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Dormancy in Reproductive Vegetative Buds in Creeping Perennials Dominating the Agricultural Weed Flora in Scandinavia

Josefine Liew
Faculty of Natural Resources and Agricultural Sciences
Department of Crop Production Ecology
Uppsala

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Abstract

Dormancy, which is the inability to initiate normal growth under otherwise favourable conditions, is an adaptation to escape sprouting prior to seasonal cold temperatures and/or drought in areas where winters are harsh or summers dry. Dormancy in woody perennials of northern temperate areas is, in general, induced by photoperiodic and/or temperature changes, and released after prolonged exposure to chilling. Besides being species specific, northern ecotypes are usually more sensitive to inductive signals than are southern ecotypes (in cold temperate areas). Dormancy in perennial weeds has been little studied, but might influence the effect of weed control measures. These often involve repeated fragmentation of the roots or rhizomes to stimulate re-sprouting, thus reducing the storage of nutrient reserves. Such measures would be a waste of energy and time if conducted during a period of dormancy. Furthermore, herbicide applications might be less efficient, since there is no or little transport to reproductive organs.

In this thesis, the autumnal growth pattern of five perennial weeds, which all propagate vegetatively from underground adventitious or axillary buds, has been studied. In an outdoor pot experiment, emergence from defoliated plants with undisturbed underground systems was followed at two weeks intervals from late July to late January/April, for 2 years. During the second year, sprouting capacity from root and rhizome fragments was also tested. Emergence was impaired in *Cirsium arvense, Equisetum arvense, Sonchus arvensis* and *Tussilago farfara* during a period in September-October. This seasonality was, however, not preserved in *C. arvense* root buds after fragmentation of the root system. Fragmented rhizomes of *Elytrigia repens*, originating from southern Sweden, sprouted less readily in September-October. The shoot-to-rhizome ratio of this species was lowest during the same period.

A climate chamber experiment suggested a photoperiodic control of sprouting from fragments of *S. arvensis*, with least sprouting in short photoperiods (12 h of light) combined with high temperature. None of the 12 combinations of photoperiods and temperatures used induced dormancy in *C. arvense.* In neither of the experiments could timing of dormancy onset be attributed to the latitudinal origin of the plants.

Keywords: dormancy, root bud, vegetative reproduction, weed biology, organic agriculture, perennial weed, weed control

Author's address: Josefine Liew, SLU, Department of Crop Production Ecology,
P.O. Box 7043, SE-750 07 Uppsala, Sweden
E-mail: josefine.liew@ slu.se

Dedication

To my grandfather, Bertil Ekander (1923-2005) for awakening my curiosity and interest in the unknown

”Allting går, bara man vill…”
”Det är alltid för tidigt att ge upp”

Contents

List of Publications

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

I Andersson L, Boström U, Forkman J, Hakman I, Liew J & Magnuski E. Sprouting capacity from intact root systems of *Cirsium arvense* and *Sonchus arvensis* decreases in autumn. *Weed Research* (in press).

II Boström U, Andersson L, Forkman J, Hakman I, Liew J & Magnuski E. Seasonal variation in sprouting capacity from intact rhizome systems of three perennial weeds (submitted manuscript).

III Liew J, Andersson L, Boström U, Forkman J, Hakman I & Magnuski E (2012). Influence of photoperiod and temperature on sprouting capacity of *Cirsium arvense* and *Sonchus arvensis* root buds. *Weed Research* 52(5), 449-457.

IV Liew J, Andersson L, Boström U, Forkman J, Hakman I & Magnuski E. Regeneration capacity from roots and rhizomes of five herbaceous perennials as affected by time of fragmentation (submitted manuscript).

Papers I and III are reproduced with the permission of the publisher.

The contribution of Josefine Liew to the papers included in this thesis was as follows:

I Together with the co-authors, planning, design and practical performance of the experiments. Did the statistical analyses (supervised by J. Forkman) and contributed substantially to the manuscript, although did not write the first draft.

II As for paper I.

III As for paper I, but wrote the main part of the paper and was the corresponding author.

IV Came up with the idea of the experiment, planned and designed it together with the co-authors (although I did not contribute much to the implementation due to sick leave during pregnancy followed by parental leave). Did the statistical analyses and wrote the main part of the paper.

Abbreviations and some definitions

GAM	Generalized additive model(s)
GLM	Generalized linear model(s)

Defoliation	The removal of aboveground biomass, including leaves, stems and flowers
Dormancy	A temporary impairment of growth (in the experiments forming the basis for the thesis - a reduction of emergence or sprouting capacity) under favourable/growth permitting conditions. Includes endodormancy and paradormancy, as defined by Lang *et al.* (1987).
Emergence	A shoot, which is visible at the soil surface, is considered as emerged.
Sprouting	Root or rhizome bud, which has grown to at least 0.5 cm in length, measured from where the outer protective parts of the bud split open to reveal the new shoot.

1 Introduction

Timing is critical for successful management of all agriculture and horticulture cropping systems. The right measure taken at the right time can make all the difference between making a profit and a complete failure. Especially in crop production, activities such as sowing, weeding, application of manure and harvests must be perfectly timed in order to obtain the most out of resources, while at the same time, minimizing expenditure in terms of effort and money. From a broader perspective, timing of events is critical to reduce the negative impact of crop production on the environment, and to mitigate climate change.

In organic farming, some of the most common practices to control perennial weeds are repeated stubble cultivation or tillage. Fragmentation of the perennial structures stimulates new sprouts to emerge, and if the treatment is repeated before the compensation point (i.e. when net allocation of energy from photosynthesis equals the energy demand for growth and development) is reached, starves the belowground root or rhizome system of stored nutrients. However, the effect may vary between species and time. There are indications that in some species there exists a period when no sprouting occurs, although the environmental conditions are close to optimal for, or at least allow growth and development. This behaviour has been referred to as *dormancy*, or a *"temporal suspension of any plant structure containing a meristem"* (Lang *et al.*, 1987, p. 373). Control measures designed to induce depletion of nutrients when plants, for physiological reasons, are incapable of growth would be a waste of labour and money. The same applies for application of systemic herbicides if no assimilates are being allocated to roots or rhizomes due to dormancy.

In this thesis, the seasonal patterns of sprouting from five of the worst perennial weeds in Scandinavian agriculture have been explored, and the inducing signals in two of them have been studied more in detail. The increased knowledge gained from the result may contribute to the

recommendations of when to carry out weeding activities, and when to avoid them. After a substantial literature review the experiments forming the basis for the thesis will be reviewed and discussed. Throughout the thesis, the term *dormancy* is used to describe an impairment of visible growth under environmental conditions that would otherwise permit normal growth and development in absence of most of the apical dominance.

1.1 The concept of dormancy from a perennial perspective

An often cited review, Vegis (1964, p. 185-186) concludes that "*dormancy is the result of a highly useful adaptation to the environmental conditions which prevail where the species or variety originates… Dormant plant organs have especially high resistance* [to unfavourable external conditions]*, thus growth cessation and the onset of dormancy before the unfavourable season begins, ensures the survival of the plant in question.*" The factors initiating dormancy vary among different species, cultivars and even among different populations, as a result of climatic adaptation to the conditions in their place of origin (e.g. Vegis, 1964; Li *et al*., 2003; Palonen, 2006; Ofir, & Kiegel, 2006; 2007).

In vegetative structures of perennial plants, dormancy is essential for plant survival under harsh conditions, such as the cold of the winter in northern Europe, or the drought of the warm summers in the Mediterranean area (Horvath *et al.*, 2003). Knowing when to grow and when to rest can make the difference between life and death. What dormant structures have in common is the absence of morphological changes (Rodhe & Bhalerao, 2007), although active physiological and molecular activity can be detected even when the depth of dormancy reaches its maximum (Anderson, 2005; Horvath *et al.*, 2006; Rodhe & Bhalerao, 2007; reviews by e.g. Anderson, Chao & Horvath, 2001; Horvath *et al*., 2003; Olsen, 2010; van der Schoot & Rinne, 2011).

Much have been written about dormancy in seeds, perennial trees and "useful" species, such as fruit trees, potted and ornamental plants, but surprisingly little is known about dormancy in vegetative buds of perennial herbaceous plants. Most research so far have been carried out on *Euphorbia esula* L. (leafy spurge, Swedish *Vargtörel*; Raju, Steeves & Coupland, 1964; Anderson, Chao & Horvath, 2001; Horvath *et al.,* 2003; 2006; Anderson *et al*., 2005; Chao *et al.*, 2006) and *Poa bulbosa* L. (bulbous bluegrass, Swedish *Knölgröe*; Ofir & Kiegel 1999; 2006; 2007), while in other species, dormancy or the absence of dormancy during a period of the year has been reported, but no further information about its initiation or release is to be found. It is often difficult to understand what different authors mean with the term *dormancy*. Lang *et al.* (1987) suggest three types of dormancy: (i) paradormancy, the

typical example is apical dominance, (ii) ecodormancy, when the environmental conditions do not permit growth, and (iii) endodormancy, when the control of absence of growth comes from factors within the affected structure. There is, however, no consensus about when to use which of these terms, nor which of them to include in the term dormancy.

1.1.1 Definitions of dormancy in the literature

In order to bring order out of the former chaos in dormancy terminology, Lang *et al.* (1987) suggested defining dormancy as *"a temporary suspension of visible growth of any plant structure containing a meristem"*. Up until then, several different terms were used and misused, many of which were imprecise and consisted of mixtures of physiological and seasonal terms. Neither were they universally applied to plants exhibiting the same type of dormancy. Some of these terms, which can be found in older literature, are listed in Table 1, classified according to type of dormancy as described by Lang *et al.* (1987).

As research developed and became more refined, especially those methods concerning molecular events, some shortcomings with the definition of Lang *et al.* (1987) became evident (Rodhe & Bhalerao, 2007). The terminology proposed is accurate for whole structures, such as buds and cambium of seeds, but is insufficient to describe the molecular activities responsible for transitions into and out of dormancy. There has also been criticism of the terms *visible* and *meristems*. The tiny little meristems are mostly far from visible and almost impossible to study in a non-destructive way (Rodhe & Bhalerao, 2007). Furthermore, *growth* consists of both cell division and cell elongation, events which can occur independently in time and space. Dormancy constitutes an inability to *resume* growth from meristems. However, growth, in terms of cell elongation, can also occur in dormant plants, if the elongating cells are situated away from the meristematic tissues. A better definition of dormancy, according to Rodhe and Bhalerao (2007), is that dormancy is "*the inability to initiate growth from meristems (and other organs and cells with the capacity to resume growth) under favourable conditions"* (p. 217). This definition holds true for dormancy in meristems, but not coat-imposed or physical dormancy in seeds. It includes axillary buds, which are incapable of growth because of apical dominance, but does not cover the type of dormancy classified as ecodormancy by Lang *et al*. (1987).

Despite these initiatives taken toward a universally accepted definition of dormancy, newer literature can still include a confusion of dormancy terms. In papers and books concerning dormancy in perennials, the nomenclature proposed by Lang *et al*. (1987) is most used, while "seed people" use other definitions. In what follows, dormancy refers to a temporary impairment of

growth under favourable conditions, that is, no visible growth when temperature and light conditions are adequate for sprouting and development. This type of dormancy is, thus, a mixture of endodormancy and paradormancy, as these dormancy types are not easily separated from each other.

Table 1. *Dormancy terms found in scientific papers before 1987 sorted according to the categories described by Lang* et al. *(1987). Table modified from the same source.*

Endodormancy	Paradormancy	Ecodormancy
After-ripening	Correlative dormancy	After-rest
Autogenic / autonomic dormancy	Correlative inhibition	Aitogenic dormancy
Constitutional dormancy	Early rest	Aitonomic dormancy
Constitutive dormancy	Predormancy	Conditional dormancy
Deep rest	Preliminary rest	Environmental dormancy
Dormancy (I-II)	Shallow dormancy	Exogenous dormancy
Early dormancy	Summer dormancy	Imposed dormancy
Endogenous dormancy	Temporary dormancy	Post-dormancy
Induced dormancy		Post rest
Innate dormancy		Quiescence
Internal dormancy		Relative dormancy
Intrinsic dormancy		
Late dormancy		
Main/middle rest		
Organic dormancy		
Permanent dormancy		
Physiodormancy		
Physiological dormancy		
Real dormancy		
Rest		
True dormancy		
Winter dormancy/rest		

1.1.2 Three types of dormancy in perennial structures

As already mentioned, Lang *et al.* (1987) divided dormancy into three categories based on the source of the dormancy-initiating signal. When the cause of the restricted growth came from physiological factors *within* the affected structure, we are dealing with *endodormancy*, innate or true dormancy according to older literature. *Paradormancy* is caused by physiological factors synthesized and transported from other structures than those affected, while *ecodormancy* is the result of *environmental conditions* which do not permit

growth. In ecodormancy, the signals are unspecific in their effects on overall plant metabolism, and involve an absence of the basic requirements for growth, such as water, nutrients and sufficient temperature. The typical example of paradormancy is apical dominance, when growth of lateral axillary buds is suppressed by the main shoot.

Vegis (1964) described "true dormancy" (endodormancy according to the nomenclature of Lang *et al.* (1987)) as "*a state in which growth or normal growth cannot be resumed, whatever the external conditions may be"*. He also described three phases of this "true" dormancy. During the first phase, *early rest* or *pre-dormancy*, plants are still able to grow, but only in a narrow range of external conditions. In the second phase, called *main rest* or *middle rest*, the meristems cannot, by any means, initiate normal growth. The *after-rest*, which is the third phase of endodormancy according to Vegis (1964), lasts until the spectrum of environmental factors permitting growth and development is widest, and the plant reaches its maximum growth capacity.

According to Lang *et al.* (1987), the source of the signals that induce endodormancy may be environmentally or endogenously derived. Their common theme is that the perception and reaction occur in the same structure that later becomes dormant.

As pointed out by Rinne and van der Schoot (2004), Lang's classification focuses on the signals responsible for dormancy induction, rather than the actual state of the dormant tissues (the meristems). The system of Lang *et al.* (1987) is thus not as straightforward as it may sound. For example, what are to be regarded as discrete structures? It is especially tricky to separate paradormancy from endodormancy. It is paradormancy if the morphogenic factor inhibiting a bud meristem is produced by the bud scales, but endodormancy if the factor is synthesized in the apex itself. It becomes even more complicated if one tries to study dormancy in living tissues when the only method to evaluate dormancy status is from growth ability (with the binomial response growing or non-growing). In such cases, there is no chance of investigating from where the controlling factor originates. Rinne and van der Schoot (2004) propose that endodormancy is the only state in which the meristems are intrinsically dormant, that is incapable of development and growth under favourable conditions, and suggest this inability is a result of impaired cell-to-cell communication via the symplasm. They describe endodormancy as an end point of a process where individual cells are incapable of communicating with each other. Their model for seasonal dormancy is based on anatomical findings in actively growing and dormant buds, and will be briefly described later.

Volaire and Norton (2006) are also sceptical about the nomenclature of Lang *et al.* (1987). According Lang *et al.* (1987), summer dormancy, which is an adaptive trait of some perennial grass species and populations of forage crops in the Mediterranean climates, is a type of paradormancy. Volaire and Norton (2006) consider it as a type of endogenous (endo-) dormancy when found in perennial species adapted to predictable long and dry summers when these plants are not under drought stress. According to them, there are two types of summer dormancy, *complete* and *incomplete*, based on the reduction of growth, senescence of aerial tissues and grade of desiccation of the surviving tissues. To be classified as complete, growth will have ceased completely for at least four weeks, most mature aerial tissues will have senesced, surviving tissues are partially or totally desiccated and resting organs, such as bulbs or swollen tiller bases may have been formed. Incomplete dormancy includes species in which growth becomes noticeably reduced, part of the aerial tissues senesces, but the leaf bases show no signs of dehydration.

Crabbé and Barnola (1996) view endodormancy in trees as an extreme point, when the seasonal rhythm shifts from periodic to episodic, that is, from relatively short periods of growth arrest to several months of dormancy.

To summarize, dormant vegetative buds can be paradormant, ecodormant or endodormant when no visible growth occurs. These events do not, however, occur separately, and the dormancy status is sometimes not easily defined. Furthermore, buds can simultaneously be controlled by several signals, and especially the endodormant state is progressively established (Horvath *et al.*, 2003).

1.1.3 Site of dormancy

There is no doubt that meristems are considered as the site of dormancy. This does not, however, mean that all meristem-containing structures are capable of establishing dormancy (van der Schoot & Rinne, 2011). As reviewed by Saure (1985) and van der Schoot and Rinne (2011), root meristems do not become dormant, as they can start to grow immediately if the temperature temporarily increases. Rather, growth in roots is suppressed. Cambium can become dormant although it is difficult to examine. According to van der Schoot and Rinne (2011), endodormancy in buds can be easily assessed based on registration of bud break or sprouting tests, something that will be further discussed below.

1.1.4 Methods to study dormancy

Unfortunately, there is no common method to study dormancy in vegetative buds – perhaps as a consequence of the absence of a commonly used nomenclature. In deciduous woody perennials, growth capacity status (i.e. dormancy status, but as dormancy is invisible, one must study something measurable) has been evaluated from isolated cultured buds, excised shoots with or without terminal buds, rooted cuttings and un-rooted shoots (Saure, 1985). The treatment conditions concerning for example temperature and light conditions for identification of dormancy vary between different studies. In general, most studies first seek to induce dormancy in samples by exposing them to various temperature or photoperiodic conditions, after which the samples are transferred to forcing conditions. Then, signs that indicate dormancy, such as bud anatomy, bud burst and shoot elongation, are continuously registered.

In parallel with dormancy acquisition, plants also establish tolerance to low temperatures (Bañuelos *et al*., 2008; van der Schoot & Rinne, 2011). At the time of release from dormancy, freezing tolerance remains high until outdoor temperatures start to rise and de-acclimation occurs. Since dormancy and freezing tolerance overlap, the mechanisms behind these processes can be difficult to separate. According to Erez *et al.* (1998), one way of doing so is to expose the endodormant bud to high temperatures, which causes a loss of hardiness, while keeping the buds dormant, given that the treatment lasts for a long enough time.

Saure (1985) mentions different measures to indicate the end of a dormant period. Examples include (i) when the buds or terminal buds show green coloration or are considerably swollen within two weeks of forcing conditions, (ii) when 50% of the buds on cuttings have green tips or (iii) when four buds on a plant have broken at warm temperatures. However, Saure (1985) means that bud break alone is not a valid determinant to evaluate whether dormancy is complete or terminated. Instead, speed of bud break is a better indicator.

In dormancy studies in trees, it is important to consider the relative position along the twig for the buds examined, since the depth of dormancy as well as the chilling requirement for its release vary between apical/terminal and lateral buds (Crabbé & Barnola, 1996; Junttila, Nilsen & Igeland, 2003). For example, in seedlings of *Betula pendula* and *B. pubescens* the basal buds of the shoots hardly developed any dormancy at all (Junttila, Nilsen & Igeland, 2003). At the same time, the terminal and upper lateral buds were unable to flush.

In perennial weeds, dormancy experiments have been done on intact plants (Ofir & Kiegel, 2006; 2007), defoliated plants with intact (undisturbed) root systems under controlled conditions (Anderson *et al.*, 2005) or fragments from

the underground system of plants grown under natural conditions (Brandsaeter *et al.*, 2010). Dormancy status has commonly been evaluated based on shoot emergence above soil level. Few, if any, studies have been done on one-node or one-bud cuttings, a method suggested by Crabbé and Barnola (1996) to remove influence of other buds when studying dormancy in tree buds.

In recent years, substantial research on gene expression, molecular events and hormone action during endo- and paradormancy has been carried out (see, for example, Anderson, Chao & Horvath, 2001; Horvath *et al.*, 2003; 2006; Anderson *et al.*, 2005; Chao *et al.*, 2006; Rodhe & Bhalerao, 2007; Horvath, 2009; Olsen, 2010; van der Schoot & Rinne, 2011). This is beyond the scope of this thesis, and will thus not be further reviewed.

1.2 Regulation of endodormancy in vegetative buds

The main focus of this thesis is the type of dormancy which persists even though the environmental conditions are optimal for growth, and although apical dominance is removed. Consequently, this section reviews how endodormancy is induced and alleviated in a number of species. Most of the examples are of woody perennials from temperate areas, while information in the literature about endodormancy regulation in herbaceous plants is sparse. Dormancy as a phenomenon seems to be evolutionarily conserved as it occurs in genetically diverse plants, such as deciduous trees, herbaceous species, seeds and tubers (Rinne & van der Shoot, 2004). Thus, it is not unlikely that herbaceous species use the same environmental clues as trees to keep track on the time of the year, for example, the length of the photoperiod and an increase or decrease of temperature. A recent review by Horvath (2009) suggests regulatory similarities between dormancy and flowering involving environmental signals, hormone action and gene expression that cause the transition from vegetative to reproductive growth or from active growth to dormancy. Moreover, there are commonalities between vernalisation and dormancy release. At the molecular level, the circadian clock and light sensing proteins seem to be involved.

1.2.1 Dormancy induction

Woody perennials

In woody perennials, length of the photoperiod and the quality of light – or more specifically, the ratio between red and far red light are the most important determinants controlling shoot elongation and growth cessation, probably mediated by phytochrome (Anderson, Chao & Horvath, 2001; Mølmann *et al.*, 2006; Olsen, 2010). Endodormancy in vegetative buds is commonly induced

when the days become shorter than a critical value which is specific for each species and population. For *Betula pubescens*, this critical photoperiod is approximately 16 hours of light (Rinne, Kaikuranta & van der Schoot, 2001). During the first period of exposure to short days, the transition to dormancy can be reversed if plants are returned to long days, but once established, endodormancy is not easily broken.

In *B. pendula*, sensitivity to photoperiodic changes varies with ecotype, with increased sensitivity (and longer critical photoperiods for dormancy induction; it is the length of the dark period which is perceived by the plants) with increasing latitude of origin (Li *et al*., 2003). Under long-day conditions (24 h of continuous light), a northern ecotype grew faster in height than a southern. When the seedlings were exposed to successively shorter days, the differences gradually decreased. The reduced photoperiods also resulted in dormancy development and cold acclimation of the buds, with an earlier start of the responses in the northern ecotype. Cold acclimation started just before dormancy development and was faster in the northern ecotype. Heide (2003) and Junntila, Nilsen and Igeland (2003) found a similar effect of latitude in *B. pendula* and *B. pubescens,* with a stronger latitudinal trend in the latter species. Heide (2003) used plants originating from different parts of Norway (56-71°N) and Denmark (56°N) grown under natural conditions between 1994 and 2002 in Ås (60°N), Norway. It was obvious that the northern populations had shorter growing periods and shed their leaves earlier than the southern populations (indicating photoperiodic control of dormancy induction). While the northernmost populations shed their leaves in late August to early September, leaf fall of the Danish populations occurred in November. However, bud burst in spring occurred within a few days in all populations.

Heide (2003) also found a strong dependency on temperature during short-day dormancy induction in first season seedlings of *B. pendula*, *B. pubescens* and *Alnus glutinosa* in controlled environmental experiments. High (21°C) temperatures during dormancy induction (10 h photoperiod) followed by subsequent chilling (5°C, 10 h photoperiod) significantly delayed bud burst, compared to plants kept at 9 or 15°C during dormancy induction. The field experiment referred to above suggested that September temperature alone explained 20% of the variation in days to bud burst, the mean temperature for September-October and August-October accounted for 26 and 29% of the variation, respectively, and March-April temperature for only 10% for the two *Betula* species.

In the phytotrone experiment by Junttila, Nilsen and Igeland (2003), dormancy induction developed most rapidly at 15-18°C during a 12 h photoperiod in the same *Betula* species. Both 9-12°C and 21°C delayed

dormancy induction, and increasing temperature from 9 to 21°C significantly increased the chilling requirement for dormancy release.

Another example of a species with photoperiodic control of growth capacity is *Prunus persica* var. *nectariana* (Li *et al.*, 2008). A long day with 16 h of light delayed dormancy induction while 8 h of light enhanced it. Buds of *Populus deltoides* responded by simultaneously acquiring freezing tolerance and developing of dormancy, when day length decreased to 8 h of light (Jian *et al.,* 1997).

Rooting of cuttings from two cultivars of *Cornus alba* taken in late September was improved in long days compared to in natural light (Whalley & Cockshull, 1976). If the cuttings were taken in mid-August, before the seasonal decrease in photoperiod was pronounced, the effect of day length of rooting was small, suggesting a critical day length for dormancy induction between 13 and 15.5 h of light. Exposure to long days throughout the winter was effective in preventing dormancy in the resulting plantlets. Short days (8 h of light) hastened bud dormancy development and leaf senescence. Returning the plants to long day conditions after three months of growth during short days did not break dormancy.

Kühn *et al*. (2009) suggest that the critical photoperiod for dormancy induction in *Vitis vinifera* 'Thompson Seadless' is between 13 and 14 hours of light. At the stage of endodormancy, the phytochromes studied were expressed uniformly, while oscillating with a diurnal rhythm during active growth suggesting photoperiodic control of dormancy in this species.

Seedlings of *Pseudotsuga menziensii* var. *meziesii* acquired endodormancy in October, after at least 3 weeks of exposure to short days, with 8 hours of light, the treatment beginning in July (Macdonald & Owens, 2010). Scanning electron microscopy of the shoot apex revealed that in endodormant apical buds, needles had been formed, but their expansion had ceased. Notably, the longest duration of the short-day treatment – six weeks – reduced root weight and shoot diameter as compared to the 3-, 4- and 5 week treatments. After one year of growth in a common garden experiment, the duration of short-day treatment in the nursery had no effect on seedling performance. In two-year-old plants of another gymnosperm, *Picea glauca*, bud set occurred after ten weeks in short days (8 h of light) at 20°C, and dormancy was attained some weeks later (Kayal *et al*., 2011).

Although photoperiod alone induces dormancy in most trees, there are some important exceptions (Olsen, 2010). Studies by Søgaard *et al.* (2008) and Granhus, Sundheim Fløystad and Søgaard (2009) suggest that high temperature during dormancy induction in short photoperiods results in deeper dormancy and later bud burst in young seedlings of *Picea abies*. By exposing 1- and 2-

year-old seedlings to short day treatments (12 h of daylight) in combination with temperatures of 9, 12, 18 or 21°C, followed by 0, 2, 4 or 6 weeks of chilling, Søgaard *et al.* (2008) showed a significant delay in the time to bud burst with increasing temperature during dormancy induction. The effect was stronger when seedlings were chilled for only 0 or 2 weeks. Under Norwegian conditions, there was also a significant effect of regions, with southern populations being more sensitive to high temperatures during dormancy induction than northern ones.

Hybrid poplar (*Populus tremula x P. alba*) induces dormancy if a short photoperiod is combined with a constant decline in temperature (Rodhe *et al*., 2007). The first sign of dormancy in this species is decreased internode elongation and formation of bud scales. Development of embryonic leaves and leaf primordia continues for a short period before the bud sets, and plants stay in this developmental stage until dormancy is broken in the spring.

In a number of species in the *Rosaceae*-family, acquisition of dormancy is regulated by temperature alone (Palonen, 2006; Sønsteby & Heide, 2008; Olsen, 2010; Heide, 2011). Heide (2011) found that in two cultivars of *Sorbus aucuparia*, growth was maintained at temperatures of 15°C or 20°C during both long (20 h of light) and short (10 h of light) photoperiods. At 9°C combined with the same day-lengths, plants ceased growth. Dormancy was, however, shallow since growth was resumed when the plants were transferred to long day conditions after prolonged periods at 9°C.

In *Rubus idaeus*, Palonen (2006) showed that photoperiod had only a minor effect on all of the six cultivars tested. If tested in the autumn, dormancy was deeper if induced in 9 hours of light compared to 18 hours of light. In the spring trial, dormancy was deeper if a long photoperiod was combined with 4°C, or a short photoperiod with 20°C. Irrespective of season, dormancy was deeper if potted plants were grown at 20°C compared to 4°C. That temperature plays a major role for dormancy induction in biennial-fruiting cultivars of *R. ideaus* has also been shown by Sønsteby & Heide (2008). Growth cessation and floral initiation in the common commercial cultivar 'Glen Ample' were controlled by cool temperatures (≤ 15°C) in combination with short days (<15 h of light). As in *S. aucuparia* (Heide, 2011), growth was maintained at 18°C, also under short day conditions, while plants at 9°C turned endodormant after 5-6 weeks of exposure.

Crabbé and Barnola (1996) suggest that temperature and photoperiod have dual effects on endodormancy, depending on the physiological state of the receptor bud.

Herbaceous plants

Although some kind of dormancy in the autumn has been observed for a number of herbaceous weedy species (Fykse, 1974; 1977; Håkansson, 1969c; Håkansson & Wallgren, 1972; Anderson *et al.*, 2005; Chao *et al*., 2006; Brandsaeter *et al*., 2010), few of them have been studied in depth. One can say that there are two model herbs, about which more information has been gained: *Euphorbia esula* and *Poa bulbosa*.

In *E. esula*, which is abundant and problematic in North America, there are three distinct phases of dormancy (Anderson *et al.*, 2005; Chao *et al*., 2006). Root and crown buds of field-grown, undisturbed plants maintain paradormancy during the active growth of the main shoot, from early spring to late September. In October, when the aerial parts of the plants have senesced or been killed by frost, the buds enter endodormancy, a state which is broken in November to early December. During the winter months, sprouting is constrained by harsh environmental conditions, that is, the buds are in an ecodormant state. Raju, Steeves and Coupland (1964), suggest not only a lower shooting capacity in the autumn, but also in June, when maximum anthesis and flowering occurs. Jia *et al.* (2006) found that gene expression does not differ much between crown and root buds. Thus, the response to environmental signals will probably be the same for both types of buds. Until recently, there was no method to induce dormancy in greenhouse-grown plants. Studies by Foley, Anderson and Horvath (2009) suggest that temperature controls both sprouting and flowering in this species. Decreasing temperatures followed by vernalisation made plants flower competent, while at the same time slowing shoot re-growth.

The perennial geophytic grass *P. bulbosa* grows actively in the mild, rainy winters, and becomes dormant in the dry summers of the Mediterranean area, where this species can be found (Ofir & Kiegel, 1999). Endodormancy in this species is either induced when the length of the photoperiod exceeds 12 h of light (Ofir & Kiegel, 1999) or when the plants are exposed to water stress (Ofir & Kiegel, 2007), although Volaire *et al*. (2009) did not detect any effect of water deficit in this species. Temperature also plays a role. Under long-day conditions, high temperature (27/22°C) accelerated dormancy onset more than did lower temperatures (22/17°C) (Ofir & Kiegel, 1999). Pre-chilling of dormant bulbs at 5°C (Ofir & Kiegel, 1999; 2006), as well as pre-exposure to short days enhanced dormancy initiation in plants grown during long days (Ofir & Kiegel, 1999). Longer periods of pre-exposure to short days decreased the number of long days required to initiate dormancy, but the effect decreased with age of the plants. The effect of pre-chilling at 5°C was smaller if plants were grown at low temperatures, and had no effect at all under short days.

Ofir and Kiegel (2006; 2007) also found that the dormancy response in *P. bulbosa* depends on the plants place of origin. Flowering ecotypes from arid or semi-arid areas entered dormancy earlier than non-flowering semi-arid and mesoic ecotypes (Ofir & Kiegel, 2006). The higher sensitivity to dormancy-inducing signals in arid ecotypes was suggested as being an adaptation, critical for survival in a hot, dry climate (Ofir & Kiegel, 2007).

Dormancy induction and release have also been studied in horticultural plants, such as *Chrysantemum* spp. In *C. morifolium*, internode elongation and flowering were reduced when plants were exposed to cool temperatures after the heat of the summer (Sumitomo *et al*., 2008a). Rosette formation in any herbaceous plant was suggested as being an adaptive response for winter survival, like terminal buds in woody plants (Sumitomo *et al*., 2008b). As leaf expansion continued during winter, although at a reduced speed, the authors suggest that dormancy in Chrysanthemums is quantitative, or a type of semi-dormancy.

1.2.2 Dormancy release

Woody perennials

While the requirements for dormancy induction vary with species and ecotype, at least in winter-dormant species (with a few exceptions), release of dormancy seems to be most dependent on one factor: exposure to low temperature during a longer period of time (Rodhe & Bhalerao, 2007). In most cases, temperatures just above freezing are required, although Rinne *et al*. (1997) have shown short-term freezing to be effective in *Betula pubescens* and *B. pendula*. In fully dormant buds of these species, the amount and speed of bud burst increased by freezing, with a stronger effect the lower the temperature.

In a number of northern deciduous trees, bud burst increased with increased duration of exposure to low temperatures (Heide, 1993a). The temperature and duration requirements vary with species and population, just as dormancy induction does. In a comparative study in Ås, Norway, Heide (1993a) found that *B. pendula* and *B. pubescens* were released from dormancy earlier than *Prunus padus* and *Populus tremula*, and two months earlier than *Alnus incana* and *A. glutinosa*. Long-day conditions reduced the thermal time to bud burst, but could not replace chilling for complete release of dormancy in any of the species. Also in *Corylus avellana*, bud burst occurred earlier in long days. In *Rubus idaeus* and *Sorbus aucuparia*, no such photoperiodic response was evident.

In *B. pubescens*, six weeks of chilling at 2°C was required for endodormant buds to resume growth (Rinne, Kaikuranta & van der Schoot, 2001). In both *B.*

pubescens and *B. pendula* (Heide, 2003; Junttila, Nilsen & Igeland, 2003), and also in *A. glutinosa* (Heide, 2003), high temperatures during dormancy induction increased the chilling requirement for dormancy release (Heide, 2003). In for example *A. glutinosa*, which has the strongest chilling requirement of the three species, bud burst occurred only after 70 and 100 days of chilling, if dormancy induction was done at 15 or 21°C, respectively. Seedlings induced at 9°C burst their buds within 60 days of forcing at 15°C. Together with results from other studies, Heide (2003) suggests that low temperatures have a chilling effect even before dormancy is fully established.

Rodhe *et al*. (2007) suggest that dormancy is gradually released, since experimental plants of *P. tremula x P. alba* alleviated dormancy faster if chilled for longer.

A period of chilling, although not necessarily freezing, is generally accepted as a prerequisite for dormancy release in deciduous fruit trees (Saure, 1985). This chilling requirement varies with species and cultivar, and is thus genetically determined. It also varies with growth stage and differs among individual buds on a particular plant. Flower buds generally have lower chilling requirements than vegetative buds, and terminal buds are released earlier than lateral ones. Interestingly, the chilling requirement for dormancy release is often similar for buds and seeds of the same cultivar, suggesting a similar control mechanism for these different organs (Saure, 1985). The chilling requirement (in terms of hours of exposure to cold temperatures) was reported to be lower for buds on isolated nodes of *R. idaeus* than on intact plants, suggesting increased resistance for the combined effect of para- and endodormancy in dormancy release (Mazzitelli *et al*., 2007). In seedlings of *B. pendula,* Junttila, Nilsen and Igeland (2003) found lateral buds to have smaller chilling requirements for dormancy release than terminal buds.

In *Malus domestica* 'Jonathan', chilling at 2-10°C enhanced bud burst, especially if the low temperature treatment was applied for a long time (Thompson, Jones & Nichols, 1975). Interruption of the cold period by higher temperatures reduced growth.

In the absence of chilling, plants respond with prolonged endodormancy as a consequence of the lack of low temperature for its release (Saure, 1985). When deciduous trees from cold-winter regions are transferred to climates where there is no period of low temperatures, they may show symptoms of, for example, (i) delayed, protracted and weak leafing, (ii) formation of bare, un-branched shoots, (iii) fast declining growth vigour and early senescence, (iv) delayed and protracted flowering due to abnormal flower development and (v) poor fruit development and irregular ripening. Also, high temperatures during the winter prolong dormancy in warm regions. In the tropics, artificial

defoliation has been shown to be effective in breaking dormancy in flower buds, while light seems to have no effect on the release from endodormancy.

The effect of the environment at the time of bud formation has been studied by Sanz-Pérez and Castro-Díez (2010). In seedlings of three Mediterranean *Quercus* species, the timing of bud burst was altered depending on the environmental conditions during the season when the buds were formed. While summer drought advanced bud burst in the two evergreens *Q. ilex* and *Q. coccifera*, moderate or intense shade delayed it. The same applied to the deciduous *Q. faginea*. Furthermore, shade and water stress inhibited budburst in lateral buds, while apical and basal buds were unaffected by the treatments.

As often is the case, there are exceptions from the general rule. Heide (1993b) found dormancy release in *Fagus sylvatica* to depend on both chilling and long days, with little variation in date of bud burst between years and ecotypes collected in Switzerland (47°30'N, 450 m elevation), Poland (49°N, 600 m), Denmark (55°45'N, 10 m) and Norway (58°40'N, 40 m), assessed under natural conditions in Norway. Once the chilling requirement was fulfilled, plants still needed photoperiods >13 h for normal bud burst, and dormancy was released faster in photoperiods >16 h. In the control species, *Carpinus betulus*, there was no similar photoperiodic response. Søgaard *et al.* (2008) found that young seedlings of *Picea abies* did not require chilling to initiate growth, although chilling advanced bud burst. However, as none of the treatments (including low and high temperature during dormancy onset, different period of chilling, different temperatures for forcing conditions and different light regimes) prevented bud burst completely, they suggest that there is no "true" bud dormancy in young seedlings of this gymnosperm.

Granhus, Sundheim Fløystad and Søgaard (2009) found that 21 days of chilling was enough to break dormancy in 1-year-old seedlings of *Picea abies*. Bud burst occurred somewhat earlier in the northernmost populations (from 66°25'), while there was no difference between populations from 60°35' and 58°35'. If a 9-week period of chilling at 0.7°C was interrupted by a 2-week period of warmer temperatures after 49 or more days of chilling, bud burst occurred earlier. A warm period given after 7-35 days of chilling did not affect the days to bud burst as compared to continuously chilled seedlings.

Borchert and Rivera (2001) suggest that endodormancy in tropical stem succulents is broken by increasing photoperiods (>12 h), occurring after the spring equinox. Bud break was highly synchronous in a number of species, and could not be enforced by rainfall. Bud break occurred 6 months earlier in the northern hemisphere compared to the southern, at any time of the year close to the equator, and the between-year variation was minimal. Taken together, this indicates photoperiodic control of bud break in this functional group of trees.

Herbaceous plants

The effects of low temperature for dormancy release in herbaceous plants are similar to those of trees. For example, Anderson *et al.* (2005) suggest that soil temperatures around 0°C or an accumulated duration of temperatures just above 0°C cause root bud dormancy release in *Euphorbia esula*. Chilling at 3°C for 42 days immediately after senescence increased the height of the longest shoot in this species, and also increased the number of stems with flower buds (Harvey & Nowierski, 1988). Furthermore, chilling increased the growth rate, with plants chilled for the longest period (56 days) having the fastest rate of growth. However, 14 days of cold treatment did not break dormancy. Similar results have been obtained for *Sonchus arvensis* (see description of this species below; Håkansson & Wallgren, 1972; Brandsæter *et al.*, 2010).

In *Zingiber mioga*, a rhizomatous perennial crop endemic to Japan (Gracie *et al.*, 2000), dormancy is released faster the longer the period of chilling. Notably, this species does not have chilling as an obligate requirement to break endodormancy, although low temperature treatment reduces the number of days from planting to emergence and the variation in emergence time among individual plants. In *Polygonatum macranthum*, a rhizomatous grass species, 120 days of chilling at 5°C was required to break dormancy in late September, while only 90 days were required in October (Takagi, 2005).

Chilling is also important for growth resumption in other plant parts than buds. In corms of the terrestrial orchid *Calpogon tuberosus*, Kauth, Kane and Vendrame (2011) found longer periods of chilling to be more effective for dormancy release and shoot growth. Expectations of longer chilling periods for corms from northern populations (Michigan, South Carolina) than for southern (Florida) were not supported. Walck *et al*. (2009) suggest that stratification at low temperatures was required to release dormancy in bulbils of *Discorea polystachya*. The bulbils were, like seeds of temperate plants, mostly dormant after dispersal, while released by the coldness of the winter. Interestingly, a linkage between the depths of seed dormancy and rhizome bud dormancy has been found in *Eupatorium rugosum* (Lau & Robinson, 2010). Buds from plants having seeds with a low degree of dormancy, sprouted earlier and produced longer sprouts in spring, compared to those with higher levels of dormancy, suggesting common regulatory influence in all reproductive parts of this species.

1.3 Seasonal cycling and dormancy models

1.3.1 Plant level

In the temperate northern area, very little growth and development occur during the cold, dry winter (Horvath *et al.*, 2003; Rodhe & Bhalerao, 2007; van der Schoot & Rinne, 2011). The seasonal cycling moves from active growth, with absence of bud sprouting caused by apical dominance (paradormancy) during spring and summer, to endodormancy in late summer and autumn, to ecodormancy, when the environmental conditions are outside the limitations permitting growth in winter. During endo- and ecodormancy, winter hardiness is also acquired and lost. Figure 1 shows a schematic sketch of the yearly cycle of a typical deciduous perennial tree, the inducing factors and how dormancy is released.

Anderson *et al.* (2005) found the lowest content of soluble sugars in crown buds of *E. esula* during paradormancy. The amount doubled or tripled during the transition to endodormancy, and increased even more when plants turned endodormant, probably as a result of metabolisation of starch.

There is also the model suggested by Vegis (1964). He suggests a successive narrowing window of growth-permitting conditions during the transition from active growth, to pre-dormancy (during which dormancy onset can be reversed if the plants are returned to non-inductive conditions, such as long days), to endodormancy. Thereafter, the spectrum of growth-permitting temperatures and photoperiods widens, as the chilling requirement is successively fulfilled.

In the Mediterranean area, where scarcity of water is a problem during summer, the cycle is the opposite. Active growth occur during the humid winter, while plants turn endodormant in spring, stay ecodormant during summer, and are released from dormancy in autumn (Volaire & Norton, 2006).

Although there is almost no difference between day lengths at or close to the equator, a number of tropical stem-succulent trees show a clear seasonality in their capacity to grow (Borchert & Rivera, 2001). Bud burst is inhibited during the normally dry period between the winter solstice and the spring equinox, even if leaves are abscised, plants irrigated or abnormal rain showers occur. The natural difference in length of the photoperiod is less than an hour here, but dormancy is nevertheless induced and broken by variations of 30 min or less.

Another conceptual model for bud dormancy has been proposed by Crabbé and Barnola (1996). According to them, the variation in sprouting readiness from spring to autumn is caused by differences in the agents inhibiting meristematic activity in buds of woody perennials. Early in the season, growth

suppression is caused by the apical meristem. Later, the control of growth suppression moves to the leaves, then to the axis tissue close to the affected bud, and subsequently, the source of suppression is found in the meristem of the bud itself; in other words, a move from remote factors (paradormancy) to stable and independent ones (endodormancy). Each bud reacts individually, causing different degrees of dormancy within the same plant. Terminal buds behave somewhat differently. These are the last ones to stop growth and form winter buds. Dormancy is deeper, but is also more readily broken. Unlike other authors (see *dormancy induction*, above), Crabbé and Barnola (1996) suggest that buds enter dormancy without any obvious influence from external factors, for example under constant conditions such as in labs. They also suggest that buds have a "memory", so that endodormancy features are influenced by the circumstances the buds were exposed to the previous season, such as temperature, location within the tree, or first or second growth flush.

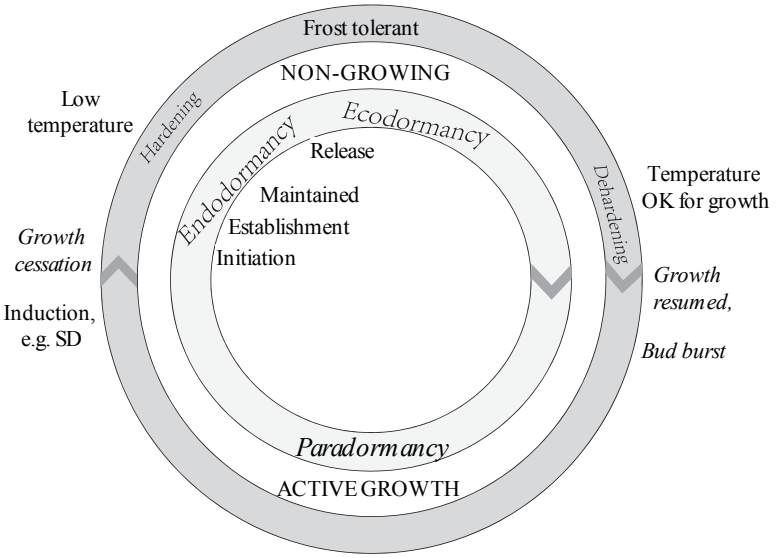

Figure 1. Seasonal dormancy cycling in a typical deciduous tree from a northern temperate climate. The inner circle shows type of dormancy, as defined by Lang *et al.* (1987), the outer the tolerance to low temperatures. Hardening is the process by which the plants become frost tolerant, and dehardening the loss of this tolerance. SD = short day. Adapted from Rodhe & Bhalerao (2007).

1.3.2 Cell level

At cell level, it has been suggested that endodormancy is caused by inhibition of the symplastic communication through plasmodesmata (Rinne, Kaikuranta

& van der Schoot, 2001). Rinne and van der Schoot (2004) proposed the seasonal dormancy cycling model presented in Figure 2 for cells of a typical (woody) perennial in a northern temperate climate. According to the model, cell-to-cell communication is interrupted during endodormancy. The plasmodesmata, which form the connection between neighbouring cells, are suggested as being blocked, turning individual cells "off-line". Environmental signals trigger the enzyme 1,3-β-D-glucan synthase, and the subsequent production of 1,3-β-D-glucan sphincters, which seal the plasmodesmata. Simultaneously, spherosomes, containing the enzyme 1,3-β-D-glucanase are produced and distributed to the cytoplasm. When endodormancy is about to be released, as a response to, for example, adequate chilling, these spherosomes line up along the plasma membranes, and associate with the plasmodesmata-sphincter complexes (i.e. the plasmodesmatal plugs). Subsequently, the digestion of the sphincter 1,3-β-D-glucan by the 1,3-β-D-glucanase re-establishes the connection through plasmodesmata, but due to limitations in the environment, no communication occurs. The cells are now in a "standby", or ecodormant state. When the environmental conditions permit, signal exchange between the re-coupled cells is resumed and the cells become "online", or active, again.

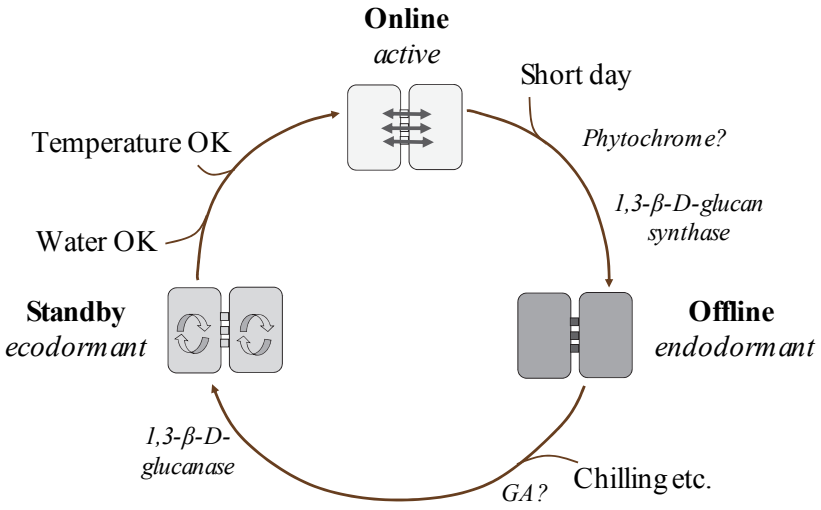

Figure 2. Dormancy cycling at the cellular level for a typical deciduous tree from a northern temperate climate. GA = Gibberellic acid. Adapted from Rinne, Kaikuranta & van der Schoot (2001).

The evidence for this model comes from ultrastructural experiments of the anatomy of actively growing, endodormant and ecodormant buds of *Populus tremula* (Jian *et al.*, 1997), *Betula pendula* and *B. pubescence* (Rinne, Kaikuranta & van der Schoot, 2001). In all these species, plasmodesmata seem to be blocked during the endodormant period, probably by 1,3-β-D-glucan, as a response to environmental factors (Rinne & van der Schoot, 2001). Jian *et al.* (1997) found a successive reduction in plasmodesmatal pore diameter when *P. tremula* transitioned from actively growing to endodormancy, and microinjections in single meristematic cells of *B. pubescence* showed cell-to-cell transport of the fluorescent dye to be definitely absent at this stage (Rinne, Kaikuranta & van der Schoot, 2001). Also the green algae *Chara corallina* has a seasonal pattern in cell-to-cell communication, with restricted intercellular transport during winter (Shepherd & Goodwin, 1992a; b).

Recently, Rinne *et al.* (2011) presented a model for the molecular events related to dormancy release in *Populus* sp., which confirmed the involvement of chilling and GA in dormancy release. External application of GA_3 has also been shown to induce sprouting in meristems of *Solanum tuberosum*, but only in the presence of cytokinin (Hartmann *et al*., 2011).

1.4 Implications of dormancy in perennials in agricultural systems

In the above, a number of species found to turn endodormant during a period of the year have been mentioned. However, there are also a number of species which grow vigorously at almost any time of the year, such as *Solanum carolinense* (Miyazaki, Ito & Urakawa, 2005)*, Phalaroides arundinacea* (Maslova *et al.*, 2007), *Elytrigia repens, Holcus mollis* and *Agrostis gigantea* (Håkansson & Wallgren, 1976). From an agronomic perspective, these species are interesting since there is no natural period of the year to avoid controlling them, if they occur as weeds.

In general, species with root buds are better protected from disturbance than rhizome species, thanks to the deeper location in soil of the former (Klimesova & Klimes, 2007). Notable exceptions include two of the species studied in this thesis, namely *Equisetum arvense* and *Tussilago farfara*, both with rhizome systems fairly deep located in soil (Leuchs, 1961; Williams, 1979; Sakamaki & Ino, 2004). Seasonal changes in the vegetative regeneration capacity of the bud bank make it particularly sensitive to timing of disturbance (Klimesova & Klimes, 2007).

Control measures for *Cirsium arvense* have been described by, among others, Tiley (2010), and for *E. repens* by Werner and Rioux (1977), but most

key features are shared with other perennials reproducing from belowground roots and rhizomes. At the seedling or post-germination stages, control is fairly simple and straightforward, using soil cultivation, herbicide treatments or cutting before flowers are formed. During this time, however, numerous reproductive organs may have been formed, and these must be handled somewhat differently. In short, the best stage to control the weed is when it has the lowest capacity for re-growth, that is when the carbohydrate root or rhizome reserves are at a minimum (e.g. Tiley, 2010). This happens just before flowering in *C. arvense* (Tiley, 2010). In *E. repens*, new rhizomes start to form when shoots have 3-4 leaves, and the compensation point (i.e. when photosynthesis is higher than the respiration for growth and developmental processes) is reached before the 5-leaf stage (Werner & Rioux, 1977). The aim is here to exhaust the underground system, to prevent replenishment for further perennation. Commonly, this is achieved by repeated soil cultivations or cutting which bring about sprouting, and make use of stored nutrients and energy. It is an advantage to bury the fragments deep, as more energy will be spent by the new shoots when they strive to reach up above soil level. Repeating the treatment when the compensation point is reached is critical for it to be effective. Efficacy also depends on seasonal timing and frequency of treatments. For example, in Southern England, farming tradition for *C. arvense* states: '*Cut in May, they are back the next day; cut in June, they will come back soon; cut in July, they will die*' (Tiley, 2010). The type of equipment, depth of working (when it comes to cultivation), duration, and integration in the cropping system will have an influence on the results, and follow-up treatments in subsequent years are critical to keep the number of weeds low. Although intensive grazing may be an alternate measure of control, many weeds have features making them less palatable to animals, and/or are toxic.

Control measures for perennial weeds also include herbicide applications. As well as for mechanical measures, timing is of importance. Not only may the herbicides only be allowed during a particular (specified) developmental stage of the plant, but also, the effect is reduced or impeded during periods of restricted growth or sprouting (Brandsæter *et al*., 2010). Thus, during periods of dormancy, mechanical as well as herbicide weed control will be inefficient, in the first case due to lack of re-growth, in the latter because of restricted growth and transport of the often systemic herbicides within plants.

1.5 Species

In their reviews, Foley (2002) and Chao *et al.* (2005) try to answer the question of which weeds are most suitable for dormancy investigations. Among the

traits characterising a good model weed are high economic impact, wide geographic distribution, close relationship to food crops, simple genetics, rapid cycling from juvenile to reproductive stage, several weedy characteristics and a broad interest from politicians and organisations. Weedy characteristics include, for example, germination in many types of environments, dormancy in seeds and vegetative organs, resistance to control measures, rapid growth to flowering, longevity of seeds and propagules, high seed output, vegetative reproduction and for perennials, deep rooting and reproduction by buds, rhizomes, tubers, bulbils, etc. The more of these traits a species possesses, the more applicable will it be as a model species.

Of the species in focus in this thesis, many of both the weedy traits and the good model weed characteristics are fulfilled. All of them propagate vegetatively and cause problems in Scandinavian agriculture. Some of them are fairly tolerant to both mechanical and chemical control measures (Håkansson, 1969a; 1969c; Håkansson & Wallgren, 1972), and some are quite deep rooted. Key features of these five perennial weeds are presented in Table 2. Below follows some information relevant to vegetative reproduction and dormancy for each species.

In general, growth and survival is favoured by vegetative reproduction as compared to establishment from seeds. In the former case, the vegetative propagule has an advantage as it is fed by the mother plant until self-sufficient. Consequently, it can spend more energy on green, photosynthesising plant parts. In contrast, the seedling must share the energy available in the seed to produce both roots and shoots, thus making it more vulnerable until the compensation point is reached. Also, it takes a longer time until new vegetative and reproductive parts can be formed.

1.5.1 Cirsium arvense (L.) Scop.

Cirsium arvense is one of the most troublesome and persistent weeds in many parts of Europe and North America (Tiley, 2010). It causes yield losses in crops and lowers usability of forage due to a deterrent effect of leaf spines on grazing animals. The species is most prevalent on waste land and disturbed areas, although frequently found in agricultural fields, especially those organically cultivated.

The biology of *C. arvense* has been described by Sagar and Rawson (1964), and recently, a very extensive review was presented by Tiley (2010). Following germination, a pair of cotyledons and a vertically growing primary root develop. A few days later, adventitious shoots begin to form on the main root, and lateral roots start to develop. Later in the season, new adventitious shoots arise from thickened regions of the lateral roots and from the lower parts

of the stem. Flowering occurs at the end of summer, after induction by long days. In autumn, the aboveground parts of the plant senesce or are killed by frost. Some of the belowground organs die off, resulting in a separation of the progeny from the mother plant. Only the thickened roots and a small number of stems survive the winter. In spring, new shoots develop from the roots established the previous season.

Regeneration from roots is possible 19 days after sowing, or when the seedlings have 2 or more leaves (Wilson, 1979). Fragments from parts other than the apical part of young, immature roots are able to produce new shoots when the root diameter exceeds 1 mm (Hamdoun, 1972). According to Hamdoun (1972), the optimum temperature for regeneration from fragments is 15°C, with no sprouting at 5°C or less. Thind (1975) found that the maximum number of shoots was produced at 25°C, although shoot formation occurred at temperatures between 5 and 30°C. At 37°C, no buds developed. An 18-week old plant was able to give rise to 930 new shoots if the root system was cut into 10-cm pieces (Nadeau & Vanden Born, 1989). On average, eight shoots per meter of root can be formed during a season, and in young roots it seems that more buds are formed when the environmental conditions are bad.

Bostock & Benton (1979) found 15% of the net production of *C. arvense* to be allocated to the vegetative reproductive organs, and 7% to seeds.

The overwintering roots are surprisingly susceptible to freezing, with -7°C and -5°C reducing survival and dry weight by 50%, respectively (Schimming & Messersmith, 1988). The relatively low tolerance to freezing temperatures might be an adaptation to the depth at which the buds are located. According to Nadeau and Vanden Born (1989), roots of *C. arvense* may reach depths of 1.8 m, which is well below the depth of normal soil tillage and furthermore, deeper than ground frost in most places where this species thrive. However, most of the roots are distributed in the topmost 20 cm of soil, with the number of bud-bearing roots declining with increasing depth. Interestingly, roots from greater depths produced more shoots than shallow roots, even more than the number of buds present at the time of sampling (Nadeau and Vanden Born, 1989).

McAllister and Haderlie (1985a) found no autumnal decrease in sprouting capacity or root bud formation in *C. arvense*. Instead, buds were most ready to sprout during the late autumn and winter, following death of the aerial shoot. Bud elongation increased with increased root temperatures (10, 20 and 30°C) and increased photoperiod (13 or 15 hours of light), and was greatest at a day/night shoot temperature of 25/15°C (as compared to 15/5 and 30/22°C; McAllister & Haderlie, 1985b). The lack of dormancy in fragments of *C. arvense* in the autumn also found by Fykse (1977) has more recently been confirmed by Grøndal, Graglia and Jensen (2003) and Brandsæter *et al.* (2010),

Table 2. *Key features of the five perennial weeds studied.*

Scientific name [a)]	***Elytrigia repens* (L.) Desv. ex Nevski ssp. *repens***	***Equisetum arvense* L.**	***Tussilago farfara* L.**	***Sonchus arvensis* L. var. *arvensis***	***Cirsium arvense* (L.) Scop.**
Alternative accepted scientific names [b)]	*Elymus repens* (L.) Gould subsp. *repens* *Agropyron repens* (L.) Beauv [f)]			*Sonchus vulgaris* Rouy subsp. *arvensis* (L.) Rouy, *Sonchus decorus* Castagne, *Sonchus humilis* N. I. Orlova	*Cirsium setosum* (Willd.) M. Bieb., *Cirsium incanum* (S.G.Gmel.) Fisch., *Cnicus arvensis* (L.) Roth, *Cirsium horridum* (Wimm. & Grab.) Stankov, non (M. Bieb. Fisch.), *Cirsium argentum* Peyer ex Vest
Common name [a)]	Common couch	Field horsetail	Colt's foot	Perennial sow-thistle	Creeping thistle
Alternative common names	couch grass, couch, dog grass, quack grass, quick grass, scutch, twitch grass [c)]		coltsfoot [c)]	field sow thistle, corn sow thistle [c, d)], creeping sow thistle, milk thistle, field milk thistle, swine-thistle, tree sow-thistle, dindle, gutweed [d)]	California thistle, Canadian thistle, field thistle, perennial thistle [c)]
Family [c)]	*Poaceae (Graminae)*	*Equisetaceae*	*Asteraceae (Compositae)*	*Asteraceae (Compositae)*	*Asteraceae (Compositae)*
Raunkiaer's life form	Chamaephyte, geophyte [g)]	Geophyte [g)]	Geophyte [h)]	Hemicryptophyte [g)]	Geophyte [g)]
Life form (including lifespan) of perennial weed with under-ground plagiotropic roots, rhizomes [e)]	Creeping perennials, tolerant to soil cultivation	Creeping perennials, tolerant to soil cultivation	Creeping perennials, tolerant to soil cultivation	Creeping perennials, plagiotropic thickened roots	Creeping perennials, plagiotropic thickened roots

Characteristics of perennial organs [e]	Rhizomes shallow, without spool-shaped swellings	Rhizomes reaching greater depths	Rhizomes reaching greater depths	Thickened roots shallow	Thickened roots reaching greater depths
Distribution in Sweden [e]	All	All	All	All	All
Abundance in arable fields in Sweden [1) e]	4	2	1	2	2
Grading of relative potential to grow and reproduce in absence of chemical or mechanical means of control in Sweden [2) e]	III: All crops	III: Potatoes, sugar beets, vegetables, spring sown cereals and oilseed crops, young leys II: Autumn sown cereals and oilseed crops, old leys	III: All crops	III: Potatoes, sugar beets, vegetables, spring sown cereals and oilseed crops II: Autumn sown cereals and oilseed crops, young leys I: Old leys	III: Potatoes, sugar beets, vegetables, spring sown cereals and oilseed crops II: Autumn sown cereals and oilseed crops, young leys I: Old leys

1) Average abundance, denoted 1-4: 1: frequent in very limited areas or under very special conditions or occurring as a more scattered weed over larger areas; 4: a frequent and, on average, abundant weed in arable fields in all, or most of the important agricultural areas in the country.

2) III: maximal; II: somewhat reduced; I: limited, -: minimal. Grading values are only comparable within each species. They do not inform on quantitative abundance or importance

a) Mossberg, Stenberg & Ericsson (1992)

b) Royal Botanic Garden, Edinburgh, U.K. Flora Europaea Database (2008; online).

c) USDA, ARS, National Genetic Resource Program. Germplasm Resources Information Network (GRIN) (2008; online)

d) Lemna & Messersmith (1990)

e) Håkansson (2003)

f) Used in older references, see reference list.

g) USDA Forest Service website (2008; online)

h) Heineken (2001; online)

although Fykse (1974) and Kvist and Håkansson (1985) found a reduced capacity for growth in the autumn. Chilling of the roots at 2°C before sprouting was tested at 18°C did not influence the number of emerging shoots, as studied by Brandsæter et al. (2010). Tørresen, Fykse and Rafoss (2010) found withering and growth cessation to occur later in the autumn for *C. arvense* than for *Sonchus arvensis* in comparative studies of pot-grown plants in Norwegian conditions.

1.5.2 Elytrigia repens (L.) Desv. Ex Nevski

Being one of the most troublesome weeds in the "cool-season" temperate areas of the world, different aspects of how to handle *Elytrigia repens* have been extensively evaluated. An old, but still relevant review of the biology of *E. repens* is the one by Werner and Rioux (1977), from which most of the information below has been extracted.

E. repens is a grass geophyte, which grows on a wide variety of soils, and occurs mainly at disturbed sites (Werner & Rioux, 1977). In particular, it infests land which has recently been abandoned, such as fallows, and may make up >90% of the biomass for several years.

E. repens propagates mainly from axillary buds, formed at the nodes of the very extensive rhizome system (Werner & Rioux, 1977). Although most buds are dormant while attached to the mother plant, some sprout to produce new shoots, and fragmentation acts as a stimulus to release buds from apical dominance. Rhizomes begin to form when the plant has only 3-4 leaves (6-8 leaves if reproduced by seeds). Long photoperiods result in heavier, thicker and more numerous rhizomes, while the aerial part of the plant remains relatively unaffected by changes in light conditions. However, more shoots are produced at reduced light levels. The rhizomes of *E. repens* are very tolerant to freezing, requiring temperatures below -20°C to reduce survival by 50% and -13°C for a similar reduction in dry mass (Schimming and Messersmith, 1988).

According to the review by Werner and Rioux (1977), there are seasonal trends in the formation of rhizomes of this species.The greatest number of new rhizomes is formed between June and August, while most photosynthesis and tillering occur in spring and autumn, unless altered by cultural practices, such as soil disturbance. According to Håkansson and Wallgren (1976), new rhizomes start to form just when the minimum dry weight of the belowground system is passed. This occurs in June under Swedish conditions.

According to Johnson and Buckholtz (1962), the activity of rhizome buds decreased from mid-April to June. The buds were dormant during June and increased their activity from July and onwards, suggesting a "late-spring-

dormancy" in this species. However, Håkansson and Wallgren (1976) found no such period of endodormancy.

Rhizome fragments of *E. repens* collected in Finland and Sweden were not dormant during a period from the beginning of July to October (Brandsæter *et al.*, 2010). A small reduction in emergence was found in late October for the Finnish populations, while the Swedish populations showed no particular pattern. Chilling of the rhizomes at 2°C prior to planting for testing sprouting willingness at 18°C did not affect the number of emerged shoots.

1.5.3 Equisetum arvense L.

The rhizomes of *Equisetum arvense* penetrate the soil deeply, probably deeper than 100 cm (Williams, 1979; Sakamaki & Ino, 2004). Besides spreading from axillary buds at the nodes of the rhizomes, this species also propagates vegetatively from tubers. Regenerative spreading from spores is rare (Sakamaki & Ino, 2004). Rhizomes are more willing to form tubers if the starch content is high. Sakamaki and Ino (2006) suggest that rhizomes produce more shoots than tubers do from the same dry mass, because of a larger number of buds on rhizomes. Thus, regeneration capacity depends on the relationship between number of buds and content of stored starch, but, importantly, as the amount of dry matter per potential shoot is larger for tubers than for rhizomes, tubers are more resistant to heavy shade and deep burial.

In cultivated soils, Williams (1979) found most of the tubers at depths greater than 50 cm, while the rhizomes occurred in the uppermost 25 cm of soil. After two years of fallow, the tubers were re-distributed to the same depths as the rhizomes, while introduction of a crop resulted in deeper distribution of both types of propagules. The weight per tuber increased with depth of occurrence. This suggests that the depth of the underground system of this evolutionary old species depends on disturbance, which in agricultural land equals management practice.

E. arvense prefers neutral soils, but is more common on acid soils due to less competition from other species there (Williams, 1979). The tubers are more sensitive to non-optimal pH than the shoots and the rhizomes. The species grows better on silty clay loam than sandy loam, and when grown in competition with wheat, the relative weight of the tubers increased as compared to shoots and rhizomes.

The tubers are sensitive to drought, while water logging is not a problem (Williams, 1979). Although little studied, they are not endodormant in November, since they germinated readily after 28 days at 15°C after collection from a sandy soil in the UK.

In Canadian studies, *E. arvense* produced shoots during the entire summer (May to September) (Cloutier & Watson, 1985). The number of new shoots decreased dramatically when the plants were subjected to drought. Rhizomes, 1 cm in length, produced shoots even if planted at a depth of 15 cm in a greenhouse. Field experiments showed the species to be extremely tolerant to mechanical disturbance, since it grew well even if hoed 16 times during the vegetation period. Kvist and Håkansson (1985) found reduced capacity to regenerate from rhizomes in September-October in one of two studied populations, probably an effect of drought in the summer months rather than dormancy.

In studies in the US, Hauke (1985) found that all rhizome buds initiated from July to September became reproductive, while those initiated in October-November remained vegetative. All buds reached a state of maturity, and then became dormant. Growth was resumed the following spring, starting with the reproductive units.

1.5.4 Sonchus arvensis L.

Sonchus arvensis is a deep rooted perennial, found in the temperate areas of the northern and southern hemisphere (Lemna & Messersmith, 1990). Although not as problematic as a weed as *C. arvense* and *E. repens*, it can locally cause significant yield and quality losses in crop plants. Apart from reproduction by seeds, vegetative propagation via numerous adventitious buds along the root system and basal parts of the stem enables a rapid spread to new areas, and resilience to disturbances.

In Sweden, shoots and new roots in established stands begin to form as soon as temperature allows (Håkansson, 1969c; Håkansson & Wallgren, 1972). New shoots develop until late July from the thickened roots in undisturbed stands. While the aerial shoots and the thin roots die in September-October, the thickened roots and some of the underground parts of the stems survive winter. Regeneration from lateral roots of *S. arvensis* is possible when the roots are 1-1.5 mm in diameter, or when the plants have 6-7 leaves, coinciding with the time of minimum dry weight of the plant. Under natural conditions in Sweden, it takes about 5-6 weeks to reach this stage in spring (Håkansson 1969c), and 3 weeks in July (Håkansson & Wallgren, 1972).

The root system of *S. arvensis* is relatively vulnerable to defoliation and burial, and if controlled before the 6-7-leaf stage is reached, it is possible to eradicate the weed by a few repetitions (2-3 according to Håkansson, 1969c). As the root system is located at shallow depths (at 5-12 cm, although able to penetrate down to 2 m depth as reviewed by Lemna & Messersmith, 1990), the roots are quite tolerant to low temperatures. Freezing at -17°C was required to

reduce survival and -15°C to reduce dry weight by 50% (Schimming and Messersmith, 1988).

As indicated by Håkansson (1969c) in Sweden, *S. arvensis* seems to develop endodormancy in the autumn. In undisturbed stands, no new shoots emerged from late July and onwards. When disturbed by fragmentation to 8-cm pieces and buried at 1.5 cm depth, re-growth from buds on roots and stem bases decreased steadily to no emergence from the beginning of September (Håkansson & Wallgren, 1972). Growth was not resumed by the end of the experimental period in the middle of October. Chilling at 2°C for one or two months released dormancy.

Also working with planted fragments of *S. arvensis*, Brandsæter *et al.* (2010) found a significant reduction in shoot emergence during a period in the autumn. The timing of this period varied with population and country. While the reduction in sprouting readiness occurred in mid-July in the two Norwegian populations, such a decrease began a month later in Denmark. Least emergence occurred in September for the Danish populations, late September to early October for the Finnish and Swedish populations, and from August to the beginning of October for the Norwegian populations. Chilling at 2°C for four weeks before sprouting was tested at 18°C, reduced the number of emerging shoots in the Swedish populations in the beginning of the test period, while chilling increased emergence towards October.

Pot-grown plants of *S. arvensis* ceased growth and withered in September-October under Norwegian conditions, as demonstrated by leaf area development and biomass distribution (Tørresen, Fykse & Rafoss, 2010). Interestingly, younger plants grew later in the autumn than older plants. The biomass of the roots increased in the autumn, while the total biomass changed little.

1.5.5 Tussilago farfara L.

In Sweden, *Tussilago farfara* is among the first wild plants to flower in spring. The seeds germinate shortly after dispersal, and a taproot is quickly formed (Ogden, 1974). During the first summer of growth, adventitious roots develop from the lower nodes of the stem. Rhizomes are later initiated from the same region. The large leaves originate at the stock (the lowest, non-rhizomatous portion of the stem). The stock also bears the flower buds, which form in the late summer or autumn, continue their development during winter and then flower the following spring. The flower buds are often visible as clusters on the stock, just at the soil surface, after senescence of the leaves in the winter (Ogden, 1974; however, in my experience, flower buds become visible in the early autumn, when the leaves are still green under Swedish conditions). Their

formation is not dependent on the number of leaves, as flower buds can be produced on rhizomes at some distance from the parent plant (Ogden, 1974). After seed dispersal, the stock dies, resulting in fragmentation of the rhizome system.

In favourable conditions, vegetative reproduction takes place even in the first season after generative dispersal by certain rhizomes growing upwards to produce new plants (Ogden, 1974). Otherwise, new shoots are formed during the flowering period the subsequent spring when leaves develop on the stock from tips of rhizomes formed the previous season. The rhizomes may grow one meter in length or more before turning upwards to produce new aerial shoots. Bostock and Benton (1979) found that potted plants produced 170 cm of rhizomes during two years of undisturbed growth. After disturbance, rhizomes of wild plants grew horizontally at shallow depths (<16 cm) during the first year, before starting to grow vertically (Leuchs, 1961). The maximum penetration depth was 61 cm. Fragments, 1 cm in length, were able to produce new shoots when buried 4-5 cm in depth or shallower. Placement at 2-3°C for eight weeks without soil did not kill the rhizomes.

Bostock and Benton (1979) found that 26% of the net production of *T. farfara* was allocated to seed reproductive organs (including accessory organs, such as penducles and capitula as well as the achenes) and 20% to the rhizomes, while Ogden (1974) recorded 3-8% of the annual net production to seeds and 3-23% to vegetative reproduction. In dense populations, relatively more energy was allocated to seeds, while in poor soils, allocation to rhizomes was favoured. The seeds are not dormant, and germinate rapidly after shedding, even under dry conditions (Bostock, 1978). Longevity was, however, short, with no seeds surviving six months of storage in soil.

In a Norwegian study, Fykse (1977) found weak endodormancy in rhizomes of *T. farfara* during the autumn. Kvist and Håkansson (1985) report a significant reduction in sprouting from newly formed rhizomes in July-August. Although no sprouting occurred four weeks after the rhizomes were fragmented, 8-10 weeks after harvest, all of them produced shoots. These were, however, dwarf-likes with short internodes, despite being grown in the dark. Cold treatment slightly above 0°C for 8 weeks in the dark restored the normal growth pattern in 20-50% of the rhizome fragments.

2 Definitions, objectives and hypotheses

2.1 Objectives

The objectives of this thesis were:

I To investigate the sprouting pattern of the five perennial weed species *Cirsium arvense*, *Elytrigia repens*, *Equisetum arvense*, *Sonchus arvensis* and *Tussilago farfara*, from late summer to early spring, from plants with intact and fragmented underground systems, in a natural environment,

II To study the impact of temperature and photoperiod on dormancy, here defined as a temporal incapacity to sprout under favourable conditions, in *C. arvense* and *S. arvensis*.

2.2 Definitions

Following the nomenclature of Lang *et al.* (1987), the definition of dormancy used in the thesis excludes ecodormancy, but covers endo- as well as paradormancy. Although the author's main interest is a type of dormancy that cannot be explained by apical dominance, the design of the experiments performed did not permit a separation between the latter dormancy types. To be able to judge whether non-sprouting behaviour is controlled by factors produced within or outside the affected bud meristem itself, experiments on the molecular level are required. However, measures were taken to remove paradormancy to some extent, for example by defoliation of the aboveground biomass (removal of paradormancy from shoots on belowground buds) or fragmentation of the root and rhizome system (removal of paradormancy from other buds). Thus, dormancy as it is used in this thesis refers rather to a reduction in the emergence or sprouting capacity (quantitative dormancy), than

an absolute absence of growth (qualitative dormancy) under favourable conditions.

2.3 Hypotheses

The hypotheses forming the basis for the experiments in this thesis were:

1. There are seasonal patterns in re-growth from roots and rhizomes, from late summer to early spring in all the species studied with the exception of *E. repens* (paper I, II, IV),
2. The capacity of re-growth from belowground buds is reduced in the autumn months, and resumed in the beginning of the winter (paper I, II, IV),
3. The seasonal trends are manifested in root and rhizome buds of whole plants after removal of the aboveground biomass (paper I, II) as well as in buds of cut fragments (paper IV),
4. The impaired sprouting capacity is a consequence of changes in the length of the photoperiod and decreasing temperatures in the late summer/early autumn months (paper III),
5. Populations from northern Sweden enter dormancy earlier than populations from the south (paper I-IV).

3 Materials and Methods

3.1 Plant materials

Plant materials used in all the experiments were originally collected from April to June 2008 in southern and northern Sweden. Details of the collections are presented in Table 3. After collection, roots and rhizomes with adherent soil were kept at 4°C until planting in late June 2008. The material for the 2009/2010-year experiments derived from plants of the same collections, which had been grown in big boxes during the 2008/2009 season and stored cold and dark during winter. Fragments of the resulting roots and rhizomes were used for establishment of new experimental plants.

All propagation and outdoor experiments took place at Ultuna (59°48.82'N, 17°38.93'E), outside Uppsala, Sweden. Potted plants grown outdoors were used in the experiments on seasonal variation, while influence of photoperiod and temperature on sprouting capacity was studied in a climate chamber (phytotrone). For the first experimental replicate of the latter, the experimental plants were established from plants grown outdoors during summer, and re-planted in a warm greenhouse in November. Plants in all other experiments were established from plants grown outdoors during the vegetation period and stored cold (4°C) and dark over winter. The daily mean temperatures during 2008 and 2009 are presented in Figure 3.

Table 3.*Coordinates (latitude and longitude) of collection site, date of collection and type of field of the collection site for the root and rhizome materials used in the experiments. Populations marked with * were used also in the paper IV experiment, those marked with † in the paper III experiment.*

Species	Population	Collection site	Date of collection	Type of field
C. arvense	S1*†	N 55°52', E 12°58'	6 May	Boarder of field
	S2	N 56°14', E 12°36'	15 April	Stubble cultivated
	S3*	N 56°2', E 14°5'	14 April	Ploughed in spring
	N1*	N 64°2', E 20°4'	2 June	Ley crop
	N2	N 63°52', E 20°12'	3 June	Oat crop
	N3*†	N 64°42', E 20°40'	4 June	Boarder, barley crop
E. repens	S1*	N 56°10', E 13°52'	14 April	Stubble cultivated
	S2	N 56°14', E 12°36'	15 April	Stubble cultivated
	S3*	N55°47', E13°32'	6 May	Fallow
	N1*	N 63°57', E 20°1'	2 June	Strawberry field
	N2	N 63°45', E 20°13'	3 June	Ley crop
	N3*	N 63°51', E 20°11'	5 June	Oat crop
E. arvense	S1*	N 56°14', E 12°36'	15 April	Stubble cultivated
	S2*	N 56°6', E 14°6'	16 April	Boarder of field
	S3	N 55°41', E 13°5'	Beginning of January	Cultivated mechanically, asparagus field
	N1*	N 63°57', E 20°1'	2 June	Strawberry field
	N2*	N 64°2', E 20°3'	2 June	Heap of rubble
	N3	N 63°51', E 20°11'	3 June	Impediment
S. arvensis	S1*	N 56°10', E 13°52'	14 April	Ploughed in autumn
	S2	N 55°26', E 13°25'	3 June	Cultivated land
	S3*†	N 55°52', E 12°58'	6 May	Clover for seeds
	N1*†	N 64°41', E 20°38'	4 June	Barley crop
	N2	N 63°9', E 17°45'	17 June	Barley crop
	N3*	N 63°9', E 17°45'	17 June	Bare soil, seed clover
T. farfara	S1	N 55°55', E 13°35'	7 July	Impediment
	S2*	N 56°14', E 12°36'	15 April	Stubble (non-cultivated)
	S3*	N 55°52', E 12°58'	6 May	Clover for seeds
	N1	N 63°57', E 20°1'	2 June	Strawberry field
	N2*	N 63°45', E 20°13'	3 June	Boarder of field, ley
	N3*	N 64°41', E 20°37'	4 June	Boarder of field, barley

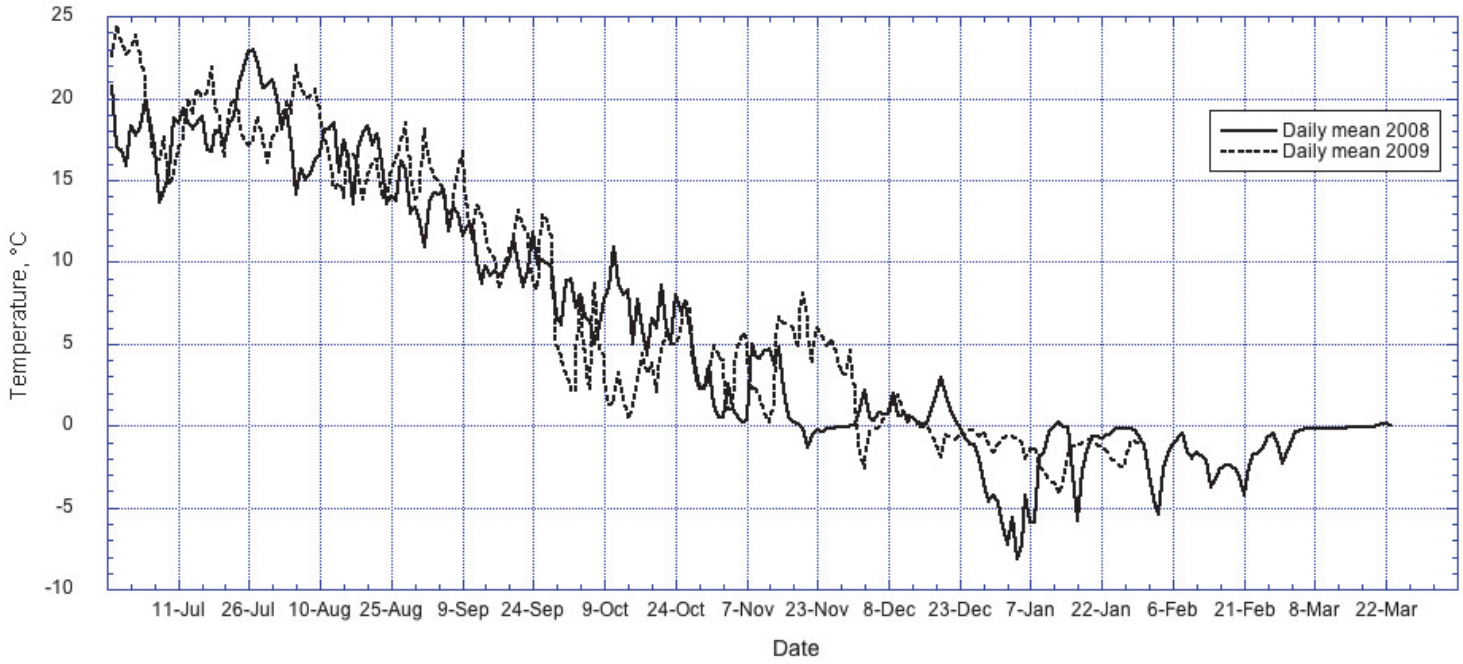

Figure 3. Daily mean soil temperatures in soil at Ultuna (59°48.82'N, 17°38.93'E) during the experimental periods 2008/2009-2009/2010.

3.2 Seasonal trends in the capacity of vegetative reproduction of plants with intact roots or rhizomes (paper I, II)

The two-year outdoor experiment, forming the basis for paper I and II, encompassed three replicates (blocks) of each of the populations presented in Table 3, i.e. 5 species x 2 regions x 3 populations, organised in a randomised block design. Plants were grown in pots, buried with the uppermost 5 cm of the pot above soil level, in a sandy soil. For *T. farfara*, the time of flower bud formation and withering was registered. Samples were taken every second week from 25 August to 16 December 2008, and thereafter on 3 additional occasions (14 January, 10 March, 7 April; in total 12 occasions) the first year, and with two-week intervals from 29 July 2009 to 25 January 2010 (14 occasions) during the second year. Aboveground biomass was removed and pots, with intact root or rhizome systems, were placed under forcing conditions (16/8 h light/dark in 17/9°C, the high temperature coinciding with the bright period) for four weeks after which time the number of emerging shoots were counted. The number of belowground shoots (of *C. arvense* and *S. arvensis*) and the dry weights of emerged and belowground shoots and roots were registered. Generalized additive models (GAMs) were used to statistically model and test the seasonal variation.

Generalized additive models (GAMs) is a computer based statistical tool, which is mainly used for exploratory purposes, but can also be used for inference (e.g. hypothesis testing). These types of models are an extension of the generalized linear models (GLMs) to applications where polynomials fail to identify curvature in the data under investigation (Hastie & Tibshirani, 1990). Spline functions or other types of smoothing functions, which allow the curves to bend in other ways than determined by, for example polynomials, replace the linear terms present in GLMs. The models are non-parametric or semi-parametric; the probability distribution of the response variable still has to be known. GAMs can be used for any probability distribution handled by GLMs (via the link function). Predictor variables can be added to the model one at the time. The additional effect of each predictor on the overall fit can be assessed through change in deviance. Thus, by including and excluding predictors, one can assess the relative importance of each predictor.

3.3 Seasonal trends in sprouting capacity from cut fragments (paper IV)

In the outdoor complete randomised experiment of paper IV, spanning over one year, plants of all five species were used. From each region, two

populations were chosen for the experiments. These are marked with an asterisk in Table 3. Plants were grown in pots, buried with the uppermost 5 cm above soil level outside Uppsala. Every second week from 29 July 2009 to 25 January 2010 (in total 14 test dates), two pots per population were used for tests of sprouting capacity from fragmented roots or rhizomes and for *E. arvense*, from the tubers. After removal of the soil, the belowground system was fragmented into pieces, 3 cm in length for *C. arvense*, 1 cm for *S. arvensis* and cut 1 cm from each side of the node for the three rhizome species. In total, up to 20 fragments and for *E. arvense*, tubers per plant (the aim was to have 20 fragments, but occasionally, this could not be achieved) were distributed equally in 2 Petri dishes, and placed in a growth chamber (17/9°C for 16/8 h in darkness) for two weeks. The number of sprouted and non-sprouted buds per Petri dish was registered and used in the subsequent analysis. Again, generalized additive models (GAMs) were used to statistically evaluate the experiment, this time studying changes in the proportion of sprouted buds producing shoots >0.5 cm over the test period.

3.4 Influence of photoperiod and temperature on sprouting capacity from *C. arvense* and *S. arvensis* (paper III)

In the climate chamber experiment of paper III, the influence of photoperiod and temperature on root bud sprouting capacity from fragments of *C. arvense* and *S. arvensis* was studied. In total 12 different treatments (3 photoperiods x 4 temperature regimes) were studied (Table 4), using 2 populations per species (one from the south and one from the north; S1 and N3 for *C. arvense*, S3 and N1 for *S. arvensis*) in 2 replicates per test day.

Sampling dates were chosen so that treatments could be compared at a day-degree basis. The experiment was repeated twice; the first experiment replicate in spring 2009, the second in the autumn the same year. At each sampling date, the root system was cut into fragments, 3 cm in length for *C. arvense* and 1 cm in length for *S. arvensis.* The aim was to use 20 fragments per plant, distributed equally in two Petri dishes.

After two weeks in a dark growth chamber at 19/15°C for 16/8 h, sprouting capacity was evaluated from the number of buds producing shoots (i) <0.5 cm (including the non-sprouted buds), (ii) 0.5-1.0 cm and (iii) >1.0 cm in length. A generalized linear model (GLM) with a multinomial distribution was used to statistically model the proportion of sprouting buds in the three categories simultaneously, thereby testing the differences between treatments over time. Within each species, separate analyses were done to test (i) the influence of a long/short photoperiod and high/low temperature (treatments A, B, C, D), (ii)

the difference between a decreasing and long photoperiod during a decreasing temperatures (treatment E and F), (iii) the difference between decreasing and constant high temperatures during decreasing photoperiod (treatment E and G), (iv) test of transition from low to high or high to low temperatures during short photoperiods (treatment H and I), and (v) test of importance of timing of transition from high to decreasing temperatures during a long photoperiod (treatments J, K and L).

Table 4. *Photoperiodic and temperature regimes and the rationale behind the choice of treatment conditions forming the basis for paper III. Photoperiods: Long (18/6 h = July), Short (12/12 h = September), Decreasing (from 18 h to 8 h in four weeks, i.e. -22 min per day = condensed period from July to September). Temperatures: High (18/12°C for 16/8 h = July), Low (12/6°C for 16/8 h = September), Decreasing (from 21°C to 4.8°C in four weeks, i.e. -0.6°C per day = condensed period from July to November).*

Treatment	Photoperiod	Temperature	Comment
A	Long	High	Control treatment; Swedish July
B	Short	High	Test if photoperiod induces dormancy
C	Long	Low	Test if temperature induces dormancy
D	Short	Low	Expected conditions for dormancy induction in *S. arvensis*; Swedish September
E	Decreasing	Decreasing	Test if both decreasing photoperiod and decreasing temperature are required to induce dormancy
F	Long	Decreasing	Assumes temperature controls dormancy; study if it is the decrease that induces it
G	Decreasing	Constant high (16°C)	Can high temperatures prevent dormancy?
H	Short	Low 2w + high 3w	Test if dormancy is induced because of changes in temperature
I	Short	High 2w + low 4w	
J	Long	High 1w + decr. 3w	If temperature controls sprouting, these treatments will tell us after how long the decrease in sprouting capacity starts, in particular to study *C. arvense*
K	Long	High 2 w + decr. 2w	
L	Long	High 1 w + decr. 1w	

4 Results

4.1 Root species (papers I, III, IV)

4.1.1 Cirsium arvense

Seasonal variation in sprouting capacity (papers I, IV)

In the study of shoot emergence from defoliated (i.e. a removal of the aerial parts) plants with intact (undisturbed) root system from July to April, it was clear that emergence was impaired in *C. arvense* during a period in the autumn (paper I). During both years, few shoots emerged from the middle of September to the middle of November. In contrast, the number of belowground shoots increased from the end of July to early December, or for an even longer period in some populations. The dry weights of the root systems increased until the arrival of the first frost in November, after which a decline was seen in most populations. Thus, low root weights could not explain the impaired emergence. A model with one curve per population fitted the data better than a less complex model with only two curves, one for populations from southern Sweden and one for populations from the north.

In contrast to emergence from intact root systems, *C. arvense* showed no seasonality in sprouting capacity if the underground system was fragmented (paper IV). The four populations behaved somewhat differently, but with no regional effect.

Influence of photoperiod and temperature on sprouting capacity (paper III)

The climate chamber experiment confirmed the lack of pattern in seasonal sprouting capacity in fragmented roots of *C. arvense.* The only significant difference in the proportion of sprouting buds were found between treatments with a decreasing photoperiod under decreasing (E) and constant high (G) temperatures ($P=0.0136$), with less sprouting under constant high temperatures.

4.1.2 Sonchus arvensis

Seasonal variation in sprouting capacity (papers I, IV)

In *S. arvensis*, a distinct seasonal pattern in emergence from undisturbed, defoliated plants was found (paper I). Few shoots emerged between mid-September to mid-November. From the beginning of December, a steady increase in the number of shoots was seen. As for *C. arvense*, a model with one curve for each population fitted the observed data better than a model based on regional origin. The reduction in emergence above soil was also reflected below soil level, with less underground shoots produced when emergence was low. As in *C. arvense*, the weight of the root system increased in the beginning of the test period, and then started to decline in most populations.

The seasonal pattern was consistent in fragmented roots (paper IV). The reduction in the proportion of sprouting buds >0.5 cm coincided with the decrease in emergence above soil, with little sprouting in September in three of the four populations. Notably, no absolute lack of sprouting could be detected, suggesting a quantitative rather than qualitative type of dormancy for this species. Again, the best model was one with an analysis by population rather than region.

Photoperiod and temperature control of sprouting (paper III)

In conclusion, the climate chamber experiment using fragments of *S. arvensis* indicated a photoperiodic control of sprouting capacity of root buds of this species, with high temperature enhancing the effects (paper III). The short photoperiod (12 h of light) severely impaired the proportion of sprouted buds, in particular if combined with a high temperature. If plants were moved from cold to warm conditions during a short photoperiod, almost significantly less sprouting occurred compared to a transfer from warm to cold conditions.

During long and decreasing photoperiods, the northern population was more sensitive to changes in temperatures than the southern. Three weeks of warm temperatures, followed by one week of cold, reduced sprouting capacity more than one or two weeks at warm temperatures, followed by two or three weeks in cold. Also, during decreasing photoperiods, fewer buds were produced at constant high temperatures than at decreasing temperatures. Both differences were present only in the northern population.

During decreasing temperatures combined with long or decreasing photoperiods, the northern population sprouted more than the southern. Over time, sprouting increased in the northern populations, while remaining relatively constant in the southern one.

4.2 Rhizome species (papers II, IV)

4.2.1 Elytrigia repens

In defoliated *Elytrigia repens*-plants with undisturbed rhizome systems, shoot emergence increased (both number and total weight) throughout the experimental period in both 2008 and 2009 (paper II). The weight of the belowground system increased 2-3-fold from late July until November-December, and then started to slowly decline. Interestingly, the weights of the emerged shoots per weight of rhizome decreased in early autumn, remained low for about 2 months and then increased again. The model by population was significantly better than a model by region.

The proportions of sprouted buds producing shoots >0.5 cm did not change much over the test period in fragmented rhizomes in populations from the northern region (paper IV). In populations from the south, however, a decrease in the proportion of sprouting buds occurred in September-October. Although there was a decline, at least 50% of all present buds sprouted at all times.

4.2.2 Equisetum arvense

Shoot emergence of defoliated plants of *Eqisetum arvense*, with intact rhizome systems, declined to almost no emergence at all from early September to late October (paper II). The weight of the rhizome system increased from the start of the experiment to October/November in 2008. In 2009, it reached a plateau in September/October. The maximum in rhizome weight coincided with the period of low emergence in November, and then started to decrease in some populations. In other populations, the rhizome weights remained high or even increased to the end of the test period, suggesting little decay and "die-off" of the belowground system during winter. A GAM by population was significantly better than a model by region or species only. The number of tubers increased throughout autumn, and one of the southern populations (S2) produced more tubers than the other populations. The total weights of the tubers produced were highest for population S2, followed by population S1, whose total weight of tubers was significantly higher than the weights of tubers from the other four populations.

In fragmented rhizomes of *E. arvense*, the proportion of sprouted buds >0.5 cm increased from the beginning of the experiment (late July) to the beginning of December in the northern populations (paper IV). From mid-December to late January, sprouting decreased. In the southern populations, few sprouts occurred from July to the beginning of October. Sprouting increased between October and December, and then decreased until the end of the experimental period (late January) in one of the populations (S1). For the other population,

sprouting remained high until the end of January. In tubers, no clear pattern of sprouting readiness could be discerned. One population (S1) reached a maximum in regenerative capacity from tubers in October, another (S2) in December, and sprouting from tubers of one of the northern populations (N2) decreased from the beginning to the end of the test period. In the other northern population (N1), sprouting from tubers decreased until the beginning of November, increased until mid-December and then started to decrease again.

4.2.3 Tussilago farfara

The undisturbed rhizome systems of *Tussilago farfara* were affected by the changing environmental conditions during autumn (paper II). The number of emerging shoots had already started to decrease in late August to early September, to reach close to zero levels two weeks later. A clear regional trend was evident, with the northern populations ceasing emergence earlier. Also, flower bud formation and withering of plants started earlier in the northern populations. Emergence was resumed in the middle of November in all populations but S3, which resumed growth much later. Although a reduction in emergence occurred, growth did not cease completely. The weight of the rhizome system increased steadily during autumn, and reached a maximum in November-December. At least in the second year of the experiment, the southern populations produced more rhizomes than the northern (the low rhizome weight of one of the southern populations during the first year of experiment was due to delayed planting, as compared to the other five populations).

Buds of fragmented rhizomes of *T. farfara* showed a distinct pattern of sprouting capacity during the autumn (paper IV). In three of the populations (N2, S1, S3), very few sprouts >0.5 cm were produced until October, after which the proportion steadily increased until end of the test period (late January). In one of the northern populations (N1), sprouting increased between late July and mid-September, remained at a constant level in September to early November, and then increased to >90% sprouting at the end of January.

5 Discussion and concluding remarks

Almost as hypothesised, there were indeed seasonal patterns in the re-growth from roots and rhizomes between late summer and early spring in all of the species investigated. Unexpectedly, biomass allocation to shoot in relation to rhizomes was reduced in defoliated plants of *Elytrigia repens*. Whether all these patterns can be referred to as "dormancy" remains to be proved. It seems likely that the reduced capacity to sprout or emerge is more quantitative than qualitative, since the proportion of sprouting buds producing shoots >0.5 cm never ceased completely. It may also be a consequence of the fact that buds respond individually to dormancy inducing signals, and are thus at different depth of dormancy (see for example the dormancy model suggested by Crabbé and Barnola (1996), described on page 29 in this thesis). Also, emergence from undisturbed root systems of defoliated *Cirsium arvensis* plants was reduced in mid-September to mid-November, while there was no decrease in the proportion of sprouted buds when the root system was cut into pieces. The lack of dormancy in fragmented roots of this species was later confirmed in the climate chamber experiment, and is in line with the findings of for example Fykse (1977), McAllister and Haderlie (1985a), Grøndal, Graglia and Jensen (2003) and Brandsæter *et al.* (2010).

The reduced capacity to sprout from undisturbed and fragmented belowground systems was most obvious in *Sonchus arvensis* and *Tussilago farfara* compared with the other species. Growth cessation occurred simultaneously in intact roots/rhizomes and in fragments, and the results were consistent in both years. This suggests photoperiodic control of sprouting readiness in these species, in line with the control of growth cessation in many woody perennials (as reviewed by e.g. Olsen, 2010; van der Schoot & Rinne, 2011) and *Poa bulbosa* (Ofir & Kiegel, 1999; 2006). Furthermore, photoperiodic induction of growth cessation also means that the signal responsible for dormancy onset is detected by the aerial parts of the plants,

probably mediated by phytochromes. Thus, it is necessary to expose whole plants to treatments in dormancy studies.

That short photoperiods (12 h of light) induced dormancy in *S. arvensis* was confirmed in the climate chamber experiment. The effect was enhanced if a short photoperiod was combined with a high temperature. Similar results have been obtained in studies on 1- and 2-year old seedlings of *Picea abies* (Søgaard *et al*., 2008; Granhus, Sundheim Fløistad & Søgaard, 2009), *Betula pendula, B. pubescens* (Heide, 2003; Junttila, Nilsen & Igeland, 2003) and *Alnus glutinosa* (Heide, 2003) where high temperature during dormancy induction under short-day conditions delayed dormancy release. From an ecological point of view, it is better to rely on a predictable factor, such as photoperiod, to detect forthcoming changes in the environmental conditions, as compared to the less predictable weather (temperature). *S. arvensis* takes this one step further, and will not be lured by a high autumnal temperature into allowing new shoots to emerge. Together with the results of Håkansson (1969c) for undisturbed plants, and Håkansson and Wallgren (1972) and Brandsæter *et al.* (2010) for emergence from planted rhizomes, the studies presented here indicate a quantitative dormancy in *S. arvensis*, manifested in plants with intact root systems as well as in fragments.

The type of dormancy shown by *T. farfara* may be an effect of the phenology of this species, described by Ogden (1974). The decrease in bud outgrowth from undisturbed rhizomes began when the first flower buds became visible. For fragmented rhizomes, bud outgrowth was impaired even in the summer, but increased later in the autumn to reach a maximum in the spring. Thus, it is possible that flower bud development is initiated by long or shortening days, and dormancy in vegetative buds is a direct effect of a reproductive phase, with the presence of newly formed, dormant flower buds acting as a controlling factor for axillary bud outgrowth.

T. farfara was also a species showing clear differences between populations from different regions. The southern populations remained green for longer, and flower bud formation started later than in the northern populations. Also, growth cessation started somewhat later in the southern plants with intact rhizome systems. The dissimilarities were present in fragmented rhizomes, although not as obvious as in relatively undisturbed plants. In *C. arvense, Equisetum arvense* and *S. arvensis*, an analysis by population were significantly better than an analysis by region. This is no proof of populations from the same regions behaving less similarly than populations from different regions, but some of the differences between regions may be an effect of differences between populations. For all four species, there was no difference in the timing of reduced emergence or sprouting, although the level of the

response variable varied. Thus, the hypothesis about northern populations initiating dormancy earlier than populations from the south proved not to be true. Li *et al.* (2003) have shown a clear relationship between the latitudinal origin and the critical photoperiod for dormancy induction in *B. pendula* leaf buds. The absence of such a dependence in the herbaceous species studied here, might be due to the better protection of reproductive units, buried fairly deep in soil instead of exposed to weather and wind high up in the air. Nevertheless, the first night with frost occurs one to two months earlier in the north of Sweden than in the south (Swedish Meteorological and Hydrological Institute, 2012). As emergence and bud sprouting capacity were already resumed in December, when days are still decreasing and short, it is not likely that both photoperiod and cold temperatures are required for dormancy release, as described for *Fagus sylvatica* (Heide, 1993b). Furthermore, in contrast to trees, herbaceous perennials have no aboveground plant parts able to perceive photoperiodic changes in the winter, and may also be covered by snow.

Søgaard *et al.* (2008) and Granhus, Sundheim Fløistad and Søgaard (2009) have shown that seedlings of *P. abies* from southern Norway are more sensitive to high temperature during autumn for dormancy induction. It is possible that the conditions in the autumn of 2009 were able to induce such a kind of reduced growth capacity in the southern, but not in the northern populations of *E. repens* used here.

The reduced capacity to emerge and sprout may also be a consequence of a photoperiodic induction of changed allocation patterns within the plant, a switch from giving priority to photosynthetic organs to instead favouring the surviving storage organs, that is roots and rhizomes. The belowground system may act as a strong sink, not allowing any production of new aerial shoots. This would explain why root and rhizome allocation continued throughout the period of low emergence and sprouting. Furthermore, emergence and sprouting capacity seems to have been resumed at a time coinciding with the start of the decrease in root and rhizome biomass, and also with the first killing frost. At this time, the environmental conditions do not permit growth in the wild. Having the capacity to regenerate from belowground buds at this time will ensure quick re-growth and production of new photosynthetic organs as soon as the temperature rises. From a survival strategy point of view, this would be wise: spend energy on storage until the shoots die off, switch to a state in which energy can be spent on reproduction as soon as the environmental conditions permit.

The studies presented here indicate that sprouting from intact rhizomes of *E. arvense* is reduced during autumn. However, the rhizomes continue to load storage compounds even late in the autumn. In tuber-producing populations,

allocation of storage compounds may be directed to tuber formation as a complement to accumulation in the rhizomes. Although little emergence occurred above soil level in this species, sprouting capacity from fragmented rhizomes increased slightly from October to December, suggesting a quantitative dormancy in rhizomes of this species as well. The sprouting pattern from tubers, however, is not easily interpreted, although it does seems like some of the populations are less ready to produce shoots from tubers in the autumn months. It is possible that the absence of dormancy in tubers, and a quantitative dormancy in rhizomes, is a consequence of stored starch, depth of distribution and ability to produce "heavy" shoots with a better capacity to survive. Compared to rhizomes, tubers contain more storage compounds, are found deeper in the soil, where they are better protected from frost, and the weight of each shoot produced by a tuber is greater (Sakamaki & Ino, 2004; 2006). Thus, the need of dormancy in tubers is reduced as compared to the tiny, more exposed rhizome buds.

The resumed emergence and sprouting in all species occurred after a few weeks of outdoor temperatures below 5°C, suggesting a chilling requirement for dormancy release.

In line with other studies on *E. repens* (Håkansson & Wallgren, 1976; Brandsæter *et al.*, 2010), no dormancy was found in the autumn, neither in undisturbed plants nor in fragmented rhizomes of plants from the northern region of Sweden. Instead, sprouting and emergence increased throughout the experimental period. For all populations, a slight reduction in the shoot weight per weight of rhizome was found in the autumn, suggesting a change in allocation pattern of storage compounds. Instead of directing the nutrient flow towards aerial shoots, which will anyway be killed by a coming winter, upload of biomass to the surviving rhizomes were prioritized. Surprisingly, there was a reduction in sprouting ability from fragments in plants from the southern region, a result not reported elsewhere. While populations from the north produced more sprouts, and showed no variation in sprouting ability during the autumn, a clear reduction in September-October was seen in the two populations from southern Sweden. It would be interesting to study the influence of light and temperature on sprouting capacity in this species, in order to better understand the process behind this behaviour. However, it has to kept in mind that even at times when sprouting was impaired, almost 50% of all available buds, that is 50% of all nodes, sprouted. With regard to the tremendous number of rhizomes one plant can give rise to during one growing season, control measures will probably still be fairly effective if undertaken while sprouting is impaired. The Swedish autumns are often wet, and from the

farmers' perspective it is better to weed mechanically at a "non-optimal" time in the autumn than not to do any weed regulation at all.

From one point of view, studies on dormancy are troublesome. The focus of interest is the *absence* of growth, something we cannot see or register. Consequently, we have to study what we *can* see, that is sprouting, emergence or cell (plant) elongation. Even if the inhibition (paradormancy) from other buds is removed by the use of single-bud cuttings, we cannot say whether a non-sprouting bud is non-sprouting because of dormancy, or simply because the bud is dead. Studies on seasonal dormancy must, therefore, be undertaken during a period long enough to both detect the decrease and after a period of little or no growth, an increase in sprouting capacity. Only then can one *assume* that the lack of growth was not caused by non-living experimental material. As most methods of studying dormancy are destructive, it is not possible to assess viability over time.

It is also possible that the forcing conditions used to test growth ability are by chance very close to or within the narrow spectra of conditions that permit growth just before the period of "deep dormancy" (endodormancy), as it is described by Vegis (1964). According to his theory, dormancy can be envisioned as a gradual tapering of the temperatures and photoperiods during which plants are able to grow. When dormancy is at its peak, the window of growth-promoting conditions is very small, or totally absent. If sampling for growth capacity are done at too long intervals, and the forcing conditions used to test sprouting or emergence are close to the narrowest spectra for the species and population in question, there is a risk of missing the period of endodormancy, and to never register a period of absence of growth. The two-week intervals used in the study of seasonal sprouting from fragments may be an example of such a case, although the experiments using plants with intact underground systems indicate a reduced capacity to emerge lasting for at least four weeks.

Taken together, the results presented in this thesis imply that control measures for *E. repens* can be undertaken at any time during the autumn; the earlier the better, to prevent further rhizome growth and nutrient upload. Concerning control measures involving fragmentation, it seems that *E. arvense, S. arvensis* and *T. farfara* are more sensitive to timing than *C. arvense*. It is, however, important to control the weeds early in the autumn to prevent allocation of storage compounds to the underground system. As shown by the experiments presented here, the dry weights of the underground systems increase, at least in some populations, until late in the autumn. Nevertheless, control measures at times when the plants are dormant will be a waste of time and energy. The desired re-growth and starvation of the belowground system

by fragmentation or defoliation will not take place. Also, herbicide applications will be less efficient since little growth, and thus, little transport of different compounds occurs.

Consequently, repeated soil cultivation, such as harrowing or tillage should be avoided in September-October if the aim is to reduce the populations of *E. arvense*, *S. arvensis* and *T. farfara*. Similarly, defoliation should be avoided during the same period if the aim is to control *C. arvense, E. arvense, S. arvensis* and *T. farfara* – there will be no emergence anyway. The best way to control *E. repens* seems to be to hit hard, cut small and bury deep, as suggested by the studies of Håkansson (1967; 1969a, b).

Finally, some recommendations for future research. The experiments forming the basis for this thesis indicate a seasonal restriction in emergence and sprouting capacity for some of the species investigated. To fully understand the dynamics of the weeds in question, both induction and release of dormancy need to be further studied. Deeper knowledge is also required concerning the seasonal allocation patterns of storage compounds. With such information at hand, it may be possible to construct models which forecast the need and efficiency of weeding or herbicide application. Such models may serve as decision support tools for farmers when planning their activities, as an important part of the integrated weed management approach recommended by governments and other stakeholders.

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