Effects of integrated pest management (IPM) on the population dynamics of the perennial weed species *Cirsium arvense* (L.) Scop

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Abstract

Cirsium arvense (L.) Scop. is a troublesome weed, causing economic losses by reducing crop yield, increasing herbicide and tillage costs, and degrading soils due to increased tillage requirements. The major control method for *C. arvense* is herbicide application, but this poses socio-environmental and herbicide resistance risks. The European Union promotes reduced dependence and sustainable use of herbicides, combined with cultural and mechanical weed control. This thesis assessed the effects of integrated weed control on the population dynamics of *C. arvense*.

For mechanical control, farmers are recommended to act when *C. arvense* is most sensitive to disturbance, *i.e.* at the point of minimum belowground weight, coinciding with 7-10 leaves per shoot. However, many farmers believe that this is too late. To estimate the compensation point (CP), defined as the minimum weight of the entire belowground structure of *C. arvense*, and identify links between initial root weight, planting depth and crop competition, three outdoor pot experiments were performed. For chemical control, farmers are recommended to spray when the majority of *C. arvense* shoots are 10-20 cm high. To assess the effects of timing and dose of herbicide application (MCPA), and crop competition on growth and development of *C. arvense*, one outdoor pot experiment and one field experiment were performed. The field experiment also assessed the effects of selective cutting.

It was found that CP for *C. arvense* occurred before 3-leaf stage and that treatment effects were minor (<0.5 leaf stages). Depletion of planted root fragments ceased on average around leaf stage 3-4, indicating that CP occurs at early leaf stages. In the pot experiment, the strongest effect of herbicide treatment was obtained by spraying with the recommended dose in the presence of a crop when the largest *C. arvense* shoot had 3-4 leaves, corresponding to maximum height 13 cm and median height 6 cm. Crop competition reduced biomass, shoot height and leaf production of *C. arvense* regardless of herbicide dose. In the field experiment, herbicide treatment at 4-5 leaves or 8-10 leaves gave similar control effects as selective cutting. Herbicide application had a more immediate effect on growth and development of *C. arvense* while selective cutting depleted the below-ground structures more gradually.

The results indicate that mechanical control of *C. arvense* should be performed earlier than previously recommended, probably before *C. arvense* reaches 3-4 leaves per shoot. Also early herbicide spraying seems to be as efficient as spraying later in the season.

Keywords: Cultural control, chemical control, compensation point, competition, creeping thistle, MCPA, mechanical control, selective cutting, spring barley.

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Dedication

To Retina Tavaziva

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 T. Verwijst, V.J. Tavaziva & A. Lundkvist. Assessment of the compensation point of *Cirsium arvense* and effects of competition, root weight and burial depth on below-ground dry weight – leaf stage trajectories (submitted manuscript).

II V.J. Tavaziva, A. Lundkvist & T. Verwijst. Effects of herbicide dose, timing of herbicide application and crop presence on growth and development of *Cirsium arvense* (manuscript).

III V.J. Tavaziva, A. Lundkvist & T. Verwijst. Effects of mechanical and chemical control on growth and development of *Cirsium arvense* under field conditions (manuscript).

IV T. Verwijst, V.J. Tavaziva & A. Lundkvist (2017). Effects of selective cutting and herbicide use in spring barley on seed production of *Cirsium arvense. Acta Agriculturae Scandinavica, Section B – Soil & Plant Science* 67:6, 562-570.

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The contribution of Varwi Jacob Tavaziva to the papers included in this thesis was as follows:

I Planned the study in collaboration with the co-authors, performed the experimental work, evaluated part of the data and wrote part of the manuscript.

II Planned the study in collaboration with the co-authors, performed the experimental work, evaluated the data and wrote the main part of the manuscript.

III Planned the study in collaboration with the co-authors, performed the experimental work, evaluated the data and wrote the main part of the manuscript.

IV Planned the study in collaboration with the co-authors, performed the experimental work, evaluated part of the data and wrote part of the manuscript.

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Abbreviations

CP	Compensation point
EU	European Union
H1	Herbicide application at 4-5 leaf stage
H2	Herbicide application at 8-10 leaf stage
IPM	Integrated pest management
IWM	Integrated weed management
MCPA	2-methyl-4-chlorophenoxyacetic acid
RD	Relative depletion
S	Selective cutting

1 *Cirsium arvense* (L.) Scop.

Cirsium arvense (L.) Scop. (creeping thistle or Canada thistle) is one of the world's most troublesome weeds and is native to Europe (Tiley, 2010). The species was given the common name Canada thistle by the early residents of New England (USA), who blamed its appearance on French traders from Canada (Brenzil *et al*., 2008). *Cirsium arvense* has a deep and wide-spreading root system, which ensures survival and rapid vegetative spread under a wide range of soil and management conditions. Its populations exhibit one of the widest ranges of clonal diversity reported for any plant species and it mainly grows in patches in arable fields (Hettwer & Gerowitt, 2004). This growth in patches is considered to be due to movement or displacement of vegetative material by tillage (Hettwer & Gerowitt, 2004).

Due to its strong competitive ability in extracting water and nutrients, *C. arvense* may cause serious economic losses if not controlled effectively (Tiley, 2010). The species has negative effects on both the levels of crop yield in the whole cropping system and the fodder quality of hay and silage. O'Sullivan *et al*. (1982, 1985) estimated that a density of 20 *C. arvense* shoots per m can decrease yield in spring barley by 34% and yield in rapeseed by 26%. In pastures, grazing animals often avoid *C. arvense* plants due to the abundant spines on leaves and shoots, leading to lower forage yield (Tiley, 2010).

Perennial weeds are considered to be more difficult to control than annual and biennial weed species, since they propagate through both vegetative structures and seeds (Lemna & Messersmith, 1990; Lundkvist & Verwijst, 2011). In organic farming, farmers often use crop rotations where both perennial and annual crops are included. Shifting between annual and perennial crops causes the growing conditions to vary in the field, which makes it more difficult for individual weed species to increase and compete efficiently with a crop. Furthermore, organic farmers often use mechanical control (soil tillage, mowing and hand weeding) to control weed growth (Pitts, 2013). Within organic farming, *C. arvense* is considered one of the worst weeds (Leth *et al.*, 2008). According to Salonen *et al.* (2011), a survey in Finland showed that the number of weeds in spring cereals had a ratio of 4:1 for organic relative to conventional farming, *i.e.* an average density of 519 weeds m^{-2} in organic farming compared with 160 weeds m^{-2} in conventional farming.

In conventional farming, *C. arvense* is often controlled by phenoxy-based compounds such as MCPA and glyphosate. MCPA (2-methyl-4-chlorophenoxyacetic acid) is an auxin-based selective herbicide which kills the weed by stimulating abnormal and uncontrolled growth (Fogelfors & Lundkvist, 2008). Glyphosate (N-phosphonomethyl glycine) is a non-selective herbicide which kills the weed by being absorbed through foliage and translocated to the growing points, where it inhibits the plant enzyme responsible for synthesis of three aromatic amino acids: tryptophan, tyrosine and phenylalanine (Kirkland, 1977).

However, over-reliance on herbicides raises some concerns about environmental pollution, health risks and development of herbicide resistance (Tilman *et al.*, 2002; Kudsk & Streibig, 2003; Vasileiadis *et al.*, 2017; Lamichhane, 2017). These concerns prompted the European Union (EU) to issue out a directive, in 2009, which states that: '*member states shall take all necessary measures to promote low pesticide-input pest management, giving wherever possible priority to non-chemical methods so that professional users of pesticides switch to practices and products with lowest risk to human health and the environment among those available for the same pest problem*'. Low pesticide input pest management systems include integrated pest management (IPM) and organic farming. IPM emphasises the growth of a healthy crop with the least possible disruption to agro-ecosystems and encourages natural pest control methods (Official Journal of the European Union, 2009). This directive requires EU farmers to shift to agricultural systems which are more environmentally friendly.

The overall aim of this thesis work was to obtain more information on the population dynamics of *C. arvense* and how it can be modified by different types of weed control strategies, such as chemical, physical and cultural control. Such information can contribute to the development of more efficient and sustainable weed control methods for *C. arvense*.

1.1 Origin and history

Cirsium arvense originated in the temperate Middle East and has been considered a troublesome weed in Europe since as early as the 16th century (Tiley, 2010; Moore, 1975). *Cirsium arvense* was introduced to North America around the 17th century, where it was brought in as a farm seed contaminant from Europe (Hansen, 1918).

In Sweden, *C. arvense* is found in most parts of the country, on arable land and meadows but also on seashores, road verges and railway embankments (Anderberg, 2011). In a farm survey in the 1920s, when tillage was the main control strategy, *C. arvense* and *Elymus repens* (L.) Gould. (couchgrass) were considered to be the most problematic weeds due to their deep-growing root and rhizome system, respectively (Adolfsson, 1996). It was difficult to fragment a deep-rooted system by tillage (Håkansson, 2003). In the 1950s, when herbicides such as phenoxy-based compounds (MCPA) emerged, the occurrence of *C. arvense* on Swedish arable land diminished. During recent decades, however, *C. arvense* has become an increasing problem due to reduced use of herbicides and an increase in organic farming, which completely bans the use of herbicides (Bellinder *et al.*, 1994; Håkansson, 2003).

1.2 Geographical distribution and habitat

Cirsium arvense occurs mainly in the temperate regions of world, *i.e.* in the northern hemisphere (Figure 1). It is native to south-eastern Europe and the Middle East and has spread throughout the whole of Europe, North America and North Africa (Moore, 1975; Tiley, 2010). In the southern hemisphere, it has been reported in South America and parts of South Africa and is now also considered a problematic weed in Australia and New Zealand (Tiley, 2010). The species is not found in the hot tropics, since it is adapted to more temperate conditions, *i.e.* it has a C_3 photosynthetic pathway and is a long-day plant (Håkansson, 2003).

Cirsium arvense is an early successional species often found on shorelines (natural habitat) and has been favoured over time by changes in the landscape caused by humans. As a result, it is also found in semi-natural habitats (road verges) and arable fields (Bommarco *et al*., 2010). *Cirsium arvense* is shade intolerant and is thus uncommon within forests, but can be found on forest edges.

Cirsium arvense thrives best in a temperature range of 0-32 °C and requires rainfall of 400-700 mm per annum (Detmers, 1927). Due to its C_3 photosynthetic pathway, the species does not thrive in areas with persistent drought or where the soil dries out easily (Håkansson, 2003). *Cirsium arvense* occurs on a wide range of soil types, but grows best in nutrient-rich and well-aerated soils. Waterlogged soils limit growth of its deep-growing root system (Tiley, 2010).

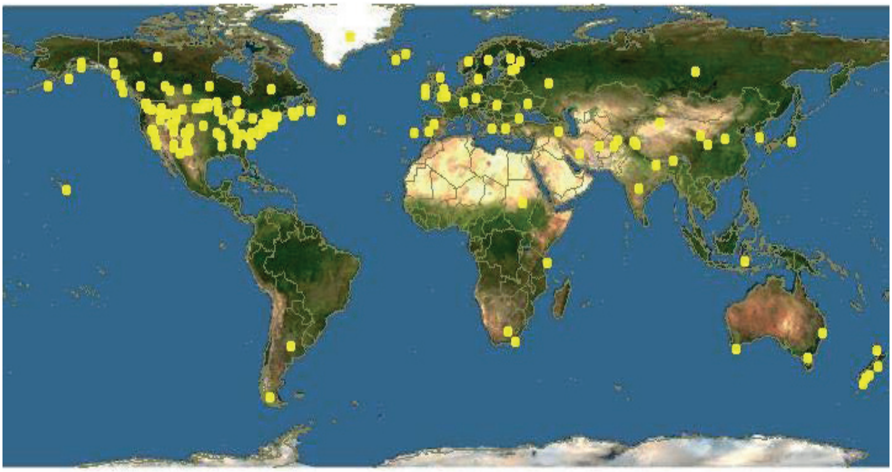


Figure 1. Global distribution of *Cirsium arvense* (Tiley, 2010).

1.3 Biology and population dynamics

The population dynamics of a weed species may be defined as the change in number of plants per unit area over time in response to weed biology, environmental factors and weed management. The weed population observed in a particular year is a function of changes that occurred throughout the previous year (Anonymous, 2017).

To optimise control of *C. arvense*, it is imperative to understand its life cycle, growth pattern and resource allocation. This knowledge can be used to predict the parts of the life cycle in which the weed is most susceptible to control measures.

1.3.1 Biology

Cirsium arvense belongs to the family Asteraceae and tribe Cardueae. It is a C_3 long-day plant with chromosome number 2n=34 and requires a photoperiod of 15 hours (Tiley, 2010). It comprises creeping horizontal and vertical roots. The horizontal roots can be as long as 5 m and give rise to aerial shoots, while the vertical roots can grow to depths of 2-5 m. Tworkoski (1992) found that the roots spread at a rate of 1 to 2 m per year and that adventitious shoots develop from the root system. The root system is extensive and can colonise an area within a short space of time. Erect stems can reach a height of 30-180 cm and are hairy, green in colour, and leafy to the apex (Moore, 1975; Tiley, 2010). The leaves alternate, spiny, with crinkled edges and green in colour. *Cirsium arvense* is dioecious and they can be 1-5 flower heads per branch. The leaves at the base and top of the stem are rather smaller than those in the middle (Tiley, 2010). Male staminate heads are globular and smaller than the flask-shaped pistillate female heads. The flowers are a distinct purple colour (Moore, 1975). The achenes are smooth, shiny and finely grooved and the pappus is grey-whitish to brown in colour (Tiley, 2010). Viable seed is produced through insect pollination, mainly honeybees and butterflies. Consequently, female and male clones must be in close proximity in order to facilitate pollination (Ellis & Ellis-Adam, 1992). Hayden (1934) found that the distance between male and female *C. arvense* plants is inversely proportional to the number of viable seeds produced, *i.e.* the shorter the distance, the larger the number of seeds produced. *Cirsium arvense* produces up to 100 seeds per flower receptacle (Derscheid & Schultz, 1960). A single plant can produce as many as 5200 seeds in one season, but the average is approximately 1500 seeds per plant in a season (Rutledge & McLendon, 1998).

Sexual reproduction in *C. arvense* helps the species to maintain genetically diverse populations which have the ability to adapt to changes in cropping systems (Hettwer & Gerowitt, 2004). It also helps the species to colonise new habits by means of wind and agricultural implements (Leth *et al.*, 2008). Vegetative reproduction ensures its multiplication and persistence in a cropping system (Håkansson, 2003).

1.3.2 Life cycle

Cirsium arvense is able to regenerate from adventitious root buds on root fragments as short as 10 mm, with a thickness of mostly 3-7 mm (Hamdoun, 1972; Håkansson, 2003). The root buds that give rise to adventitious shoots can arise at any point along the root system or fragment (Donald, 1994). These are traits which ensure the persistence and success of *C. arvense* (Nadeau & Vanden Born, 1989). In the U.S., over-wintering roots develop new underground roots and shoots in January and begin to elongate in February (Nuzzo, 1997). As the soil temperature starts to rise in spring, primary aerial shoots of *C. arvense* start to emerge on the soil surface (Moore, 1975). In Canada, shoot emergence occurs in late March or early April (Tiley, 2010). In Sweden, shoots emerge about 10-15 days after spring has commenced, *i.e.* in March-April (Håkansson, 2003). According to Donald (2000), shoots start to emerge from adventitious root buds after a heat sum accumulation of 197 °C day (by day 91, *i.e.* in March). Shoot emergence usually commences when the average weekly temperature reaches 5 °C and is optimal when the temperature is about 8 °C (Hodgson, 1968). After shoot emergence, a rosette of leaves develops and, as the air temperature continues to rise, the stem elongates (Tiley, 2010). Rapid growth of about 3 cm day^{-1} occurs in June, levelling off in July and by August growth will have ceased (Moore, 1975). Flowering occurs in the middle of July and the pappus emerges late in July or early in August (Tiley, 2010). In August, winds help to disperse the pappus during dry days and, from late September, mature stems start senescing and eventually die due to frost and low temperatures. The aboveground shoots disappear in winter, until spring comes again (Moore, 1975). Secondary shoots which emerge in late summer or early autumn normally develop only into rosettes. These usually develop where plants were mown or treated with herbicides during the summer and grow with less vigour (Tiley, 2010). They ultimately die off because of frost and low temperatures.

According to Håkansson (2003), the success and persistence of *C. arvense* is chiefly dependent on its vegetative reproduction. However, Heimann & Cussans (1996) concluded that the contribution of sexual reproduction to the spread and survival of *C. arvense* is rather under-estimated. Thus, its success is due to a combined contribution from both vegetative and sexual reproduction (Solé *et al.*, 2004). A soil seed bank with dormant seeds builds up and when environmental conditions become conducive they germinate, with a germination rate of up to 95% (Hayden, 1934). Roberts & Chancellor (1979) concluded that most seeds emerge within a year after dispersal, while Thompson *et al.* (1997) considered the seedbank to be rather extensive. New seedlings often germinate in spring, when temperatures fluctuate from 10 to 28 °C (Bakker, 1960). When seedlings emerge, they develop a fibrous tap root and within 10 weeks the main root thickens and gives rise to lateral roots, which spread out horizontally (Håkansson, 2003). The same process as for vegetatively reproduced shoots then begins.

1.3.3 Population dynamics and resource allocation

A single seedling in a newly invaded area can form a large patch of shoots through vegetative propagation of the root system. Consequently, *C. arvense* occurs as clumps of shoots or in patches throughout the field (Moore, 1975). Environmental conditions greatly impact on the regenerative capacity and ability of *C. arvense* (Sciegienka *et al.*, 2011). Basically, when the environmental conditions become conducive, in spring, a flash of shoots emerge. Shoot numbers gradually increase from March to June. The abundance of the weed is dependent on the history of infestation, environmental conditions and the effectiveness of control strategies. A study by Hayden (1934) reported an incidence of 180 shoots per m^2 in an oat field infestation which had been established for 25 years. When the plant begins flowering in mid-July the number of shoots levels off. From late September onwards, the number of shoots starts to decline as they begin to senesce (Tiley, 2010). They then die because of frost and low temperatures. According to Andersson *et al.* (2013), *C. arvense* avoids sprouting in autumn and undergoes apical dormancy due to low air temperature and drought. Growth only resumes in spring when air temperature rises again.

Nutrients are stored as food reserves in the root system and in spring they produce large amounts of aboveground biomass, so *C. arvense* competes with the cultivated crop (Thomsen *et al.*, 2015). The reserves are mainly stored as carbohydrates, with inulin and sucrose being the principal carbohydrates found in *C. arvense* roots according to Tworkoski (1992). This was confirmed by Nkurunziza & Streiberg (2011), who found that the dominant carbohydrate reserves in belowground parts of *C. arvense* are fructo-oligosaccharides. During the onset of growth in spring, there is a decline in the amount of carbohydrates due to root respiration and supplementation of photosynthesis for shoot growth (Moore, 1975). McAllister & Haderlie (1985) observed that the content of carbohydrate reserves in autumn was much higher (26% of fresh weight) than in spring, after the onset of growth (3% of fresh weight). The lowest amount of carbohydrate reserves in the root system is usually observed in early June, when there is zero net assimilation of nutrients between the shoots and the roots (Welton *et al.*, 1929; Hodgson, 1968). This state is known as the compensation point and coincides with the minimum regenerative capacity of the root system (Graglia *et al.*, 2006). Thus *C. arvense* is considered to be most susceptible to disturbance when it reaches the compensation point. According to earlier studies by Dock-Gustavsson (1997), the compensation point occurs when *C. arvense* has attained a phenology of 8-10 expanded leaves. Consequently, farmers in Sweden are advised to control *C. arvense* mechanically at this stage. Thomsen *et al.* (2011) studied the effects of root length, burial depth, competition and cutting on growth and development of *C. arvense* in Norway. They did not formally refer to the compensation point, but when growing *C. arvense* without competition, a minimum below-ground dry weight was suggested to coincide with a phenological stage of approximately 3-7 leaves.

A surge in photosynthesis in late summer replenishes the carbohydrate root reserves, as photoassimilates are sent from the aboveground shoots into the root system for storage. As autumn approaches, the new roots continue to grow and they begin to become dormant, preparing for overwintering (Hein & Wilson, 2004). This theory is supported by Håkansson (2003), who concluded during this period there is no shortage of food reserves in the root system, but the rate of emergence of new shoots is minimal. Late in the autumn, aboveground structures are killed off by frost and low temperatures. During winter, respiration diminishes *C. arvense* root biomass. In the similar perennial weed species *Sonchus arvensis* L. (creeping sow-thistle), root biomass may be reduced by about 30-

40% during the winter period (Tørresen *et al.*, 2010; Verwijst *et al.*, 2013).

1.4 Control methods

Weed control strategies may be classified into four different categories: cultural, mechanical, chemical and biological.

1.4.1 Cultural control

Cultural control is the deliberate alteration of the production system, either the cropping system itself or specific crop production practices, to reduce weed populations or weed-induced yield losses (Herzog & Funderburk, 1986). Melander *et al.* (2005) states that the main goal for cultural methods is to "*reduce weed competition through the enhancement of crop competitive ability*", by using competitive varieties and appropriate sowing/planting pattern and fertilisation strategies.

Weed - crop competition

Weeds occupy a similar trophic level as crop plants, and thus they compete for the same resources (nutrients, water, light and space). The crop has to possess a competitive advantage over weeds in order to reduce or delay growth and development of weeds (Bond & Grundy, 2001). At the seedling stage, *C. arvense* is susceptible to shading and competition for light from neighbouring plants in crop stands (Tiley, 2010). When the crop plants are taller at the early stages of *C. arvense* development, then competition for light is stronger (Boström & Fogelfors, 1999). Pilipavicius *et al.* (2011) observed that increasing crop stand density of spring barley augmented its competitive ability against *C. arvense* and annual weeds such as *Chenopodium album* L. (fat-hen) and *Stellaria media* (L.) Vill. (chickweed). Graglia *et al.* (2006) also showed that interspecific competition from a crop in an agricultural system is a reliable control strategy against *C. arvense*. In Norway, Thomsen *et al.* (2011) found that using green manure comprising a mixture of *Phacelia tanacetia* (lacy phacelia), *Vicia sativa* L. (common vetch), *Trifolium pratense* (red clover) and *Lolium multiforum* (Italian ryegrass) reduced *C. arvense* growth by up to 90%. However, Lukashyk *et al.* (2007) concluded that perennial weeds are difficult to control by crop competitiveness. The presence of multiple plants in a given soil volume can trigger nutrient stress in a given plant, as neighbouring plants take up limited resources (Craine & Dybzinski, 2013). A study by Mohammaddoust-e-Chamanabad *et al.* (2007) showed that crop rotation and fertiliser application increased nutrient uptake by spring barley and consequently its competitiveness over weeds was enhanced.

Crops

Cereal crops have early vigour and thus possess a greater competitive advantage over weeds than other crop species such as peas, oilseed rape, potato and soyabean (Boström & Fogelfors, 2000; Teasdale *et al.*, 2007). In Canada, studies have shown that the choice of crop is imperative in decreasing *C. arvense* populations, *e.g.* the abundance of *C. arvense* decreases in lucerne crops but increases in soyabean crops (Schreiber, 1967). The choice of cultivar can also have an effect on weed suppression. Grundy *et al.* (1993) showed that a winter wheat variety with longer straw suppressed weeds more than a modern variety with shorter straw.

Cover crops are mainly used as a catch crop between or within main crops to prevent soil erosion or leaching of nutrients and, in the process, they also serve as weed suppressors (Håkansson, 2003; Melander *et al.*, 2013). In Sweden, undersown cover crops such as hairy vetch (*Vicia villosa* L.), birdsfoot trefoil (*Lotus corniculatus* L.) and white clover (*Trifolium repens* L.) are mostly used in spring cereals (Aronsson *et al.*, 2015). However, in a four-year study by Brandsæter *et al.* (2011), red clover undersown in a cereal crop did not significantly reduce the growth of *C. arvense*, *S. arvensis* or *E. repens*.

Crop rotation

Weeds usually grow together with crops that have similar life cycles. When using a crop rotation where monocotyledonous crops are continuously sown, a certain type of weed flora will develop. When including a dicotyledonous crop in the rotation, the environmental conditions to which the weed flora has adapted will be altered. The choice of crop and rotating species with different seasonal and growing cycles as the weed can markedly diminish the competitive effects from the weed (Bàrberi & Casio, 2001). The use of ley crops has been shown to be effective in combating *C. arvense* in Swedish agricultural systems. The competitiveness of ley crops, coupled with mowing at regular intervals, has been proven to be quite an effective control tool for *C. arvense* (Håkansson, 2003).

1.4.2 Mechanical control

Mechanical control involves physical disturbance of the environment with the aim of directly killing or desiccating weeds (Lundkvist & Verwijst, 2011). Weed plants are uprooted, dismembered and buried. Germination and establishment of weeds is promoted by altering the soil environment and weed seeds/roots/rhizomes are moved vertically and horizontally, affecting the emergence, survival and competitiveness of the weeds (Mohler, 2001).

Ploughing

In Sweden, ploughing is mainly carried out in the autumn after crop harvest, or in the spring. It usually involves deep ploughing, with mouldboard ploughing being the most popular method in Sweden (Håkansson *et al.*, 1998). Ploughing helps to control *C. arvense* by killing the aboveground shoots, fragmenting the roots and burying them deeper in the soil or bringing them up to the soil surface where they are exposed to desiccation. Fragmenting roots results in increased number of buds that can produce shoots. However, the more deeply buried and smaller the root fragments, the more energy is required for sprouting shoots to reach the soil surface. This leads to fewer and less competitive shoots emerging (Håkansson, 2003). Studies by Dock-Gustavsson (1997) found that short root fragments (7 cm) of *C. arvense* buried deep had reduced regeneration capacity compared with longer fragments (21 cm). In Sweden, the normal ploughing depth is 20-25 cm, depending on the soil type (Håkansson *et al.*, 1998). This means that below 25 cm, the root system of *C. arvense* remains intact and can therefore be the source of new shoots emerging. According to Thomsen *et al.* (2013), most of the root biomass of *C. arvense* is found in the upper 40 cm of the soil profile, with 84% found within 7-40 cm (Hodgson, 1968).

Stubble cultivation

Stubble cultivation is mainly performed in autumn, just after crop harvest, using a cultivator. In Sweden, the normal cultivation depth is 10-15 cm (Håkansson *et al.,* 1998). Stubble cultivation controls perennial weeds by fragmenting roots which function as vegetative propagules and spreading them within the soil profile (Lundkvist & Verwijst, 2011). As mentioned above, increased burial of root fragments inhibits *C. arvense* emergence, while root fragments located on the soil surface are subject to desiccation or freezing, provided the weather conditions are suitable (Håkansson, 1971).

Harrowing, weed harrowing and inter-row hoeing

Harrowing is used to prepare the seedbed, kill weed seedlings or level the soil surface. In cereals, spring-tine or chain harrows are mostly used, depending on soil type (Lampkin, 1990). Weed harrowing is usually carried out just before or after sowing, so as to give the crop a competitive advantage over already emerged weed seedlings by uprooting and burying them in soil (Bond & Grundy, 2001). In perennials, harrowing can fragment roots which are close to the soil surface (Lundkvist & Verwijst, 2011). However, it is difficult to control perennials with a vigorous root system such as *C. arvense* with a single harrowing (Håkansson, 2003).

Inter-row hoeing controls weeds between the crop rows to a depth of 5-10 cm through soil coverage, uprooting or root cutting (Mohler, 2001; Melander *et al.*, 2005). The method is used in row crops (maize, potatoes, sugar beet) but also in cereals sown with larger row spacing (>18 cm). Hoeing is most efficient against annual weeds, but may also give some control effects on perennial weeds with a rather shallow underground root/stem system (Lundkvist & Verwijst, 2011).

Mowing

Mowing involves cutting or defoliation of the aboveground parts of weeds using a mechanical implement. Mowing prevents or reduces the process of photosynthesis, so photosynthetic assimilates are prevented from being allocated to the roots (Andersson *et al.*, 2013). This leads to reduced size of the overwintering root system and, in turn, the subsequent shoot population is also regulated (Bourdot *et al.*, 2006; Graglia *et al.*, 2006). When *C. arvense* shoots are cut off, emergence of new shoots is stimulated due to the breaking of apical dominance, known to be exerted by the main shoots (Andersson *et al.*, 2013). Therefore, if mowing is repeated, nutrient reserves stored in the roots are depleted (Graglia *et al.*, 2006). In addition to the removal of photosynthetic capacity, mowing during the rainy season may accelerate the weakening and decaying of belowground structures when rainwater enters the cut ends of the mature *C. arvense* shoots (Bourdot, 2011). According to Bourdot *et al*. (2016), the frequency of mowing within a growing season is inversely proportional to the rate of *C. arvense* shoot population decline.

Many success stories involving repeated mowing of *C. arvense* have been reported. Derscheid *et al*. (1961) observed that a cover crop, *Bromus inermis* Leyss (smooth brome), combined with repeated mowing for three years, resulted in almost 90% suppression of *C. arvense.* This was corroborated by Graglia *et al*. (2006), who also observed that competition from a cover crop combined with frequent mowing greatly reduced the regenerative capacity of *C. arvense*. *Medicago sativa* (lucerne) mown twice a year has been shown to reduce *C. arvense* populations significantly after four years (Wilson *et al*., 1999).

In the past, mowing of *C. arvense* was only possible after harvesting of cereal crops (Tiley, 2010). However, a new method for controlling *C. arvense* in cereals, selective cutting, has been developed in Sweden. The implement involved (CombCut®; Figure 2) selectively cuts the aboveground parts of *C. arvense* and combs through the cereal crop without damaging it (Anonymous, 2016; Lundkvist *et al.*, 2011).

Figure 2. CombCut® machine, which selectively cuts *C. arvense* and combs through the cereal crop without damaging it. Photo: Jonas Carlsson.

1.4.3 Chemical control

Chemical control involves the use of herbicides to kill and control weeds, which is an effective way of controlling weeds.

Commonly used selective herbicides to control *C. arvense* in cereal production and in pastures are hormone herbicides (phenoxy-based) such as MCPA (Moore, 1975). Non-selective and residual herbicides such as glyphosate (N-phosphonomethyl glycine) have been used to control *C. arvense* in non-crop areas and after crop harvest in the autumn (Tiley, 2010). *Cirsium arvense* is killed when glyphosate's biologically active compound is absorbed and translocated to the underground storage organs (Moore, 1975). However, *C. arvense* may be difficult to control in autumn due to dormancy and early withering or senescing of the leaves. Hence it is better controlled in the growing season with selective herbicides combined with non-selective herbicides after harvest (Tørresen *et al.*, 2010; Andersson *et al.*, 2013). Herbicides currently used in Sweden for controlling *C. arvense* are listed in Table 1.

Due to environmental and societal considerations, ways to mitigate or reduce the use of herbicides have to be developed. With this in mind, this thesis investigated whether reduced dosage and timing, *i.e.* the most effective time to spray *C. arvense*, could help in sustainable use of herbicides.

Table 1. *Herbicides used for controlling* Cirsium arvense *in different types of crops (Swedish Board of Agriculture, 2017)*

Crop	Herbicide (product name)	Active ingredient
Spring cereals	MCPA 750	Dimethylamine salt
	Ally 50 ST	Metsulfuronmethyl
	Gratil 75 WG	Amidosulfuron
	Mustang forte	Aminopyralid & Florasulam
Winter cereals	Matrigon 72 SG	2-Pyridinecarboxylic acid
	Mustang forte	Aminopyralid & Florasulam
Maize	Callisto	Mesotrione
	Matrigon 72 SG	2-Pyridinecarboxylic acid
	Titus 25 WSB	Rimsulfuron
	Harmony 50 SX	Tifensulfuromethyl
Oilseed rape	Galera	Picloram & Clopyralid
	Matrigon 72 SG	2-Pyridinecarboxylic acid
Ley	Ariane S	Clopyralid, Fluroxypyr & Dimethylamine salt

1.4.4 Biological control

Biological control involves the use of living organisms to suppress and control weed infestation. The advantage of using biological control is that it offers a low-cost and host-specific control approach for *C. arvense* (Berner *et al.*, 2015).

A phytophagus stem-mining weevil, *Hadroplontus litura* F., has been identified as a potential biological control agent for *C. arvense* (Gramig *et al.*, 2015). The adults feed on leaf tissue, mate and lay eggs. When the larvae develop they burrow into the stem of *C. arvense* and feed from the inside, thereby causing dislodging of the shoots (Zwolfer & Harris, 1966). However, *H. litura* is not significantly effective in suppressing *C. arvense* on a large scale and requires several years to show a significant effect (Burns, 2013). Reduction in *C. arvense* abundance, size and flowering has been observed after 10 years of exposure to *H. litura, Urophora cardui* L. (gall fly) and *Larinus planus* F. (seedhead weevil) (Markus & Larson, 2011).

Fungi have also been shown to be potentially effective biological control agents for *C. arvense* (Moore, 1975). The fungus *Sclerotinia sclerotiorum* has been used successfully in the control of *C. arvense* in pastures in New Zealand (Tiley, 2010). Studies by Brosten and Sands (1986) showed that 20-80% of *C. arvense* shoots were killed after applying *Sclerotinia sclerotiorum*. However, this fungus is not host-specific to *C. arvense* and is known to infect commercial crop plants (Kluth *et al.*, 2005). In Denmark, the fungus *Phomopsis cirsii* has been shown to have potential for use as a mycoherbicide, as it causes stem canker and dieback on *C. arvense*. The fungus with the greatest potential for use as a mycoherbicide is *Puccinia punctiformis* (Muller *et al.*, 2011). It is an obligate rust fungus that is host-specific and can systemically infect *C. arvense*, resulting in permanent infection of the root system (Berner *et al.*, 2015). Combined inoculation of *Phoma destructive* and *Puccinia punctiformis* has been found to reduce a *C. arvense* population from 60% to 5% cover within three years (Kluth *et al.*, 2005).

Despite the above, according to Tiley (2010) biological control has minimal effect with respect to controlling *C. arvense* on a large scale. A combination of biocontrol agents and herbicides might prove more effective and curtail the current over-reliance on herbicides by farmers.

1.4.5 Integrated pest management (IPM)

Due to emerging herbicide resistance, government legislation and adverse effects on food safety and the environment, the sole reliance on herbicide weed control has become somewhat controversial in recent years (Bellinder *et al*., 1994; Boström & Fogelfors, 2000; Bastiaans *et al*., 2008). According to Muller & Collins (2012), there is a need to fully understand how the different control strategies complement each other, in order to maintain weed populations below the economic damage level without over-reliance on herbicides.

The Food and Agriculture Organization of the United Nations (FAO) defines integrated pest management (IPM) as the "*careful consideration of all available pest control techniques and subsequent integration of appropriate measures that discourage the development of pest populations and keep pesticides and other interventions to levels that are economically justified and reduce or minimize risks to human health and the environment*" (FAO, 2017).

The term IPM was first coined by entomologists in the 1960s with respect to problems emanating from heavy reliance on insecticides (Thill *et al*., 1991). Recently, it has been expanded to encompass all the plant protection disciplines, namely entomology, nematology, plant pathology, weeds science, horticulture, agronomy, ecology, economics and systems science (Swanton, 1996). Integrated weed management (IWM) is a component of IPM used by weed scientists. The term IWM has been used consistently by weed scientists since the 1970s (Walker & Buchanan, 1982). The main goal in IWM is to maintain weed populations below the economic damage level by combining several control strategies such as tillage, herbicide application timing and rates, cover crops, mowing and crop choice and competition (Elmore, 1996; Boström & Fogelfors, 1999). Combining two or more treatments within an integrated management strategy may provide more effective control of *C. arvense* than each treatment alone (Burns *et al*., 2013). According to Grekul & Bork (2007), long-term control of *C. arvense* by herbicides is enhanced with annual spring fertilisation. Burns *et al*. (2013) found that the biological agent *Hadroplontus litura* (stem-mining weevil), when combined with competition from *Helianthus annuus* (common sunflower), suppressed *C. arvense* to some degree.

2 Overall aims and objectives and specific hypotheses

The overall aim of this thesis was to obtain more information on the population dynamics of *C. arvense* and how it can be modified by different types of weed control strategies. Such information can assist in the development of more efficient and sustainable weed control methods for this weed species.

2.1 Paper I

The specific objective in Paper I was to assess, by means of curve fitting procedures, the influence of competition, planting depth and root weight on the phenological stage at which the compensation point, defined as minimum dry weight of belowground biomass, occurs in *C. arvense*. Effects of leaf and leaf stage definition and choice of leaf range and model on the estimates of compensation point were also assessed.

The following hypotheses were tested:

- The compensation point likely occurs before *C. arvense* has developed 3 leaves
- Relative depletion of the belowground system at the compensation point is lower at a lower initial root weight compared to higher initial root weight
- Effects of leaf, leaf stage definition and choice of leaf range and model do have minor effects on the CP estimates, relative to the difference targeted in the first hypothesis.

2.2 Paper II

The specific objective in Paper II was to assess effects of timing of herbicide application, herbicide dose and crop presence on growth and development of *C. arvense*. The effect of a control method is strongly dependent on targeting *C. arvense* at its most vulnerable developmental stage. This is assumed to be at the compensation point. In Paper I, the results showed that compensation point occurred just before the 3-leaf stage.
The following hypotheses were therefore tested:

- Herbicide application close to 3-leaf stage gives the strongest control effect on *C. arvense*
- Presence of a crop increases the control effect of herbicide treatments
- A reduced herbicide dose gives the same control effect as the recommended dose.

2.3 Paper III

The specific objective in Paper III was to evaluate and compare the effects of a selective cutting treatment on *C. arvense* (shoot and biomass production) and spring barley (grain yield) with two herbicide treatments (MCPA) applied at two phenological stages of *C. arvense*. All treatments were applied over two consecutive growing seasons in two different spring barley crops sown on the same soil.
The following hypotheses were tested:

- Herbicide treatment reduces *C. arvense* shoot numbers and aboveground biomass production faster and to a higher degree than selective cutting
- Early herbicide application is more effective than late herbicide application
- Control treatments give stronger effects in the second year
- Herbicide treatments give higher crop yields than selective cutting.

2.4 Paper IV

The specific objective in Paper IV was to test the control effect of selective cutting (CombCut®) with regard to its ability to restrict seed production of *C. arvense* and compare it with the control effect of a herbicide (MCPA) applied at two different phenological stages of *C. arvense*.

The following hypotheses were tested:

- Herbicide treatment restricts seed production per unit area more than selective cutting
- Early herbicide application decreases seed production per unit area more than late application
- Individual seed weight is not affected by weed control method
- Number of seeds per shoot, flower receptacle and unit area is affected by weed control method
- Herbicide treatment decreases the number of shoots per unit area more than selective cutting, but selective cutting decreases shoot numbers compared with no treatment.

3 Material and methods

3.1 Site

All experiments were conducted either in pots in an outdoor net enclosure (Papers I & II) or in the field (Papers III & IV) at Ultuna (59˚48’N, 17˚39’E, 5 m above sea level), close to Uppsala, Sweden. The soil in the experimental field is a heavy clay, which was ploughed prior to sowing in all field experiments.

3.2 Plant material

The plant material used for all experiments was *C. arvense* and spring barley (*Hordeum vulgare* L. var. SW Waldemar). Spring barley and root fragments of *C. arvense* with a fresh weight of 0.8 and 2.4 g comprised the plant material for experiments in Papers I and II. The root fragments were obtained from a *C. arvense* root bank kept at SLU, Ultuna. The root bank was stored from October-June in pots with a soil volume of 0.012 m^3 in a dark cold room at a temperature of +2 to +4 °C. In June, the pots were taken from the cold store and the roots were replanted and fertilised with 70 kg N ha^{-1}. The soil was then kept moist during the growing season (June-October).

In Papers III and IV, a naturally established population of *C. arvense* and spring barley sown at a nominal density of 400 kernels m^{-2} was used for experiments

3.3 Experimental designs

3.3.1 Paper I

Paper I comprised three outdoor pot experiments and a *C. arvense* leaf definition assessment. Pots, with a volume of 12 litres and a surface area of 0.064 m^2 were filled with soil, consisting of 85% moderately composed peat, 15% sand, total N-content of 0.057 kg m^{-3}, and NPK proportion of 2:1:2 (Hasselfors Garden AB, Sweden) and irrigated just before planting. One day prior to planting of each of the experiments, *C. arvense* roots were harvested from the plant bank. Roots with a diameter of approximately 3-5 mm were then cut in pieces with a mean fresh weight of 0.8 or 2.4 g, respectively. Each root piece contained at least two adventitious buds. To estimate the initial dry matter content (DMC) in the root pieces, twenty root fragments with a length of 14 cm were weighed, dried and weighed again. After planting of one root fragment per pot, the pots were irrigated and fertilized with 60 kg N ha^{-1} and the soil was kept moist during the complete growing season.

In experiment 1 (planted on June 4th 2013), the experimental factors were planting depth, root weight and competition from spring barley. The experiment was a split-plot design with competition randomised to main plots. Planting depth (5 and 15 cm) and root weight (0.8 and 2.4 g) were completely randomised to subplots within the main plots. To avoid the effect of shading, plants subjected to competition were separated from those without competition (Figure 3). Twelve harvests were performed following the phenological development stage of the most developed shoot per experimental unit (from emergence to 12-leaf stage). In total, the experiment consisted of four blocks × eight subplots × 12 leaf stages, *i.e.* 384 experimental units. Thirty-two extra pots were planted (4 for each of the experimental combinations) which were used to replace pots where *C. arvense* did not emerge within the original experiment.

In experiment 2 (planted on June 20th 2014), a randomised block design with five blocks was used. The experimental factors were planting depth (5 and 15 cm) and root weight (0.8 and 2.4 g). Six harvests, at distinct phenological development stages (3-8 leaves) of *C. arvense* were performed. In total, the experiment consisted of (five blocks × two levels of planting depth × two levels of root weight × six leaf stages) *i.e.* 120 experimental units. Twenty extra pots were planted (5 for each of the experimental combinations) which were used to replace pots where *C. arvense* did not emerge within the original experiment.

In experiment 3 (planted on June 20th 2014, root weight 2.4 g and planting depth 5 cm), the design was completely randomised and the experimental factor was crop competition. Six harvests, connected to phenological development (3-8 leaves) of *C. arvense,* were performed. In total, the experiment comprised 5 replicates × 2 competition levels × 6 leaf stages, *i.e*. 60 experimental units.

A leaf definition for *C. arvense* was calibrated by collecting 49 shoots covering a range from 1 to 13 leaves and having two researchers independently assess the developmental stage of each shoot.

Figure 3. Set-up for experiment 1 in Paper I, showing *C. arvense* plants subjected to competition from spring barley separated from those without competition to avoid the effect of shading. Photo: Monika Welc.

3.3.2 Paper II

During June–September 2014, a pot experiment was conducted outdoors in a net enclosure at Ultuna close to Uppsala, Sweden (59°48’N, 17°39’E) to assess effects of herbicide dose, timing of herbicide application and presence of a crop. A randomised block design with five blocks was used. The experimental factors were herbicide treatment (control, 50% and 100% of recommended dose), timing of herbicide application and crop presence (with and without spring barley). Timing of herbicide spraying followed six phenological development stages of *C. arvense* (3-8 leaves). The herbicide treatments were performed indoors in a closed ventilated spray chamber designed to resemble field spray treatments (Kristensen, 1992a, b) (Figure 4).

In advance, it was randomly determined which experimental units should be (i) planted with spring barley, and (ii) sprayed at a particular phenological stage. At each herbicide treatment, corresponding control treatments were harvested to assess growth and development of *C. arvense*. Another 10 control units (five units with *C. arvense* and five units with *C. arvense* + spring barley) to be used as controls at harvest were included in the experiment. In total, the experiment consisted of (five blocks × two levels of competition × three levels of herbicide treatment × six leaf stages) + 10 control units, *i.e.* 190 experimental units.

Figure 4. Ventilated spray chamber used for herbicide treatments in the experiment in Paper II.

3.3.3 Papers III and IV

During 2015-2017, a field experiment was performed at Ultuna close to Uppsala, Sweden to assess effects of selective cutting and herbicide applications repeated at the same site two years in a row, on the growth and development of C. arvense under field conditions. The field experiment was laid out as a randomised block design with three blocks, four treatments and two replicates per block, *i.e.* 24 experimental plots, each measuring 3 m × 15 m. Treatments consisted of a control (C), an early herbicide application (H1) at an average of 4-5-leaf stage of *C. arvense*, a late herbicide application (H2), at the 8-10 leaf-stage, and a selective cutting, simulating CombCut© action (S), after shoot elongation around an average of 10-leaf stage, just before spike formation of the barley.

Figure 5. Tractor-drawn planter, planting spring barley in the field with a naturally established population of *C. arvense*.

3.4 Measurements

3.4.1 Paper I

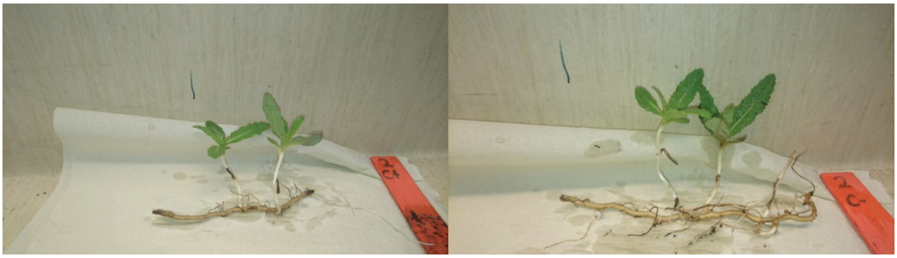
Experiments 1-3

Harvests were taken following each leaf stage, *i.e.* emergence to 12-leaf stage (experiment 1) or 3-8 leaf stage (experiments 2 and 3) (Figures 6-9). We considered a leaf stage to be reached when the shoot with most leaves per experimental unit had reached that stage, i.e. the most developed leaf was five cm long and the leaf surface area had flattened out. At each harvest, numbers of aboveground and belowground shoots of *C. arvense* were counted and the developmental stage of all shoots per experimental unit was estimated. The plants were separated into an aboveground component, the initially planted root fragment, and a belowground component, comprising belowground shoots parts and newly developed roots. All roots, regardless of dimensions, were carefully retrieved and washed to remove growth substrate. The plant components were dried at 60 ºC for 24 h and weighed.

Assessment - leaf definition

In order to evaluate the assessment techniques for developmental stage of *C. arvense* used in this study compared with those used by Dock Gustavsson (1997), a calibration of leaf definition was performed on 13 September 2013 at Ultuna, Uppsala, Sweden. Forty-nine *C. arvense* shoots, covering a range from 1 to 13 leaves, were collected from cereal fields near Uppsala and brought to a laboratory. The developmental stage of each shoot was then independently assessed by myself and Dock Gustavsson.

Figure 6. Cirsium arvense plant harvested at time of emergence.


a. C+, leaf stage 2

b. C-, leaf stage 2


c. C+, leaf stage 3

d. C-, leaf stage 3


e. C+, leaf stage 4

f. C-, leaf stage 4

Figure 7. Photographs depicting *C. arvense* leaf stages 2-4 under competition (C+) (a, c, e) and non-competition (C-) (b, d, f) from spring barley.

a. C+, leaf stage 5 b. C-, leaf stage 5

c. C+, leaf stage 6 d. C-, leaf stage 6

e. C+, leaf stage 7 f. C-, leaf stage 7

Figure 8. Photographs depicting *C. arvense* leaf stages 5-7 under competition (C+) (a, c, e) and non-competition (C-) (b, d, f) from spring barley.

a. C+, leaf stage 8 b. C-, leaf stage 8

c. C+, leaf stage 9 d. C-, leaf stage 9

Figure 9. Photographs depicting *C. arvense* leaf stages 8-9 under competition (C+) (a, c) and non-competition (C-) (b, d) from spring barley.

3.4.2 Paper II

Harvest at spraying

When herbicide treatments had been performed, the corresponding control treatments were harvested. The first harvest was taken when spraying was performed at 3-leaf stage of *C. arvense*. In each pot, the height of the largest shoot was measured and the phenological stage of each *C. arvense* shoot was recorded. The *C. arvense* plants were partitioned into aboveground parts (leaves and stems) and belowground parts [belowground shoots, old root (originally planted root fragment), new roots and fine roots]. The samples were dried at 105 ºC for 24 hours and weighed. No measurements were performed on spring barley. The same procedure was used for harvests at the 4-8 leaf phenological stages. Total plant weight per experimental unit was estimated by adding the weights of aboveground and belowground parts. Average phenological stage per experimental unit was calculated by adding the phenological stage for each shoot and dividing by the number of shoots.

Final harvest

In September, all herbicide-treated experimental units and the additional control units were harvested following the procedure described above.

Shoot height measurements

To estimate relationships between median and maximum shoot height, *C. arvense* shoots were measured in the beginning of June 2017 in a field experiment near Uppsala, Sweden (Paper III). The experiment was sown with spring barley and contained naturally occurring *C. arvense* populations. In each of the 24 experimental plots, shoot height was measured within an area of 20 m^2.

3.4.3 Paper III

Experimental year 2015

On July 13, the effects of the control treatments were evaluated. In each experimental plot, four subplots each measuring 0.25 m^2 were randomly selected. Height and number of shoots of *C. arvense* were recorded. All aboveground plant material was cut and separated into *C. arvense*, spring barley and other weeds. The samples were dried at 105 °C for 24 hours and dry weight was recorded.

On September 7 (final harvest), a similar assessment of the control measures was performed as described above. However, spring barley was separated into two components before drying, *i.e.* ears and straw. After drying, ears were divided into grains and awns. The ears consisted of about 80% grains and the grain yield (15 % water content) was estimated as:

$$\text{Grain yield} = (0.80 \times \text{ear weight}) \times 1.15$$

Experimental year 2016

On June 10 (before control treatments) and September 15, number of *C. arvense* shoots in each plot (45 m^2) was recorded.

On September 15, four subplots, each measuring 0.25 m^2, were randomly selected in each experimental plot. All aboveground plant material was cut and separated into *C. arvense,* spring barley (ears and straw) and other weeds. The samples were dried at 105 °C for 24 hours and dry weight was recorded.

Experimental year 2017

Number of *C. arvense* shoots was counted in each of the experimental plots within an area of 20 m^2 on June 3. No weed control treatments or harvesting were done during this year.

3.4.4 Paper IV

In the experiment described in Paper IV, number of *C. arvense* shoots in each experimental unit was counted before the treatments (June 10, 2016) and just before crop harvest (September 15, 2016).

Changes in number of seeds per flower receptacle and average seed weight were recorded from the onset of seed production until seed production during autumn 2016 (sampling occasions: August 22, August 30, September 6 and September 15) (Figure 10). On each sampling occasion, a maximum of five mature flower receptacles containing seeds just prior to shedding were randomly chosen from each experimental plot. However, some experimental plots contained less than five mature flower receptacles, and in these plots all mature flower receptacles were sampled. These seeds were cleaned (the pappus was removed), dried (105 °C for 24 hours), counted and weighed.

At crop harvest (September 15, 2016), total number of shoots per area and number of shoots leading to mature seeds at crop harvest were counted. Cumulative numbers of flower receptacles which had shed mature seeds over the season were assessed by randomly sampling a maximum of 10 seed-producing shoots per experimental unit plot and counting the number of mature flower receptacles on these. A mean value for the number of mature flower receptacles per shoot was calculated and multiplied by the number of shoots that had produced mature seeds, giving the total number of flower receptacles per plot. Records of daily average precipitation for the period August-September 2016 were retrieved from the Ultuna Meteorological Station.

Figure 10. Seeds of *C. arvense* attached to the pappus and flower receptacles just before seeds are released.

3.5 Statistical analyses

3.5.1 Paper I

To estimate at which leaf stage (S_{CP}) and total below-ground dry weight (DW_{CP}) the compensation point occurred, second and third order polynomials (Dell Inc., 2015) were used to fit observed below-ground weight (DW) against leaf stage (S) categorized by blocks. Also, relative depletion of the below-ground system at the compensation point (RD_{CP}) was calculated by solving the second- and third-order polynomial models for their respective S_{CP}-values, giving dry weight of the below-ground structure (DW_{CP}) at CP. Before the analyses, total below-ground dry weights were log transformed to make the variance homogeneous.

To evaluate the effects of the categorical variables and their interactions on the S_{CP} and relative depletion of the below-ground system at the compensation point (RD_{CP}), analyses were performed using a mixed model with fixed effects of root weight (0.8 and 2.4 g), planting depth (5 and 15 cm), competition (with and without spring barley), model choice (second and third order polynomial), assessment technique [Dock Gustavsson(DG) and Tavaziva (T)], and their interactions, and random effects of assessment technique within leaf stage range (SAS Institute, 2011) (experiment 1). Estimated CP values that were either negative or greater than 12 were removed from the dataset. Estimations of CP using the second order polynomial model with the full range (0-12 leaves) in experiment 1 were all negative and therefore all were excluded from the statistical analysis.

The datasets from experiments 2 and 3 were amalgamated and analysed together since they contained observations from the same season and leaf range. To evaluate the effects of the categorical variables and their interactions on the S_{CP} and RD_{CP}, analyses were performed using a mixed model with fixed effects of root weight, planting depth, competition, model choice, assessment technique, and their interactions, as specified under experiment 1, except for the missing root weight of 0.8 g and planting depth of 15 cm in experiment 3 and missing competition in experiment 2. In addition, fixed effects of experiment (experiments 2 and 3), and random effects of assessment technique within experiment and blocks within experiment (SAS Institute, 2011) were used. The Kenward-Roger method for calculation of degrees of freedom was used in the analyses. Differences in least square means were tested using t-tests.

3.5.2 Paper II

The models for the experiment described in Paper II were fitted using the mixed and glm procedures in the SAS system (SAS Institute, 2012). Prior to the statistical analysis, belowground weight, total weight, maximum shoot height and average phenology of *C. arvense* were square root-transformed to make the variance homogeneous.

The effects of treatments on belowground weight, total weight, maximum shoot height and average phenology of *C. arvense* at harvest were evaluated using mixed models. Differences in least square means were tested using the lsmestimate function.

The combined effects of crop, herbicide dose and phenology on belowground weight, total weight, maximum shoot height and average phenology of *C. arvense* at harvest were evaluated using a general linear model.

The effects of crop and herbicide dose on changes in belowground weight, total weight, maximum shoot height and average phenology over time (between spraying and harvest) were assessed by general linear models. Tukey’s test was used to perform pairwise comparisons between phenological stages.

Linear regression analysis (Dell Inc. 2015) was used to establish the relationships between median and maximum shoot height.

3.5.3 Paper III

In Paper III, all models were fitted using the mixed procedure in the SAS system (SAS Institute, 2012). To make the variance homogeneous, number of shoots, total weight, and shoot weight of *C. arvense*, grain yield and straw weight of barley, and weight of other weeds were squared root transformed prior to the analysis of variance.

Repeated measures analysis was performed to evaluate the changes in the number of shoots of *C. arvense* over time and treatment. The models contained fixed effects of treatment, time, block and the interaction treatment × time. Time was included as a repeated factor in the model. Tukey’s test was used to adjust the P-values.

Repeated measures analyses were also performed to evaluate the effects of treatment on the biomass of *C. arvense*, grain yield, straw and other weeds. The model contained fixed effects of treatment, year, block, plot and the interactions treatment × year, treatment × block, year × block and treatment × year × block. Year was included as a repeated factor in the model. Tukey’s test was used to adjust the P-values.

3.5.4 Paper IV

In order to make the variance homogeneous, prior to the analysis of variance the number of shoots per unit area, number of seeds per flower receptacle, average seed weight and total seed weight per flower receptacle were square root-transformed.

To evaluate changes in the number of shoots over time and treatment [*i.e.* between early (June) and late summer (September)], repeated-measures analysis was performed using a mixed model containing fixed effects of treatment, time, block and the interaction treatment × time. Time was included as a repeated factor in the model.

The effects of treatment in decreasing number of shoots between June and September and the percentage of seed-producing shoots were evaluated using the mixed model including fixed effects of treatment, block and their interactions.

To evaluate changes in the number of seeds per flower receptacle, average seed weight and total seed weight per flower receptacle over the four sampling times, repeated-measures analysis was performed using a mixed model containing fixed effects of treatment, sampling time, block and the interaction treatment × sampling time. Sampling time was included as a repeated factor in the model.

Non-linear regression analysis (Dell Inc. 2015) was used to establish relationships between the number of seeds per flower receptacle and the proportion of rainy days during a 10-day period prior to sampling

4 Results and discussion

4.1 Compensation point and phenological development (Paper I)

The aim of the study presented in Paper I was to assess the phenological stage at which the compensation point (CP) occurs and to investigate how CP is affected by factors such as crop competition and (artificial) soil tillage (root weight and burial depth). Methodological issues pertaining to the estimation of CP were also addressed, in order to further improve estimation of CP based on aboveground phenology as a diagnostic tool for optimising the timing of mechanical and physical control of *C. arvense*. In the study, the focus was on assessment of the CP and therefore the assumption that the CP coincides with a plant stage of minimum regenerative capacity was not tested.

4.1.1 Effects of competition, root weight and planting depth

Regardless of crop competition, root weight and planting depth, the minimum belowground dry weight of *C. arvense*, *i.e.* CP, occurred before the most developed shoot had reached the 3-leaf stage (Figure 11) (see also Table 2 in Paper I). These results support the hypothesis that the CP likely occurs before *C. arvense* has developed 3 leaves. This explains farmers' experience that a better control effect is achieved when mechanical control is performed at earlier leaf stages than currently recommended.

Relative depletion, *i.e.* weight loss with respect to the belowground system at the CP, was significantly greater at a higher initial root weight than at a lower initial root weight in experiments 2 and 3, but not in experiment 1 (see Table 2 in Paper I). This partly supports the hypothesis that relative depletion of the belowground system at CP is smaller at a lower initial root weight than a higher initial root weight. Dock Gustavsson (1997) also found that weight loss of the belowground system, in absolute terms, was greater at CP for initially heavier root fragments compared with lighter fragments. This was expected, as loss of weight by allocation and respiration can be quantified in terms of relative weight loss (Verwijst *et al.*, 2013). Torssell *et al.* (2016) noted that lighter root fragments delay sprouting and phenological development of *Sonchus arvensis* L. and attributed that to less depletion of lighter roots, since they have a smaller proportion of stored carbohydrates and proteins than lignified tissues. Anbari *et al.* (2011) also found a delay in sprouting and phenological development of *S. arvensis* with increasing root fragmentation. These results suggest that fragmentation of roots leads to lower availability of resources not only per plant, but also per unit area available for regeneration.

Dock Gustavsson (1997) and Thomsen *et al.* (2011) refer to plant physiological theory and attribute the relative performance of their planted roots to the amount of stored carbohydrates, which is assumed to be proportional to root size, and used root length as a proxy for the initial amount of available carbohydrates. However, a random sample of equal root lengths, even when using root thickness classes, would give a certain variance in root weight and thereby a larger variance around S_{CP}-estimates. We standardized for initial root weight, which we think is a better proxy for root reserves than length, to minimize this source of variation. This approach is also sustained by knowledge about the internal regulation of bud sprouting: The number of shoots produced per unit length is known to be reduced for longer root parts (Nadeau & Van den Born 1989) due to apical dominance (Hunter 1995). Leathwick *et al.* (2006) found that recruitment of shoots was not influenced by the number of buds per unit dry mass of root. Another advantage of starting with a known root weight at planting is that we can calculate the relative root depletion/ replenishment over the time / phenology trajectory studied.

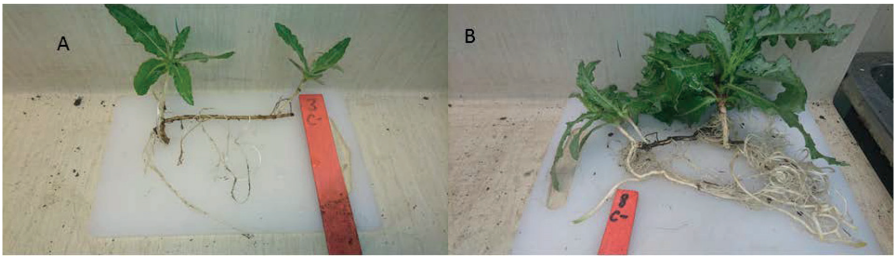


Figure 11. Cirsium arvense plant regenerated from a root fragment with a fresh weight of 2.4 g at (A) 3-leaf stage and (B) 8-leaf stage.

4.1.2 Effects of leaf and leaf stage definition

With regard to CP estimation, the differences in leaf definition (last developed leaf either >5 cm long regardless of leaf expansion or >5 cm and the leaf surface had flattened out) were negligible (see Table 2 in Paper I). This is due to the fact that both estimates coincided around the 4-leaf stage, which is relatively close to the CP (see Figure 1 in Paper I).

In the study, a certain leaf stage was considered to be reached when the most developed shoot of an experimental unit had produced the prescribed number of leaves. This method provided a more rapid assessment than finding the mean or median number of shoots in a population as done by Dock Gustavsson (1997). The median and mean leaf number per shoot at population level per experimental unit initially coincided with each other, but became significantly different from the maximum number of leaves per shoot above leaf stage 3 and 4 in experiments 1 and 2-3, respectively (see Figures 2 A and B in Paper I). This means that using the mean, median or maximum would not lead to significant differences in the estimated CP when the CP occurs at early leaf stages (1-3). It should be noted that the differences in methodology do not explain why the CP occurred at earlier leaf stages than estimated by Dock Gustavsson (1997).

4.1.3 Effects of model choice and leaf range

To obtain statistically comparable S_{CP} estimates on a continuous scale, curve fitting was used. The results showed that the results were sensitive to model choice when estimating the leaf stage (S_{CP}) at which minimum belowground dry weight is obtained. Moreover, estimates of minimum belowground dry weight and relative depletion of initially planted roots at S_{CP} were sensitive to model choice. Using a second order polynomial model with the full range (0-12 leaves) in experiment 1 gave negative estimations of S_{CP}. This is due to the fact that this function is symmetrical around the estimated S_{CP}, while the belowground dry weight-leaf stage course is non-symmetrical and dominated by its right tail. Shortening the right tail by reducing the leaf range from 12 to 8 improved the situation by generating a higher number of valid ($0<S_{CP}<12$) values, thereby causing choice of leaf range also to affect the results. To include the value at which the S_{CP} was estimated earlier (Dock Gustavsson, 1997), the leaf range extended to 8 was kept. However, a third order polynomial function proved to be flexible enough to fit the belowground dry weight-leaf stage course when using the entire leaf range (see Figure 2 in Paper I). While effects of both model choice and leaf range were significant, they were far too small (all <1 leaf stage) to explain the differences between the S_{CP} found in this study (1.05- 2.12) regardless of treatment (see Table 2 in Paper I) and the S_{CP} values for *C. arvense* reported previously (Dock Gustavsson, 1997; Nkurunziza & Streibig, 2011; Thomsen *et al.*, 2011).

4.1.4 Definition of S_{CP} (components of belowground weight)

The results of the experiments presented in Paper I are consistent with each other, but differ from previous findings by Dock Gustavsson (1997) who found that the S_{CP} of *C. arvense* occurred at later leaf stages than observed in Paper I. In controlled experiments with *S. arvensis* (Tavaziva, 2012; Verwijst *et al.*, 2014), similar results have been obtained, *i.e.* it has been found that the S_{CP} occurs earlier than reported previously by Håkansson (1969). There is one notable difference with regard to sampling procedure between the present work and that by Dock Gustavsson (1997) and Håkansson (1969). In this thesis work, all roots were retrieved regardless of dimensions, while in the other two studies, roots of diameter 1 mm or more, markedly thickened by secondary growth, were used. From graphs presented by Dock Gustavsson (1997), it is evident that the first sampled roots (>1 mm in diameter) were retrieved after reaching the S_{CP}, *i.e.* at an average leaf stage of >8 leaves per shoot. This causes underestimation of the belowground weight, especially for the early leaf stages, because all roots are <1 mm in diameter during these stages. In the study by Dock Gustavsson (1997), the production of belowground plant parts, especially at early leaf stages, was actually larger than accounted for, and thereby the *C. arvense* plants had reached and passed the S_{CP} that would have been identified when including the entire belowground system. Assuming that new roots attain a secondary thickening past leaf stage 8 and that roots account for the major part of below-ground biomass at this stage, the majority of below-ground biomass is not accounted for when discarding roots < 1 mm in diameter, and may be the reason for the difference in S_{CP}-estimates provided by Dock-Gustavsson (8-10 leaves) and this study (< leaf stage 3). This may also explain why Thomsen *et al.* (2011), who also included roots < 1mm, inferred a lower S_{CP}-value (3-7 leaves) than Dock-Gustavsson (1997). It cannot be ruled out that ecotypes of *C. arvense* may differ with regard to dry weight – leaf stage trajectories and that different ecotypes were used in the different studies. Fogelfors and Lundkvist (2009) concluded that *C. arvense* is susceptible to selective pressure exerted by intensification of agriculture, and this may well encompass the position of the S_{CP}.

The reason for only sampling roots >1 mm in diameter given by Dock Gustavsson (1997) is that: '*The minimum dry weight of underground regenerative organs occurs at a definable point of areal shoot development.*' Roots with diameter <1 mm were probably not sampled because they were considered to lack regenerative capacity. However, even if those roots do not have the capacity to produce viable shoots, they may well contribute to regeneration by means of resource acquisition and allocation if they remain functional and attached to regenerative structures after an eventual disturbance.

4.2 Biomass production and population dynamics (Papers II and III)

The effects of crop presence, herbicide dose and timing of herbicide application on biomass production and population dynamics of *C. arvense* were addressed in Paper II. In Paper III, the effects on *C. arvense* and spring barley of selective cutting and early and late herbicide spraying over two consecutive growing seasons in two different barley crops sown on the same soil were assessed.

4.2.1 Effects of competition (Paper II)

The presence of spring barley significantly reduced biomass, shoot height and leaf production of *C. arvense*, regardless of herbicide dose (see Table 2 in Paper II). The presence of spring barley reduced *C. arvense* belowground and total dry weight by 83% (from 27.6 to 4.6 g plant^{-1} and 69.2 to 11.8 g plant^{-1}, respectively). It also reduced *C. arvense* maximum shoot height by 24% (from 53.2 to 40.2 cm). The reason was probably that *C. arvense* is susceptible to reduced light from shading and competition by neighbouring plants in crop stands and grassland (Bakker, 1960; Edwards *et al.*, 2000). Shaded plants produce fewer shoots with fewer flowers than plants growing in an unshaded environment (Bakker, 1960). When growing together with taller or more rapidly growing crop stands like cereals, growth and development of *C. arvense* is therefore usually strongly reduced (Tiley, 2010).

4.2.2 Effects of herbicide dose (Paper II)

Spraying with 50% of the recommended dose of MCPA gave weaker control effects on *C. arvense* than the recommended dose (see Table 2 in Paper II). Even when herbicide application was combined with a competitive crop (spring barley), the effect of reduced dose was significantly lower than the effect of the recommended dose. MCPA is an auxin-based herbicide which acts by accelerating uncontrolled cell growth (Fogelfors & Lundkvist, 2008). In low doses, it might have had a synergistic effect on weed growth and, instead of killing the weeds, promoted growth of *C. arvense*. This is in agreement with results from a study on perennial weeds (*C. arvense* and *Sonchus arvensis* L.), where reduced herbicide dose gave an increase in aboveground biomass compared with the recommended dose (Fogelfors & Lundkvist, 2008). A reduction in herbicide dose may give sufficient control effects on weed communities dominated by annual species. Sufficient weed control effects have also been obtained when spraying with reduced herbicide doses against annual weeds in competitive cereal crops (Salonen 1992, Lundkvist 1997).

Also, Boström and Fogelfors (1999) stated that it is possible to maintain the weed flora on acceptable levels by using 50% lower doses than normally recommended together with appropriate tillage strategies.

4.2.3 Effects of timing of herbicide application (Papers II and III)

In the controlled experiment (Paper II), the strongest weed control effects were observed after spraying with the recommended dose (100%) when the largest *C. arvense* shoot had reached 3-4 leaf stage (Paper II). On assessing biomass growth over time (from spraying to harvest), no significant increase in biomass was observed for those plants compared with plants treated at the 5-8 leaf stage (see Figures 1A, B in Paper II). Herbicide application on all treatment occasions (3-8 leaves) inhibited shoot elongation and leaf development over time (see Figures 2 and 4 in Paper II). The smallest shoot heights and number of leaves at harvest were observed when spraying was carried out at 3-4 leaf stage. Thus the hypothesis that herbicide treatment at close to 3-leaf stage would give the best control effect was supported (Paper II).

In the field experiment (Paper III), herbicide treatment at 4-5 leaf stage (H1) and 8-10 leaf stage (H2) gave the same control effects on shoot number and aboveground biomass production. Both treatments were equally efficient in suppressing growth of *C. arvense* as compared with the control plots (see Figure 2 in Paper III). The hypothesis was that early herbicide treatment is more effective than late herbicide treatment was therefore not supported.

The results in Paper II can probably be attributed to the fact that, when using herbicides, *C. arvense* needs to have developed a sufficient number of shoots and leaf area to be able to absorb and translocate the active ingredient down to the root system. At the 4-leaf stage, maximum shoot height was about 13 cm (see Figure 2 in Paper II), while the corresponding median height in a field experiment was about 6 cm (see Figure 3 in Paper II). The results presented in Paper II differ slightly from the current recommendation in Sweden, which is to spray slightly later, when the majority of the shoots are at a height of 10-20 cm (Jordbruksverket, 2017b; Widen & Johansson, 2015, 2016).

The results in Paper III showed that herbicide treatment at 4-5 leaf stage (H1) and 8-10 leaf stage (H2) had similar control effects, *i.e.* both significantly reduced shoot number and aboveground biomass of *C. arvense*. The strong control effects obtained at H1 are in accordance with the results of Paper II. When spraying at H1, about 50 % of the shoots had developed 4-5 leaves while the remaining shoots have fewer leaves. *Cirsium arvense* had then passed the compensation point (likely before 3-4 leaves), i.e. the developmental stage at which a plants rate of photosynthesis equals the rate of respiration (Håkansson 2003, Paper I) but had also developed enough leaf area to absorb and translocate MCPA. Surviving shoots as well as new emerging shoots continued to develop and grow in the plant stand after spraying. However, growth and development of the weed was strongly set back giving the crop a competitive advantage (Figs. 2, 3). When spraying later in the season (H2), *C. arvense* had been subjected to crop competition resulting in reduced development and growth (Bakker 1960, Edwards *et al.* 2000, Paper II). More *C. arvense* shoots had emerged and developed in the plant stand at H2 compared to H1. About half of the shoots had developed 8-10 leaves while the remaining shoots had fewer leaves. Herbicide treatment at H2 targeted and killed more shoots compared to H1. Together with crop competition, spraying reduced growth of *C. arvense* (Figure 2 in Paper III) and enhanced crop yield (Figure 3 in Paper III). The results illustrate the complexity farmers are facing when deciding optimal spraying occasion.

Spring barley

In the field experiment (Paper III), grain yield and straw production by spring barley were significantly higher in 2016 compared with 2015. Both herbicide treatments (H1 and H2) gave significantly higher grain yield (4754 and 4800 kg ha^{-1}, respectively) than in the control plots (2197 kg ha^{-1}). These results show that the herbicide treatments reduced the competitive effects of *C. arvense*, thereby favouring growth and development of the crop.

Other weeds

In the field experiment (Paper III), *Elymus repens, Tussilago farfara* L. (coltsfoot) and *S. arvensis* were found on the experimental site. Herbicide treatment also reduced the total biomass of these weeds (from 70 g m^{-2} to 17-20 g m^{-2}).

4.2.4 Effects of selective cutting (Paper III)

Cirsium arvense

On assessing the number of *C. arvense* shoots in 2017, after two selective cutting during the growing seasons of 2015 and 2016, the results showed that herbicide spraying reduced shoot number more effectively than selective cutting (Figure 1) but that both methods were equally efficient in reducing *C. arvense* biomass (Figure 2). Also, stronger control effects were observed the second year (Figures 1, 2). When using herbicides, a large proportion of the shoot population is killed more immediately while selective cutting depletes the below-ground structures more gradually (Parr & Way, 1988). Also, selective cutting targets shoots above a certain height (6 cm in this experiment) and leaves smaller shoots (< 6 cm) unharmed while herbicide spraying may affect a larger part of the shoot population. The control effect of selective cutting may also be attributed to the presence of a competitive crop (spring barley). Wilson & Kachman (1999) found that pastures with perennial grasses mowed twice a year during three years reduced the abundance of *C. arvense* with about 90 %. Also Derscheid *et al.* (1961) reported a 90 % suppression of *C. arvense* when mowing during three years was combined with competition from a perennial grass species.

Spring barley

Compared with the control, selective cutting gave significantly higher grain yield (2250 kg ha^{-1} and 3780 kg ha^{-1}) and straw production (see Figures 4a, b in Paper III). The results showed that selective cutting was as effective as a herbicide treatment.

Other weeds

No effects of selective cutting were observed on the other perennial weeds present at the site since the selective cutting (mimicked by using scissors) only targeted the *C. arvense* plants, thereby leaving the other weeds unaffected.

4.3 Generative reproduction (Paper IV)

The effects on seed production by *C. arvense* of selective cutting and early and late herbicide spraying over two consecutive growing seasons in two different barley crops sown on the same soil were assessed in Paper IV.

4.3.1 Effects of herbicide spraying and selective cutting

Number of shoots

From June to September 2016, the number of *C. arvense* shoots decreased in all treatments, by 32, 88, 86 and 60 % of the values in June in C (control), H1 (early herbicide treatment), H2 (late herbicide treatment) and S (selective cutting), respectively (see Figure 2 in Paper IV). The decrease in H1 and H2 was significantly larger than in S ($P<0.001$) and the decrease in S was significantly larger than in C ($P<0.001$). Of all shoots present in the control, 80% produced seeds at harvest 2016. Both the herbicide applications (H1 and H2) and selective cutting (S) treatments significantly reduced the number of seed-producing shoots to a few percent (see Figure 3 in Paper IV). The hypothesis that herbicide treatment decreases the number of shoots per unit area faster and to a greater degree was thereby supported.

Herbicide treatment killed a large proportion of the shoot population, while repeated cutting gradually reduced the number of shoots (see Figures 1 and 2 in Paper IV). In essence, this means that herbicide use, with respect to shoot population, has a more immediate effect and may have a positive impact on the yield of the current crop. More shoots survived after selective cutting than in the herbicide treatments, but selective cutting delayed the phenological development so much that the remaining season was too short to permit abundant seed production. Thus selective cutting led to a shoot reduction in the longer term. These results are consistent with findings by Graglia *et al*. (2006) and Lukashyk *et al*. (2008) that frequent mowing leads to a population reduction in *C. arvense*.

Seed production over time

Number of seeds per flower receptacle differed between treatments and changed over time from the onset of seed production until crop harvest. No significant interaction between treatment and time was observed (see Table 1 in Paper IV). Treatment H2 led to a significantly greater reduction in average number of seeds per receptacle (49) than treatments S (59), H1 (64) and C (67). Over time, number of seeds per flower receptacle was lowest in the second week (47) and increased over the third week to 69 in week four for all treatments. There was a significant negative correlation between the number of seeds per flower receptacle and the proportion of rainy days during a 10-day period prior to sampling (see Figure 4 in Paper IV). Average weights per seed differed significantly between treatments, but not over time (see Table 1 in Paper IV). Average seed weight was 0.91 mg, while H1 and S had significantly lower seed weight (0.63 and 0.78 mg) compared with H2 and C (1.04 and 1.19 mg). Within treatments, no significant correlations were found between seed weight and number of seeds per flower receptacle. However, irrespective of treatment and sampling time, there was a low ($r^2 = 0.12$) but significant ($P=0.013$) positive correlation between average seed weight and average number of seeds per flower receptacle. Cumulative seed weight per flower receptacle was significantly higher in the control (0.081 g) than in treatments H1, H2 and S (0.049, 0.053 and 0.047 g, respectively) (see Table 1, Figure 5 in Paper IV). Thus the hypothesis that number of seeds per flower receptacle is affected by weed control treatments was partly supported.

Seed production per shoot

The number of mature flower receptacles per seed-producing shoot at harvest was around 28 in the control (C), and was significantly reduced ($P=0.001$) to about 5 by selective cutting (S). For the early and late herbicide treatments (H1 and H2), the average values were 6 and 14 respectively, but with a large variation, and thus they did not differ significantly from the values obtained in C and S. The cumulative number of seeds per seed-producing shoot was 1870 in the control, significantly differing ($P=0.001$) from the number of seeds produced by shoots under selective cutting (260 seeds shoot^{-1}). Productive shoots in the H1 and H2 treatments produced on average

400 and 680 seeds shoot^{-1} but with a large variation, thereby not differing significantly from those in treatments C and S.

Seed production per area

Cumulative seed production in 2016, in terms of number of seeds per m^{2}, was significantly reduced, by three orders of magnitude, by all three treatments (5-20 seeds m^{-2}) compared with the control (6600 seeds m^{-2}). The same pattern was observed for total seed weight per m^{2}: In the control, *C. arvense* produced about 7.8 g seeds m^{-2}, while the total seed weight ranged from 0.003 to 0.014 g m^{-2} in the other treatments. The hypothesis that early herbicide application decreases seed production per unit area more than late herbicide application was not supported, because both treatments were equally effective in restricting seed production by preventing shoots from developing mature seeds before harvest (see Figure 3 in Paper IV). Moreover, the hypothesis that herbicide treatment restricts seed production more than selective cutting was not supported, since all weed control treatments were equally successful in preventing seed production per unit area by reducing the number of shoots that produced seeds (see Figure 3 in Paper IV).

4.3.2 Effects of precipitation

Seed-set by *C. arvense* was negatively affected by precipitation, *i.e.* the higher the number of rainy days, the less seed-set was observed (see Figure 4 in Paper IV). This can be attributed to the fact that seed-set by *C. arvense* greatly relies on pollination by honeybees (Derscheid & Schultz, 1960), which do not fly during rainy days (Percival, 1947).

5 Conclusions and future research

Compensation point

- The compensation point of *C. arvense*, when determined on basis of the entire belowground plant weight, occurs before the 3-leaf stage
- Mechanical control should be performed at earlier phenological stages than previously recommended.

To evaluate the results from this study, experiments to assess if and how the compensation point of *C. arvense* varies under field conditions should be performed. The major aim would be to provide farmers and extension officers with a diagnostic tool that enables timely and efficient control of those weeds

Biomass production and population dynamics

- Growth and development of *C. arvense* with respect to below-ground and total dry weight is most efficiently suppressed when spraying is carried out with the recommended dose of MCPA 750 when the largest shoot has developed three-four leaves.
- Presence of a crop increases the control effect of herbicide treatment

At 4-leaf developmental stage, the shoot population had a maximum shoot height of about 13 cm and a median shoot height of 6 cm. This indicates that herbicide spraying might be performed earlier than previously recommended (when most shoots have reached a height of 10-20 cm). However, to confirm these results, more studies in a controlled environment and in field conditions are needed.

- With respect to aboveground biomass and crop yield, repeated selective cutting (mowing) is as effective as herbicide treatment in suppressing growth and development of *C. arvense* under field conditions.

Thus selective cutting can be used as a sustainable control strategy and can also be included as part of an integrated weed management (IWM) system for *C. arvense*. More long-term experiments should be conducted in order to confirm these findings.

Generative reproduction

- Seed production by *C. arvense* is greatly impeded by early and late herbicide treatments and by repeated selective cutting.

Thus all these treatments can be part of an IWM strategy to effectively control seed production of *C. arvense* in a sustainable way. More long-term experiments should, however, be conducted in order to confirm these findings.

References

Adolfsson, E. (1996). Ogräskontroll i svenskt lantbruk under tidigt 1900-tal - analys av en samtida enkät. *Svensk Botanisk Tidskrift*, 90: 199-214.

Anbari, S., Lundkvist, A. & Verwijst, T. (2011). Sprouting and shoot development of *Sonchus arvensis* in relation to initial root size. *Weed Research,* 51: 142-150.

Anderberg, A. (2011). Åkertistel, *Cirsium arvense* (L.) Scop. *Den virtuella floran*. Naturhistoriska riksmuseet. Available at: http://linnaeus.nrm.se/flora/di/astera/cirsi/ cirsarv.html [2017-10-10]

Andersson, L., Boström, U., Forkman, J., Hakman, I., Liew, J & Magnuski, E. (2013). Sprouting capacity from intact root systems of Cirsium arvense and Sonchus arvensis decrease in autumn. *Weed Research,* 53: 183–191.

Anonymous. (2009). Directive 2009/128/EC of the European Parliament and of the Council of 21 October 2009 establishing a framework for Community action to achieve the sustainable use of pesticides. *Official Journal of European Union,* 309/71–86.

Anonymous. (2016). CombCut®. Available at http://www.justcommonsense.eu/en/. Accessed November 3, 2017.

Anonymous. (2017). Plant and soil science eLibrary. Available at http://passel.unl.edu/pages/informationmodule.php?idinformationmodule=998689386&topicorder=3&maxto=7. Accessed November 2, 2017.

Bakker, D. (1960). A comparative life-history study of *Cirsium arvense* (L.) Scop. and *Tussilago farfara* L., the most troublesome weeds in the newly reclaimed polders of the former Zuiderzee. *The Biology of Weeds* (ed. J.L. Harper) pages 205-222. Blackwell Scientific Publications Ltd, Oxford, UK.

Bastiaans, L., Paolinir, R. & Baumann, D.T. (2008). Focus on ecological weed management: what is hindering adoption? *Weed Research*, 48: 481–491.

Ba'rberi, P. & Cascio, B. (2001). Long-term tillage and crop rotation effects on weed seedbank size and composition. *Weed Research*, 41: 325-340.

Bellinder, R.R., Gummesson, G. & Karlsson, C. (1994). Percentage-driven government mandates for pesticide reduction: The Swedish model. *Weed Technology,* 8: 350-359.

Berner, D.K., Smallwood, E.L., Cavin, C.A., McMahon, M.B., Thomas, K.M., Luster, D.G., Lagopodi, A.L., Kashefi, J.N., Mukhina, Z., Kolomiets, T. & Pankratova, L. (2015).

Asymptomatic systemic disease of Canada thistle (*Cirsium arvense*) caused by *Puccinia puntiformis* and changes in shoot density following inoculation. *Biological control,* 86: 28-35.

Bommarco, R., Lönn, M., Danzer, U., Pålsson K-J. & Torstensson P. (2010). Genetic and phenotypic differences between thistle populations in response to habitat and weed management practices. *Biological Journal of Linnean Society,* 99: 797-807.

Bond, W. & Grundy, A.C. (2002). Non-chemical weed management in organic farming systems. *Weed Research,* 41: 383–405.

Boström, U. & Fogelfors, H. (1999). Type and time of autumn tillage with and without herbicides at reduced rates in southern Sweden. 2. Weed flora and diversity. *Soil and Tillage Research*, 50: 283-293.

Boström, U. & Fogelfors, H. (2002). Long-term effects of herbicide-application strategies on weeds and yield in spring-sown cereals. *Weed Science,* 50: 196-203.

Boudôrt, G.W., Basse, B. & Cripps, M.G. (2016). Mowing strategies for controlling *Cirsium arvense* in a permanent pasture in New Zealand compared using a matrix model. *Ecology and Evolution,* 6: 2968-2977.

Boudôrt, G.W., Hurrell, G.A., Saville, D.J. & Leathwick, D.M. (2006). Impacts of applied *Sclerotinia sclerotiorum* on the dynamics of a *Cirsium arvense* population. *Weed Research,* 46: 61-72.

Boudôrt, G.W., Hurrell, G.A., Skipp, R.A., Monk, J. & Saville, D.J. (2011). Mowing during rainfall enhances the control of *Cirsium arvense. Biocontrol Science and Technology,* 21: 1213-1223.

Brandsæter, L.O., Bakken, A.K., Mangerud, K., Riley, H., Eltun, R. & Fykse H. (2011). Effects of tractor weight, wheel placement and depth of ploughing on the infestation of perennial weeds in organically farmed cereals. *European Journal of Agronomy*, 34: 239–246.

Brenzil, C., Holm, R., Hunter, J., Johnson, E. and Kirkland, K. (2008). Canada Thistle and its control. Saskatchewan Ministry of Agriculture Fact Sheet. http://www.agriculture.gov.sk.ca/Canada_Thistle_Control.

Brosten, B.S. & Sands, D.C. (1986). Field trials of sclerotinia-sclerotiorum to control Canada thistle (*Cirsium arvense*). *Weed Science,* 34: 377-380.

Burns, E.E., Prischmann-Voldseth, D.A. & Gramig, G.G. (2013). Integrated management of Canada thistle (*Cirsium arvense*) with insect biological control and plant competition under variable soil nutrients. *Invasive Plant Science and Management,* 6: 512-520.

Craine, J.M. & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology,* 27: 833-840

Dell Inc. (2015). Dell Statistica (data analysis software system), version 13. software.dell.com.

Derscheid, L.A. & Schultz, R.E. (1960). Achene development of Canada thistle and perennial sow-thistle. *Weeds,* 8: 55-62.

Detmers, F. (1927). Canada thistle, *Cirsium arvense* Tourn. Field thistle, creeping thistle. *Ohio Agricultural Experiment Station Bulletin 414,* 45 pp. Ohio University Press, Athens, Ohio, USA.

Dock Gustavsson A-M. (1997). Growth and regenerative capacity of plants of *Cirsium arvense*. *Weed Research,* 37: 229-236.

Donald, W.W. (1994). The biology of Canada thistle (*Cirsium arvense*). *Review of Weed Science,* 5: 77-101.

Donald, W.W. (2000). A degree-day model of *Cirsium arvense* shoot emergence from adventitious root buds in spring. *Weed Science,* 48: 333-341.

Edwards, G.R., Bourdôt, G.W., Crawley, M.J. (2000). Influence of herbivory, competition, and soil fertility on the abundance of *Cirsium arvense* in acid grassland*. Journal of Applied Ecology*, 37: 321–334.

Ellis, W.N. & Ellis-Adam, A.C. (1992). Flower visits to *Cirsium arvense* and *Carduus*. *Entomologische Berichten* (Amsterdam), 52: 137-140.

Elmore, C.L. (1996). A reintroduction to integrated weed management

Fogelfors, H. & Lundkvist, A. (2008). Selection in *Cirsium arvense* (L.) Scop. and *Sonchus arvensis* L.: Susceptibility to MCPA on different types of farmland in Sweden. Acta Agric Scand Sect B – *Soil Plant Science,* 58: 82-87.

Food and Agriculture Organisation of the United Nations. (2017). Integrated Pest Management. Available at: http://www.fao.org/agriculture/crops/thematic-sitemap/theme/pests/ipm/en/. Accessed November 3, 2017.

Graglia, E., Melander B. & Jensen, R.K. (2006). Mechanical and cultural strategies to control *Cirsium arvense* in organic arable cropping systems. *Weed Research*, 46: 304-312.

Gramig, G.G., Burns, E.E. & Prischmann-Voldseth, D.A. (2015). Predicting developmental timing immature Canada thistle stem-mining weevils, *Hadroplontus litura* (Coleoptera: Curculionidae). *Environmental entomology,* 44: 1085-1094.

Grekul, C.W. & Bork, E.W. (2007) Fertilization augments Canada thistle (*Cirsium arvense* L. Scop.) control in temperate pastures with herbicides. *Crop Protection,* 26: 668-676.

Grundy, A.C., Froudwilliams, R.J., & Boatman, N.D. (1993). The use of cultivar, crop seed rate and nitrogen level for the suppression of weeds in winter wheat. *Brighton Crop Protection Conference*: *Weeds - 1993*, Volumes 1-3.

Hamdoun, A.M. (1972). Regenerative capacity of root fragments of *Cirsium arvense* (L.) Scop. *Weed Research,* 10: 128-136.

Hansen, A.A. (1918). Canada thistle and methods of eradication. *U.S. Department of Agriculture*. Farmers Bulletin. 1002. Page 15

Hayden, A. (1934). Distribution and reproduction of Canada thistle in Iowa. *American Journal of Botany,* 21: 335-373.

Håkansson, I., Stenberg, M. & Rydberg, T. (1998). Long-term experiments with different depths of mouldboard ploughing in Sweden. *Soil and Tillage Research,* 46: 209-223.

Håkansson, S. (1969). Experiments with *Sonchus arvensis* L. I. Development and growth, and the response to burial and defoliation in different developmental stages. *Annals of the Agricultural College of Sweden,* 35: 989–1030.

Håkansson, S. (2003). *Weeds and Weed Management on Arable Land: An Ecological Approach*. CAB International, Wallingford, UK.

Heimann, B. & Cussans, G.W. (1996). The importance of seeds and sexual reproduction in the population biology of *Cirsium arvense* – a literature review. *Weed Research,* 36: 493-505.

Hein, G.L. & Wilson, R.G. (2004). Impact of *Ceutorhynchus litura* feeding on root carbohydrate levels in Canada thistle (*Cirsium arvense*). *Weed Science,* 52: 628-633.

Herzog, D.C. & Funderburk, J.E. (1986). Ecological bases for habitat management and pest cultural control. pp. 217-250. In M. Kogan (ed.), *Ecological Theory and Integrated Pest Management Practice*. John Wiley and Sons, New York.

Hettwer, U. & Gerowitt, B. (2004). An investigation of genetic variation in *Cirsium arvense* field patches. *Weed Research,* 44: 289–297.

Hodgson, J.M. (1968). The nature, ecology and control of Canada thistle. *United States Department of Agriculture Technical Bulletin 1386.* United States Department of Agriculture, Washington, DC, USA.

Hunter J.H. (1995). Effect of bud vs rosette growth stage on translocation of 14C-glyphosate in Canada thistle (*Cirsium arvense*). *Weed Science* 43: 347–351.

Jordbruksverket. (2017b). Välkommen till Ogräsdatabasen. Available at: http://www.jordbruksverket.se/etjanster/etjanster/odling/ograsdatabas.4.35974d0d12179bec28580002385.html . Accessed November 2, 2017.

Kluth, S., Kruess, A. & Tscharntke, (2005). Effects of two pathogens on the performance of *Cirsium arvense* in a successional fallow. *Weed Research* 45, 261–269.

Kirkland, K.J. (1977). Glyphosate for control of Canada thistle of summer fallow. *Canada Journal of Plant Science,* 57: 1015-1017.

Kristensen JL. 1992a. Experimental pot sprayer. User's manual. Department of Weed Control, Research Centre for Plant Protection, Flakkebjerg, Slagelse, Denmark.

Kristensen JL. 1992b. Research equipment for laboratory experiments with herbicides. In: Combellack JH, Levick KJ, Parsons J, Richardson RG, editors. Proceedings of the First International Weed Control Congress; 1992 February 17-21; Melbourne (Australia): Weed Science Society of Victoria Inc. ISBN 0 9599210 4 4.

Kudsk P, Streibig C. 2003. Herbicides – a two-edged sword. Weed Res. 43:90–10

Lamichhane, J.R. (2017). Pesticide use and risk reduction in European farming systems with IPM: An introduction to the special issue. *Crop Protection,* 97: 1-6.

Lampkin, N. (1990). *Organic Farming*. Farming Press Books. Ipswich, UK.

Leathwick, D.M., Bourdot, G.W., Hurrell, G.A. & Saville, D.J. (2006). Intraspecific plant density effects in *Cirsium arvense*. *New Zealand Journal of Agricultural Research* 49: 13–24.

Lemna, W.K. & Messersmith, C.G. (1990). The biology of Canadian weeds. 94. *Sonchus arvensis* L. *Canada Journal of Plant Science,* 70: 509-532.

Leth, V., Netland, J. & Andreasen C. (2008). *Phomopsis cirsii:* a potential biocontrol agent of *Cirsium arvense. Weed Research*, 48: 533-541.

Lukashyk, P., Berg, M. & Kopke, U. (2008). Strategies to control Canada thistle (*Cirsium arvense*) under organic farming conditions. *Renewable Agriculture and Food Systems*, 23: 13-18.

Lundkvist, A. (1997). Influence of weather on the efficacy of dichlorprop-P/MCPA and trihenuron-methyl. *Weed Research,* 37: 361–371.

Lundkvist, A. and Verwijst, T. (2011). Weed Biology and Weed Management in Organic Farming. *Research in Organic Farming*. Edited by Raumjit Nokkul, ISBN 978-953-307-381-1, Hard cover, 186 pages, Publisher: InTech, Chapters published December 16, 2011 under CC.

MacAllister, R.S. & Haderlie, L.C. (1985). Seasonal variations in Canada thistle (*Cirsium arvense*) root bud growth and carbohydrate reserves. *Weed Science,* 33: 44-49.

Melander, B., Munier-Jolain, N., Charles, R., Wirth, J., Schwarz, J., van der Weide, R., Bonin, L., Jensen, P.K. & Kudsk, P. (2013). European perspectives on the adoption of nonchemical weed management in reduced-tillage systems for arable crops. *Weed Technology,* 27: 231-240.

Melander, B., Rasmussen, I.A., Bàrberi, P. (2005). Integrating physical and cultural methods of weed control: examples from European research. *Weed Science*, 53: 369–381.

Mohammaddoust-e-Chamanabad, H.R., Asghari, A., Tulikov, A.M. (2007). The effects of weed-crop competition on nutrient uptake as affected by crop rotation and fertilizers. *Pakistan Journal of Biological Sciences,* 10: 4128-4131.

Mohler, C.L. (2001). Mechanical management of weeds, In: *Ecological Management of Agricultural Weeds*, Editors: Liebman, M; Mohler, C. L. & Staver, C. P., pp. 139–209, Cambridge University Press, ISBN 0-521-56068-3, Cambridge, UK.

Moore, R.J. (1975). The biology of Canadian weeds. 13. *Cirsium arvense* (L.) Scop. *Canada Journal of Plant Science,* 55: 1033-1048.

Mueller-Schaerer, H. & Collins, A.R. (2012) Integrated weed management. *Encyclopedia of Environmental Management.*

Muller, E., Jud, P. & Nentwig, W. (2010). Artificial infection of *Cirsium arvense* with the rust pathogen *Puccinia punctiformis* by imitation of natural spore transfer by the weevil *Ceratapion onopordi. Weed Research,* 51: 209-213.

Nadeau, L.B. & Vanden Born, W.H. (1989). The root system of Canada thistle. *Canadian Journal of Plant Science,* 69: 1169-1206.

Nkurunziza, L. & Streibig J.C. (2011). Carbohydrate dynamics in roots and rhizomes of *Cirsium arvense* and *Tussilago farfara*. *Weed Research,* 51: 461–468.

Nuzzo, V. (1997). *Element Stewardship Abstract for Cirsium arvense*. The Nature Conservancy, Virginia, USA https://www.invasive.org/browse/subinfo.cfm?sub=2792

O'Sullivan, P.A., Kossatz, V.C., Weiss, G.M. & Dew, D.A. (1982). An approach to estimating yield loss in spring barley due to Canada thistle. *Canada Journal of Plant Science,* 62: 725-731.

O'Sullivan, P.A., Weiss, G.M. & Kossatz, V.C. (1985). Indices of competition for estimating rapeseed yield loss due to Canada Thistle. *Canada Journal of Plant Science,* 65: 145-149.

Parr, T.W., Way, J.M. (1988). Management of roadside vegetation: The long-term effects of cutting. *Journal of Applied Ecology* 25: 1073–1087.

Percival, M. (1947). Pollen collection by *Apis mellifera*. *New Phytologist,* 46: 142-165.

Pilipavicius, V., Romaneckiene, R. & Romaneckiene, K. (2011). Crop stand density enhances competitive ability of spring barley (*Hordeum vulgare* L.). *Acta Agriculturae Scandinavica, Section B – Soil & Plant Science,* 61: 648-660.

Pitts, J. (2013). Organic farming vs Conventional farming, www.healthguidance.org/entry/11320/1/Organic-Farming-vs-Conventional-Farming.html

Roberts, H.A. & Chancellor, R.J. (1979). Periodicity of seedling emergence and achene survival in some species of *Carduus, Cirsium* and *Onopordum. Journal of Applied Ecology,* 16: 641-647.

Rutledge, C.R. & McLendon, T. (1998). *An assessment of exotic plant species of Rocky Mountain National Park.* Department of Rangeland Ecosystem Science, Colorado State University, Page 97. Northern Prairie Wildlife Research Center Home Page. http://www.npwrc.usgs.gov/resource/othrdata/explant/explant.htm

Salonen, J. (1992). Yield responses of spring cereals to reduced herbicide doses. *Weed Research*, 32: 493–499.

Salonen, J., Hyvönen, T. & Jalli, H. (2011). Composition of weed flora in spring cereals in Finland – a fourth survey. *Agricultural and Food Science,* 20: 245-261.

Sciegienka, J.K., Keren, E.N. & Menalled, F. D. (2011). Impact of root fragment dimension, weight, burial depth, and water regime on *Cirsium arvense* emergence and growth. *Canadian Journal of Plant Science*, 91: 1027–1036.

Solé, M., Durka, W., Eber, S. & Brandl, R. (2004). Genotypic and genetic diversity of the common weed *Cirsium arvense* (Asteraceae). *International Journal of Plant Sciences,* 165: 437-444.

Swanton, C.J. & Murphy, S.D. (1996). Weed science beyond the weeds: The role of integrated weed management (IWM) in agroecosystem health. *Weed Science,* 44: 437-445.

Tavaziva, V.J. (2012). *Effects of competition on compensation point and phenological development in Sonchus arvensis L.* Master Thesis. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Thill, D.C., Lish, J.M., Callihan, R.H. & Bechinski, E.J. (1991). Integrated weed management: A component of integrated pest management: A critical review. *Weed Science,* 5: 648-656.

Thompson, K., Bakker, J.P. & Bekker, R.M. (1997). *The Soil Seed Banks of North West Europe: Methodology, Density and Longevity*. Cambridge University Press, Cambridge,UK.

Thomsen, M.G., Brandsæter, L.O. & Fykse, H. (2011). Sensitivity of *Cirsium arvense* to simulated tillage and competition, *Acta Agriculturae Scandinavica, Section B – Soil and Plant Science,* 61: 693–700.

Thomsen, M.G., Mangerud, K., Riley, H. & Brandsæter, L.O. (2015). Method, timing and duration of bare fallow for the control of *Cirsium arvense* and other creeping perennials. *Crop Protection,* 77: 31-37.

Tilman D, Cassman KG, Matson PA, Naylor R & Polasky S. (2002). Agricultural sustainability and intensive production practices. *Nature*, 418: 671–677.

Tiley, G.E.D. (2010). Biological flora of the British Isles: *Cirsium arvense* (L.) Scop. *Journal of Ecology,* 98: 938-983.

Torssell, B., Eckersten, H., Lundkvist, A. & Verwijst, T. (2016). Modelling *Sonchus arvensis* root biomass allocation to below-ground shoot and fine root growth. *Acta Agriculturae Scandinavica, Section B – Soil and Plant Science,* 66: 476–482.

Tworkoski, T. (1992). Developmental and environmental effects on assimilate partitioning in Canada thistle (*Cirsium arvense*). *Weed Science,* 40: 79-85.

Tørresen, K.S., Fykse, H. & Rafoss, T. (2010). Autumn growth of *Elytrigia repens*, *Cirsium arvense* and *Sonchus arvensis* at high latitudes in an outdoor pot experiment. *Weed Research,* 50: 353–363.

Vasileiadis, V.P., Dachbrodt-Saaydeh, S., Kudsk, P., Colnenne-David, C., Leprince, F., Holb, I.J., Kierzek, R., Furlan, L., Loddo, D., Melander, B., Jørgensen, L.N., Newton, A.C., Toque, C., van Dijk, W., Lefebvre, M., Benezit, M. & Sattin, M. (2017). Sustainability of European winter wheat- and maize-based cropping systems: Economic, environmental and social *ex-post* assessment of conventional and IPM-based systems. *Crop protection,* 97: 60-69.

Verwijst, T., Eckersten, H., Anbari, S., Lundkvist, A. & Torssell, B. (2013). Weight loss in overwintering below-ground parts of *Sonchus arvensis* under current and temperature-elevated climate scenarios in Sweden. *Weed Research*, 53: 21–29.

Walker, R.H. & Buchanan, G.A. (1982) Crop manipulation in integrated weed management systems. *Weed Science,* 30: 17-24.

Welton, F.A., Morris, V.H. & Hatzler, A.J. (1929). Organic food reserves in relation to the eradication of Canada thistle. *Ohio Agricultural Experiment Station Bulletin 441.* United States Department of Agriculture, Washington, DC, USA.

Widén, P. & Johansson, L. (2015). Bekämpning av tistel i vårsäd. Sverigeförsöken 2015, 63–65. Available at: http://www.sverigeforsoken.se/se/sok.asp. Accessed November 3, 2017.

Widén, P. & Johansson, L. (2016). Bekämpning av tistel i vårsäd. Sverigeförsöken 2016, 63–65. Available at: http://www.sverigeforsoken.se/se/sok.asp. Accessed November 3, 2017.

Zwolfer, H. & Harris, P. (1966). *Ceutorhynchus litura* (F.) (Col. Curculionidae) A potential insect for biological control of thistle. *Canadian Journal of Zoology,* 44: 23-26.

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