a further accurate value of time to final response, I suggest that the seeds used to experiments are rather distributed to more points in time than was done here (where the more or less conventional method of using 100-200 seeds distributed to 3-4 Petri dishes was used). If using 50 seeds to each of ten points over a time period instead of 100 seeds to each of five points over the same time period, the result from each single point in time will be less exact, but the overall response over time will be more well-described. If not using the Petri dishes as replicates, a number of dishes per treatment then function as safety; if one is lost for some reason (seeds overgrown with mould, substrate drying out, the dish crushed) there is still something left. Therefore, the number of dishes per test could be regarded as the insurance requested, and can be determined by space available, kind of seeds (especially size) and total time period of incubation.

In addition to the graphs intended to visualize dormancy pattern, there are also graphs describing germination preferences (Fig. 4[IV]). Average overall germination in light during daytime and in continuous darkness at the four temperature regimes used were calculated as the fraction of germination in the environment giving most germination per species. This allows comparisons of general germination preferences for the different species, neutralizing differences between species depending on general differences in eagerness to germinate.

4.4. COMPARISONS OF SEED DORMANCY AND GERMINATION

4.4.1. DORMANCY PATTERN

All species increased germination in response to one or more environmental event, and therefore, I regard all species as having some kind of seed dormancy pattern.

For *Papaver,* the dormancy pattern was similar for all included species; warm stratification reduced dormancy. Because of substantial germination, in suitable environments, for *Papaver aculeatum* when fresh, that response was mainly manifested when tested in darkness, but also at the lowest temperature, for this species (Fig. 1[II]). For the *Papaver* collected in Sweden (Table 1), the germination response following warm periods was distinct in the warm climate (Fig. 3[I]). However, despite the degree of dormancy being reduced during a warm period, germination also occurred during spring in annual cycles, both when subjected to light during daytime all year (Figs 3[I], 3[II]) and, more pronouncedly, when transferred from continuous darkness to light during daytime simultaneous with the start of spring (Fig. 7). Thus, even though cold stratification *per se* does not reduce the degree of dormancy of *Papaver aculeatum* (Fig. 1[II]), *Papaver rhoeas* (Baskin *et al.* 2002) or *Papaver argemone* and the two *Papaver dubium* subspecies (ongoing study; data not shown), germination can occur after a cold period when subjected to annual temperature changes.

When *Papaver rhoeas* is subjected to burial in soil outdoors and regularly tested for germination in a controlled environment with light during daytime, it shows an increased degree of dormancy in the middle of the winter, both in Sweden (Milberg & Andersson 1997) and in Spain (Cirujeda *et al.* 2006). These results show that there is a dormancy cycle, with induction of dormancy during cold periods. However, the results also indicate that induction of dormancy during a winter period, which follows a warm period that has previously reduced dormancy, does not lead to such a high degree of dormancy as fresh seeds had; this conclusion is supported by results from Baskin *et al.* (2002). In the artificial annual cycles used here, with light during daytime all year, germination in autumn, and a little in winter and early spring, was the rule in the warm climate (Fig. 3[I]). This is probably a result of reduction of dormancy during summer, and suitable temperatures during sufficient times, for germination during autumn. The germination in spring in the intermediate and cold climate may be explained by seeds being on the way to germinate before winter, but the actual germination being postponed until suitable temperatures, or sufficient temperature sum, occurred in spring. Thus, dormancy patterns direct these *Papaver* towards a mainly winter annual behaviour in warmer climates, and substantially a summer annual one in colder climates when seeds are not buried after dispersal (Figs 3[I], 3[II]). However, if transference from being buried to being exposed at a soil's surface occurs, spring germination is highly possible also in warm climates (Fig. 7).

The dormancy pattern for *Lamium* was similar for the four species investigated, and also similar to *Papaver:* degree of dormancy was reduced during warm periods (Fig. 4[III]). The *Lamium* species reduced dormancy even more during dry storage than during warm stratification, which led to more overall germination, germination at lower temperatures, and germination in darkness, which did not occur after stratification (Fig. 4 [III]). When *Lamium* was sown outdoors, germination occurred both in autumn and spring (Fig. 1[III]). Thus, *Lamium*, as well as *Papaver*, can germinate after a cold period, even though cold stratification does not decrease the degree of dormancy (Fig. 4 [III]) but on the contrary increases it (Baskin & Baskin 1984a [*Lamium amplexicaule*], 1984b [*Lamium purpureum*], Milberg & Andersson 1998 [*Lamium hybridum*]). Because dry storage reduced the degree of dormancy more efficiently than warm stratification (Fig. 4 [III]), it is possible that germination in spring may occur in response to dormancy reduction during such winters as 2004/2005 (Fig. 1[III]), *i.e.* when a lack of snow cover and freezing temperatures gave an environment similar to dry storage. As for *Papaver*, it is also possible that spring germination occurs as a result of the germination process being delayed at low temperatures during autumn and winter.

The studied Asteraceae species belong to different genera, and therefore it is not surprising, despite co-occurrence where collected, that there were larger differences between them than within *Papaver* and *Lamium*. None of the Asteraceae had a dormancy pattern similar to the studied *Papaver* and *Lamium*.

Bidens pilosa and *Galinsoga parviflora* responded principally quite similarly: they showed a positive response to all pre-treatments, and responded faster to warm stratification than to the other pre-treatments, but they differed by *Galinsoga parviflora* reducing dormancy much quicker (Fig. 4[IV]). *Guizotia scabra*, *Parthenium hysterophorus* and *Verbesina encelioides* all responded more quickly and more pronouncedly to cold stratification than to other pre-treatments (Fig. 4[IV]). However, there were considerable differences in dormancy patterns among these species: *Guizotia scabra* responded nearly as well to dry storage and warm stratification as to cold stratification, *Parthenium hysterophorus* did not respond to dry storage, and *Verbesina encelioides* did not respond to warm stratification (Fig. 4[IV]). *Tagetes minuta* differed from the other species by only expressing considerable reduction of degree of dormancy when subjected to dry pre-treatment, which was observable only for the treatments in darkness because of the extensive germination in light already when fresh (Fig. 2[IV]). Because five out of six Asteraceae species responded with reduced degree of dormancy to two or three pre-treatments (Fig. 4[IV]), time *per se* is probably as important as specific environmental events for dormancy reduction for these species. In the field, the species had a similar emergence pattern during the season following dispersal (Fig. 5[IV]). Thus, different dormancy patterns do not, for these species, hinder simultaneous germination during certain circumstances.

4.4.2. GERMINATION PREFERENCES

All included species germinated, at least to some extent, when provided with water and a suitable temperature, and light promoted germination for all species. Thus, I conclude that there is no additional special environmental requirement for germination for any of the species.

Germination of all *Papaver* investigated was promoted by light, but was not completely inhibited by continuous darkness (*cf.* Fig. 3[I] and 4[I], Fig. 1[II]). The different species had different temperature preferences. Compared to *Papaver rhoeas* and *Papaver dubium*, *Papaver argemone* and *Papaver aculeatum* preferred lower temperatures for germination, being restricted from germination at 30/20°C regardless of life story until subjected to the high temperature (Figs 1[I], 3[I], 1[II], 3[II]). The temperature preferences were important for directing germination timing during autumn in more detail than achieved solely by dormancy pattern. For *Papaver aculeatum*, germination of seeds with starting point in summer was delayed until early autumn in the warm climate because of germination being inhibited at 30/20°C, but occurred immediately after onset of incubation in the intermediate and cold climates (Fig. 3[II]). For *Papaver argemone*, germination during the autumn of each year occurred later than for the other species in the warm climate (Fig. 3[I]), also when subjected to transference from continuous darkness to light during daytime at the end of summer (Fig. 7), because *Papaver rhoeas* and *Papaver dubium* accepted higher temperatures for germination (Fig. 1[I]).

All four *Lamium* species preferred the highest temperatures tested, 25/15 and 30/20°C, for germination, and light during daytime strongly favoured germination (Fig. 4[III]). After dry storage, the most efficient environment tested for reduction of degree of dormancy, all species germinated to some extent also at 15/5°C, and in darkness at all temperatures, but germination was always favoured by the higher temperatures and light (Fig. 4[III]). The reluctance to germinate at low temperatures is important for not allowing germination too late in autumn (Fig. 1[III]); directing, at least a part of, the seeds that have reduced dormancy during summer to spring germination.

In addition to different dormancy patterns, germination preferences differed between species. *Bidens pilosa* and *Galinsoga parviflora* preferred the highest temperatures tested, *Guizotia scabra* and *Parthenium hysterophorus* 25/15°C, *Verbesina encelioides* the lower temperatures and *Tagetes minuta* had no clear temperature preference within the studied range (Fig. 2[IV]). The difference in germination preferences may lead to difference in emergence timing in temperate climates. For example, all species germinated considerably after a cold stratification period of 20 weeks (winter), but because of differences in temperature preferences, *Galinsoga parviflora*, *Tagetes minuta* and *Verbesina encelioides* would germinate early in spring (they all accept 15/5°C for germination after cold stratification if provided with light, Fig. 2[IV]) while *Bidens pilosa*, *Guizotia scabra* and *Parthenium hysterophorus* would postpone germination until higher temperatures occur later in spring or in early summer.

4.4.3. DORMANCY STRENGTH

Dormancy strength was the characteristic of the three used to describe dormancy and germination that varied most within species. Nevertheless, species and interactions including species were important exploratory factors for germination results (Papers I, III, IV). Thus, despite the large variation within species, there seem to be general differences in dormancy strength for the studied species, also within genera.

Dormancy strength affected the overall response of the different *Papaver*. *Papaver dubium* ssp. *lecoqii* had the strongest dormancy, not reducing dormancy considerably during any incubation temperature (Fig. 1[I]), nor in annual cycles (Fig. 3[I]), nor when subjected to changes between darkness and light during different circumstances (Figs 4, 7). Also *Papaver argemone* had a relatively strong dormancy; even though it responded distinctly to germination after summer periods in the warm climate (Fig. 3[I]), only about 50% germination was achieved during 2.5 years. Even though *Papaver rhoeas* and *Papaver dubium* ssp. *dubium* germinated at similar temperatures (Fig. 1[I]) and achieved nearly full germination after three autumns in the warm climate (Fig. 3[I]), the species differed in dormancy strength. *Papaver dubium* ssp. *dubium* had its peak in germination during the second autumn while *Papaver rhoeas* germinated about equally in the first and the second autumns (Fig. 3[I]). Thus, *Papaver rhoeas* had weaker dormancy than the other species collected in Sweden (Table 1). *Papaver aculeatum* had much weaker dormancy than the other included *Papaver*. This resulted in nearly full germination within 30 days in annual cycles when provided with suitable temperature regime from onset of experiments (Fig. 3[II]). *Papaver aculeatum* also easily reduced the degree of dormancy during warm stratification after having increased it during cold stratification (Fig. 2[II]).

For the *Lamium* species, dormancy strength constituted the largest difference between species: *Lamium amplexicaule* had the strongest, with degree of dormancy only slightly reduced during warm stratification, and substantial germination did not occur until 24 weeks of dry storage for any of the seed batches (Fig. 3[III]). *Lamium hybridum* had the weakest dormancy; fresh seeds of several batches germinated to some extent (Fig. 2[III]) and after dry storage for 12 or 24 weeks, all seed batches germinated to at least 50% in both light and darkness at 25/15°C, which did not occur during any circumstances for the other species (Fig. 3). *Lamium confertum* and *Lamium purpureum* had about the same dormancy strength, responding at the same magnitude to all treatments (Fig. 4[III]). Compared to one population of each *Lamium amplexicaule* and *Lamium purpureum* from Kentucky (Baskin & Baskin 1984a, 1984b), all the *Lamium* collected in Sweden had stronger dormancy. This could be a result of adaptation to environments; both summers and winters are colder in Sweden than in Kentucky, and the strong dormancy may then be an adaptation to partly restrict germination in autumn.

In addition to differences in seed dormancy pattern and germination preferences among the studied Asteraceae species, there were also differences in dormancy strength. *Tagetes minuta* had very weak dormancy, with fresh seed germinating readily in suitable environments (Fig. 6, Taylor *et al.* 2005). *Parthenium hysterophorus* and *Bidens pilosa* had relatively strong dormancy, not reaching full germination and requiring a long time in pre-treatment to achieve full germination, respectively (Fig. 2[IV]). Other studies on *Bidens pilosa* (Fenner 1980a, 1980b) and *Parthenium hysterophorus* (Pandey & Dubey 1988, Navie *et al.* 1998, Tamado *et al.* 2002) reported more germination than for the batches tested here (Fig. 6). Thus, there seem to be considerable differences in dormancy strength within these species, which could be a result of variations between populations as well as between generations (*cf. Lamium*, Fig. 3[III]). *Galinsoga parviflora* and *Verbesina encelioides* had weak dormancy and responded with nearly full germination after 2.5 weeks in the most favourable pre-treatment, while *Guizotia scabra* needed more time for full response (Fig. 2[IV]). The difference in dormancy strength is probably important in environments without pronounced dry periods; for example, *Tagetes minuta* would germinate directly after seed dispersal in irrigated fields, while the other species studies here would remain ungerminated for different time periods (*cf.* Fig. 6[IV]).

4.5. IMPLICATIONS FOR THE FIELD

4.5.1. GERMINATION STUDIES VS EMERGENCE IN NATURE

Of course, results from germination studies give understanding of germination, not of establishment, nor of reproduction success. The example of *Conyza bonariensis* and *Conyza canadensis* (Fig. 2) suggests that, for *Conyza bonariensis*, it is bad germination timing, resulting from a broad niche for germination (Karlsson & Milberg ms 1), not a lack of suitable germination environments, that restricts distribution to warmer parts of the world. Such a pattern is contradictory to the hypothesis of broader niches leading to larger ranges (Brown 1984). When Thompson & Ceriani (2003) tested that hypothesis from a large number of studies conducted by HA Roberts and co-workers within the UK, they found no relationship between seasonal distribution of emergence and distribution range. As the two *Conyza* indicate, it may, at least in some cases, be the opposite: a broad niche tolerated for germination restricts distribution to a more limited range than a tighter germination niche. Thus, to draw conclusions from experimental germination studies into the field situation includes taking into account the possibility for a seedling to survive at any specific time for germination.

4.5.2. PAPAVER

In this study, *Papaver* germinated outdoors in both autumn and spring (Fig. 5[I]). For *Papaver rhoeas*, emergence outdoors during both the autumn for sowing and the following spring, but not during the consecutive year, has been previously reported in Sweden (Baskin *et al.* 2002). In England, all four *Papaver* studied here emerged during both spring and autumn for five years when mixed with soil that was disturbed three times a year (Roberts & Bodrell 1984a), while McNaughton & Harper (1964) regarded them as summer annuals, and Brenchley & Warington (1930) recorded *Papaver* spp. seedlings mainly in autumns, a little in springs but not during summers, when soil samples were taken three consecutive years, kept moist and subjected to frequent distribution, and kept in near-natural temperatures in a greenhouse for 2.5 years.

The germination pattern with a considerable fraction of *Papaver* emerging in spring (Figs 7, 3[I], Roberts & Boddrell 1984a, Baskin *et al.* 2002) cannot be explained by results from conventional stratification of fresh seeds: no, or nearly no, germination of *Papaver rhoeas* occurred in germination tests after periods of up to 12 weeks at 1°C in darkness, while 50-100% of the same seed batches always germinated both in autumn and spring, at the same test temperatures, after being buried in soil for two or three years (Baskin *et al.* 2002). From the experimental setup with annual cycles one can observe that *Papaver* germinates both autumn and spring even when not subjected to burial in soil followed by transference to soil surface and light, which *per se* is known to promote germination for some species (Scopel *et al.* 1991). However, the observation of the phenomenon with germination after both warm and cold periods is not easily explained. The suggestion above, *i.e.* that dormancy is reduced during warm periods but not equally much induced during cold periods and/or that seeds are initiated to germinate during autumn but because of low temperature the actual germination is postponed until spring, seems to me as the most plausible.

Even though *Papaver aculeatum* is regarded as a weed in South Africa (Bromilow 2001) and Australia (Parsons & Cuthbertson 2001), and has well-timed emergence there, the establishment of *Papaver aculeatum* in colder parts of the world may be restricted. It has weak dormancy and germinates at low temperatures (Fig. 3[II]), and may therefore germinate too readily late in autumns after dispersal, and may not be able to survive the winter as a seedling. If not germinating, for example after burial, cold periods increase dormancy (Fig. 2[II]) and 20/10°C is too low for dormancy reduction (Fig. 3[II]). Thus, dispersal and germination after a first year with spring-sown seeds could lead to a lack of germination analogous to the situation for autumn-started Fouriesbourg seeds in the cold climate (Fig. 3[II]). Realistically, there is little possibility for early summer dispersal in a cold climate (even if autumn-germinated seedlings survive winter, spring is short), thus, the summer-started seeds in the cold climate should not be treated as a realistic model for established populations. However, if seeds are spread to the warmer parts of the Americas, Europe and Asia, germination ecology *per se* should probably not limit the distribution of *Papaver aculeatum*. A parallel case is *Papaver rhoeas* which has spread from its origin at the east coast of the Mediterranean (Kadereit 1990) to become regarded as a weed in several, not too cold, parts of the world (Holm *et al.* 1997).

4.5.3. LAMIUM

When *Lamium* seeds were sown on top of soil outdoors in Sweden, the largest fraction germinated in autumns (Fig. 1[III]). Even though the four *Lamium* species studied, that are the only annual *Lamium* present in the wild in Sweden (Krok *et al.* 2001), are regarded as weeds in the area used for this study (Kindberg 1880, Genberg 1992), autumn emergence seem not to be a performance suitable for the environment, with *Lamium purpureum* partly being an exception. Plants of different ages of *Lamium amplexicaule*, *Lamium confertum* and *Lamium hybridum* that were present during autumn at the cultivation sites died during the winters when observed: these winters were quite different when considering temperature and protecting snow cover. Seeds from plants that germinated in summer or early autumn and flowered in autumn were not ripe before winter. Thus, the possibility for successful reproduction is low for autumn-germinated plants of these three species. *Lamium purpureum* survived winter better, yet far from completely, and could therefore grow, flower and disperse earlier in spring and summer than the other (Paper III). However, *Lamium purpureum* also failed to produce ripe seeds from the plants that flowered during autumn. Thus, autumn germination in Sweden is a drawback also for this species.

The autumn germination of *Lamium* is a logical result of dormancy reduction during warm periods (Fig. 4[III]), while the results imply that other factors are important to take into consideration to understand the more favourable spring germination. Germination in spring may occur in response to dormancy reduction during such winters as that of 2004/2005 (Fig. 1[III]), *i.e.* similar to dry storage. In England, both *Lamium amplexicaule* and *Lamium purpureum*, collected in three different years, germinated in both spring and autumn during all three years they were observed when mixed with soil that was disturbed three times a year (Roberts & Boddrell 1983). Another explanation for spring emergence is germination requirements: if temperatures are too low during autumn and winter, there will be a delay of germination until spring. That explanation presupposes that dormancy is not induced during winter, which is known to occur during cold stratification

(Baskin & Baskin 1984a [*Lamium amplexicaule*], 1984b [*Lamium purpureum*], Milberg & Andersson 1998 [*Lamium hybridum*]). Dormancy is probably not induced during cold periods when seeds are too dry, as may be achieved by freezing. On the contrary, such winters as 2005/2006 that, because of snow cover, provide an environment similar to cold stratification at soil surface (Fig. 1[III]), would be well suited for inducing dormancy in *Lamium*.

Annual *Lamium* species have been shown to be able to survive in the soil for long periods. Ødum (1965) used archeologically dated soil samples from Denmark and Sweden and found *Lamium amplexicaule* and *Lamium purpureum* that germinated after circa 450 and 650 years, respectively, and reported evidence, based on germination in excavation sites, of *Lamium hybridum* germinating after at least 160 years in soil. When a mowed lawn was established covering a natural weed seed flora on former arable soil in Oxford, emergence of *Lamium amplexicaule* varied between soil samples taken over years, but did not decline substantially over 20 years (Chancellor 1986). Further, each plant can produce a large number of seeds (*e.g.* Holm *et al.* 1997). Germination of fresh seeds in the field is low (Fig. 1[III]) because of a high degree of dormancy (Fig. 2[III]) that is not easily reduced (Fig. 4[III]). Further, germination preferences do not allow germination at so low a temperature as 15/5°C or in darkness at any temperature if not first subjected to a dry period (Fig. 4[III]). Thus, germination is restricted to a limited part of each cohort during limited periods of each year, even if seeds are not buried in soil where germination is prevented because of lack of light. This explains how soil seed banks of the four *Lamium* investigated here are easily formed, persist over long periods of time, and are not easily reduced even by soil cultivation in the Swedish climate.

4.5.4. ASTERACEAE

The weather during the study period in Ethiopia (Fig. 5[IV]) was normal for that time of the year; thus, seeds dispersed in autumns are normally subjected to a relatively long dry period before being imbibed for a number of consecutive days. Most emergence in pots occurred soon after the first rains in February (Fig. 5[IV]), similar to the germination after 12 weeks of storage before the onset of incubation (Fig. 6[IV]). In the field, there was a second peak of emergence in late March to early April (Fig. 5[IV]). From comparisons of continuous incubation with incubation interrupted by dry periods (Fig. 6[IV]), the extent of field emergence seems to be more an effect of time than of the actual dry periods *per se*. Thus, dry periods may only marginally affect total emergence as long as seeds are lying on the soil surface, but, of course; dry periods are important for emergence timing. In the field, emergence in irrigated fields and in fields subjected to dry periods is therefore probably about the same according to the amount of seedlings, but more extended in time when continuously irrigated (Fig. 6[IV]). Because of germination being favoured by light for all species, soil disturbance will affect emergence by burying seeds, *i.e.* preventing germination, or by bringing seeds to soil surface, *i.e.* favouring germination.

The emergence timing in the field can be explained by dormancy reduction, expressed as increased germination in light, during a dry period for *Bidens pilosa*, *Galinsoga parviflora*, *Guizotia scabra* and *Verbesina encelioides*, even though a dry period was not the most efficient environmental circumstance for dormancy reduction for any of them (Fig. 4[IV]). For *Tagetes minuta,* the emergence pattern was a result of germination readily occurring in light at the studied temperatures when imbibed, and for *Parthenium hysterophorus* it was mostly a matter of time from first imbibition (Fig. 6[IV]), similar to *Parthenium hysterophorus* collected in Australia when sown outdoors (Navie *et al.* 1998), even though that seed batch germinated more readily overall than the two investigated here. Thus, co-occurrence, and simultaneous emergence, in environments similar to the studied, for the six investigated species is achieved despite different dormancy patterns (Figs 4[IV], 5[IV]).

All Asteraceae except *Guizotia scabra* are considered serious or principal weeds in several countries in warmer parts of the world (Holm *et al.* 1979, Bromilow 2001, Parsons & Cuthbertson 2001), but only *Galinsoga parviflora* is established in the cooler temperate climate in northern Europe (Rothmaler *et al.* 2000, Krok *et al.* 2001, Lid & Lid 2005). For *Galinsoga parviflora*, the kind of emergence pattern in Kentucky (Baskin & Baskin 1981b) is similar to the one described for *Conyza canadensis* (Fig. 2), that is, that the most important factor to direct germination toward spring for the species in cooler climates is germination being favoured by higher temperatures (Fig. 2[IV]), thus preventing germination in autumn, and allowing the species to over-winter as seeds. This species, probably originating from mountainous areas in Central America (Canne 1977), achieves proper germination timing in various climates (Fig. 5[IV], Baskin & Baskin 1981b).

Tagetes minuta and *Verbesina encelioides* are reported as very rare occasional species in the cold temperate climate in Norway (Lid & Lid 2005), showing that there are at least some dispersal events to that area. It is possible that the establishment of these species in colder climates is obstructed because similar problems as hypothesized for *Conyza bonariensis* (Fig. 2); that is, not being adapted to winter survival as seedlings and not restricting germination during autumn. However, I suspect that species performing as *Parthenium hysterophorus* and *Bidens pilosa* could be able to establish in colder climates without any further adaptation. Because of a relatively strong dormancy, a dormancy pattern with reduction in response to cold periods (4[IV]) and restricted germination at lower temperatures (Fig. 2[IV]), a substantial part of a cohort from an initial successful plant could over-winter as seeds, reduce the degree of dormancy during winter, germinate in early summer, disperse in autumn but not germinate at the prevailing low temperatures, and then over-winter again as seeds.

4.6. REFLECTIONS ON EVOLUTION

Sometimes differences within species can be correlated to local circumstances, thus probably being local adapted ecotypes (*e.g.* Probert *et al.* 1985, Skordilis & Thanos 1995, Meyer & Allen 1999, Ramakrishnan *et al.* 2004) but sometimes the differences between populations are rather unexplained variations (*e.g.* Schütz & Milberg 1997, Andersson & Milberg 1998, Cirujeda *et al.* 2006, Pezzani & Montaña 2006). Thus, some caution is appropriate when drawing conclusions about whether a performance is a result of local adaptations or not; just because a seed batch shows a dormancy and germination pattern that suit where it grows does not imply that it has adapted to that site, as concluded El-Keblawy & Al-Ansari (2000) about *Portulaca oleracea* from three countries. An example of differences between batches that could easily be explained by local adaptation, if not taking lack of replication into account, is *Papaver aculeatum*.

The two populations used for collection of *Papaver aculeatum* were the farthest apart (about 850 km north-south) used for one species for these studies, and even though the general impression of the two sites was similar at the moment of collection, there are differences in location (Roundvlei at circa 100 m a.s.l. and relatively close to the coast, Fouriesbourg circa 2000 m a.s.l. and in the inland), and the two sites differ by Fouriesbourg having colder winters. When stratified in coldness, the Fouriesbourg seed batch induced dormancy more pronouncedly than the Roundvlei seed batch (Fig. 1[II]). In the annual cycles, that difference between batches was clearly observable in the cold climate with autumn start for the experiment: few seeds germinated during the first autumn, while Roundvlei, but not Fouriesbourg, seeds germinated to a high extent the following spring and summer (Fig. 3[II]). The Fouriesbourg population may, because of the cold winter, have had a stronger impetus to restrict germination during periods with warmer weather during winters; thus being evolutionarily favoured by more completely, than the Roundvlei population, restricting germination after the yearly onset of winter coldness. However, one seed batch from each of the two sites is too little to use as a basis for inferring local adaptations; the difference observed could as well be a result of unexplained variation between populations and/or generations.

In addition to the difficulty of comparisons *per se*, there are also difficulties in determining if a particular characteristic is an adaptation to the site or merely a phylogenetically conservative one. The way suggested here to describe seed dormancy and germination characteristics, by not using discrete groups or morphology, may help in determining what ecologically important characteristics are meaningful to study in an evolutionary perspective. Evaluations of how and how much theses characteristics differ between closely related co-occurring species, such as the *Papaver* and *Lamium* studied, may give a conceptual model for interpreting degrees of evolutionary conservatism.

It seems like the general dormancy pattern is a conservative characteristic for the co-occurring *Papaver* studied here; the degree of dormancy was reduced during warm periods. Germination preferences have probably been adjusted when or after new taxa evolved; *Papaver argemone* was the only one to not germinate at the highest temperature. Thus, germination preferences seem to be less conservative than the general dormancy pattern. Dormancy strength, highly variable between seed batches, but also species-specific (Fig. 3[I]), seems to be the most easily changeable character involved in germination.

Papaver aculeatum belongs to the same clade as, for example, *Papaver rhoeas* but has no documented close relative (Carolan *et al.* 2006), being the only species of *Papaver* sect. *Horrida* (Kadereit *et al.* 1997). The four *Papaver* collected in Sweden have probably evolved in the Mediterranean region (Kadereit 1990), while *Papaver aculeatum* originates from southern Africa (Kadereit 1988). *Papaver aculeatum* demonstrated principally the same dormancy pattern as the four other *Papaver* species, *i.e.* dormancy reduction during warm periods (*cf.* Fig. 3[I] and Fig. 3[II]). The germination preferences of *Papaver aculeatum* was more similar to *Papaver argemone*, *i.e.* germination was restricted at high temperature, than to the closer relative *Papaver rhoeas*, thus again suggesting that germination preferences is a more easily changeable characteristic than dormancy pattern. The dormancy strength of *Papaver aculeatum* was much weaker than for the other *Papaver*, thus; not reflecting that *Papaver aculeatum* is closer related to *Papaver rhoeas* and *Papaver dubium* than are *Papaver argemone* to any of the other included *Papaver* (Carolan *et al.* 2006).

One *Papaver* species, *Papaver somniferum*, a close relative to *Papaver rhoeas* and *Papaver dubium* (Kadereit *et al.* 1997, Carolan *et al.* 2006), has been reported to have weak dormancy without a requirement for a warm period before germination (Bare *et al.* 1978, Grime *et al.* 1981). These results may depend on the fact that *Papaver somniferum* ssp. *somniferum*, which has been cultivated since ancient times, has lost its dormancy because of selection by man. Bare *et al.* (1978) described their study object as a "cultivated plant", and only *Papaver somniferum* ssp. *somniferum*, the cultivated type, are known to occur outside the Mediterranean region in Europe (Tutin *et al.* 1964, Kadereit 1986). Therefore, the population at Sheffield (Grime *et al.*, 1981) was probably naturalized *Papaver somniferum* ssp. *somniferum*, not the wild type *Papaver somniferum* ssp. *setigetum*.

The four *Lamium* had similar dormancy pattern; reduction during warm periods, and more pronounced, during dry periods (Fig. 3[III]). Also the germination preferences were similar, with most germination at the highest temperatures tested and germination in darkness only after dry storage (Fig. 4[III]). Another Lamiaceae, *Galeopsis speciosa*, that occurs in the same environment as, and sometimes co-occurs with, the *Lamium* studied here decreases its degree of dormancy during cold stratification, but not during warm stratification or dry storage, and germinates at low temperatures (Karlsson *et al.* 2006). Also two other Lamiaceae, not co-occurring with the studied *Lamium* but occurring in cold temperate climates, decrease dormancy during cold periods (*Collinsonia canadensis* [Albrecht & McCarthy 2006], *Lycopus europaeus* [Brändel 2006]). Thus, within the Lamiaceae family different dormancy patterns and germination preferences occur.

Despite being the closest related of the *Lamium* included here (Mennema 1989), there were large differences in dormancy strength between *Lamium hybridum* and *Lamium purpureum* (Fig. 4). Thus, for the *Lamium* studied it seems like dormancy pattern and germination preferences are more evolutionarily conservative than dormancy strength, analogous to *Papaver*.

The studied Asteraceae are far from as closely related as the included *Papaver* and *Lamium*. Considering the relatively small seasonal temperature differences in the study area and in the areas of origin for the species, it is noteworthy that five of six species from different genera clearly responded to cold pre-treatment (Fig. 4[IV]). That could be explained by dormancy pattern being an evolutionarily conservative characteristic; the response could remain from before development of the actual species, from hypothetical ancestral populations at high altitude or latitude where dormancy reduction during cold periods was favourable. Alternatively, the response could be a result of evolution of a seed dormancy pattern with distribution of germination of each cohort over time regardless of current environment, thus, dormancy reduction during a cold period may have been a response neither useful, nor harmful, during the evolution of the present species.

Together, these result leads to the hypothesis that dormancy pattern is an evolutionarily conservative characteristic, dormancy strength is relatively easily changed and germination preferences is intermediate. If correct, dormancy pattern hardly changes even if that should lead to a more appropriate germination timing, as if the *Lamium* in Sweden switched to reduce degree of dormancy during cold, instead of warm periods, which should lead to a more easily-achieved spring germination. Instead, it seems like increasing of dormancy strength, an easily-changed characteristic, may partly function as a method for directing towards spring germination for the Swedish *Lamium*. The characteristic with hypothesized intermediate evolutionary conservatism, germination preferences, interact with dormancy strength to reduce the possibility for autumn germination, by partly restricting germination at low temperatures (Fig. 4[III]).

4.7. CONCLUSIONS

General seed dormancy and germination performances may, in an ecological perspective, be described by dormancy pattern, germination preference and dormancy strength. These characteristics are supposed to be mutually independent seed characteristics, and each is regarded as continuous, allowing comparisons also for species with similar responses. For two groups of species from different genera, *Lamium* and *Papaver*, the general dormancy pattern was relatively similar: dormancy was reduced during warm periods. The characteristic germination preference, as temperature range accepted for germination, was genus-specific with *Lamium* preferring higher temperatures than *Papaver*, but there were also smaller-scale species-specific differences within the genera. Dormancy strength was to some extent species-specific, but highly variable. Comparisons of one group of co-occurring Asteraceae species of different genera showed differences in dormancy pattern. Such differences can be visualized and evaluated by plotting response time and achieved germination in two-dimensional graphs, giving species-specific pictures.

Dormancy pattern and germination preferences explained how *Papaver* can perform as winter annuals in warmer climates, but mainly as summer annuals in colder climates, without local adaptations. For *Lamium*, the results indicate a local adaptation of increasing dormancy strength: in the relatively cold climate in Sweden, a strong dormancy restricted a part of each cohort from germinating during autumn, thus preventing winter mortality. For the Asteraceae, five of six species clearly responded to cold pre-treatment, which is noteworthy considering the small seasonal temperature differences in the study area and in the areas of origin for the species. The six Asteraceae achieved similar emergence timing in the field by responding to different environmental factors. Together, the results from the included fifteen species indicate that dormancy pattern is an evolutionarily conservative characteristic, dormancy strength is relatively easily changed, and germination preference is intermediate.

ACKNOWLEDGEMENTS

I am most thankful to my supervisor Professor Per Milberg for always encouraging me, for being courageous enough to not suppress my ideas, and for all the fruitful discussions leading to new questions and experiments. I am also very thankful to Professor Emeritus Jan Landin for all the discussions about ecology, science and principles. A number of people have given me (in various mixes[!]) friendship, inspiration, practical assistance and help to endure at IFM biology: Abdulrazak Abdulahi, Alireza Taab, Almaz Alemu and co-workers, Anna Eklöf, Anneli Pedersen Brandt, Annelie Andersson, Åsa Jönsson, Birgitta and Tord Björk, Bo Ebenman, Carina Sundberg, Carol and Jerry Baskin, Christina Lindqvist, Daniel Karlsson, Daniel Wondimu, Elisabeth Lundkvist, Ewa Sandberg, Frida Lögdberg, Gizela Maluszynska, Gunilla Sjunnesson, Hristina Bojcevska, Håkan Lättman, Ilse Rasmussen, Ingevald Abrahamsson, Ingrid Johansson, Jennie Håkansson, Jenny Stendahl, Johan Bergstedt, John Dickie, Karin Tonderski, Ken Thompson, Kerstin Johansson, Kerstin Nyström, Kjell Carlsson, Lars Andersson, Lars Eldefors, Lars Höglund, Lisa Thorén, Lotta Borrvall, Maria Christianou, Mekonnen Takaro, Per Arne Björklid, Peter Reneby, Robin Probert, Roger Malmberg, Rolf Karlsson, Ronny

Lock, Sofia Bastviken, Stefan Kokalj, Susanne Andersson, Tamado Tana & Tomas Östholm. The staff at the Linköping University library has been great in finding the literature I have searched for, the IFM computer group have provided support whenever needed and David Lawrence has indefatigably corrected my written language. Finally, I like to thank my mother Inger and father Arne for always supporting me and put up with me when I have been hopelessly asocial and spent all my time with my seeds. Funding was provided by Formas (The Swedish Research Council for Environment, Agricultural and Spatial Planning).

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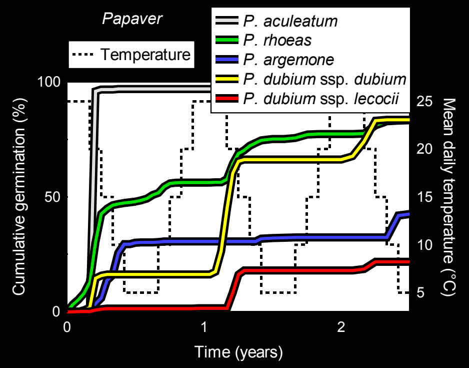

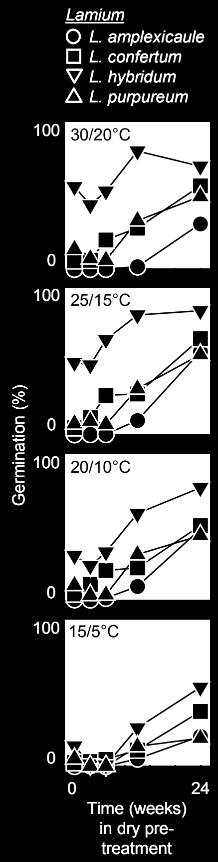

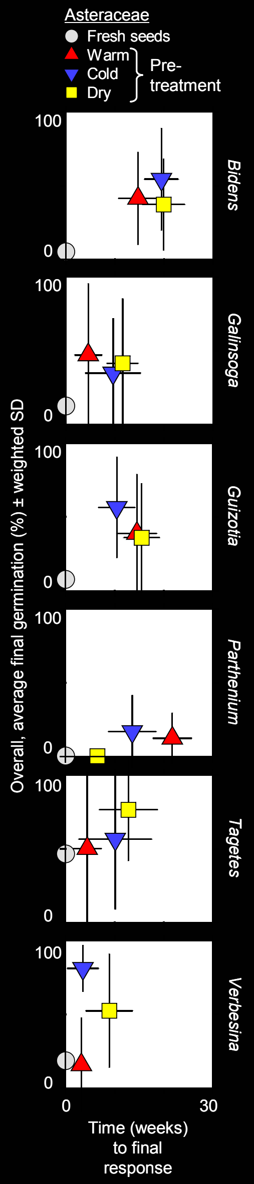

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Linköping University
INSTITUTE OF TECHNOLOGY

Linköping Studies in Science and Technology
Dissertation No. 1088
Linköping University
Department of Physics, Chemistry and Biology
Division of Ecology

Linköping, Sweden, 2007
Printed by LiU-Tryck, Linköping 2007