Population dynamics of the perennial weed species *Sonchus arvensis* L.

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Abstract

Sonchus arvensis L. is a perennial weed that is widely prevalent in annual crops in northern Europe and can cause substantial yield losses. The abundance of *S. arvensis* has increased recently, primarily due to expansion of organic farming and increased use of reduced tillage. This thesis assessed the effect of mechanical control measures on the population dynamics of *S. arvensis* and sought to predict the impact of temperature on sprouting of *S. arvensis* under variable climate conditions. An outdoor box experiment was performed to evaluate the effect of initial root fragment size on subsequent growth of *S. arvensis*. Four artificial populations of *S. arvensis* with differing initial root length but with the same total root length per area were planted (20 roots of 5 cm, 10 roots of 10 cm, 20 roots of 5 cm and 4 × 20 cm + 4 × 5 cm roots). A pot experiment was performed in darkness to assess the impact of initial root length (5 and 10 cm), temperature (4, 8 and 18 °C) and planting depth (3, 10 and 17 cm) on belowground shoot elongation and emergence time of *S. arvensis*. The data from this pot experiment were used to model shoot emergence rate as a function of temperature and to predict emergence time under climatic variation.

Degree of root fragmentation was found to strongly influence plant performance in terms of shoot emergence time, aboveground shoot numbers, rosette size, flowering, biomass production and seed production. Compared with larger root fragments, small root fragments of *S. arvensis* produced more numerous but smaller-sized aboveground shoots, which emerged later in the beginning of the growing season and had lower generative capacity in terms of seed and root production. Root fragmentation by mechanical control measures resulted in a change not only in the frequency of aboveground shoots originating from *S. arvensis* root fragments, but also in the height of these shoots. Temperature significantly affected sprouting and emergence time of *S. arvensis*, with an increase in temperature causing an increase in the rate of *S. arvensis* belowground shoot elongation. Variations in temperature between years under field conditions (in central Sweden) resulted in larger variations in emergence time than differences in root fragment weight. An average increase in mean air temperature of about 3 °C would cause earlier emergence, approximately equal to the difference between the earliest and latest year in the present climate.

Keywords: biomass production, emergence time, model, nitrogen allocation, perennial sow-thistle, pre-emergence growth, roots, root fragmentation, seeds, temperature

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Dedication

To my family

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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 S Anbari, A Lundkvist & T Verwijst (2011). Sprouting and shoot development of *Sonchus arvensis* L. in relation to initial root size. *Weed Research* 51(2), 142-150.

II S Anbari, A Lundkvist, J Forkman & T Verwijst (2015). Population dynamics and nitrogen allocation of *Sonchus arvensis* L. in relation to initial root size. *Acta Agriculturae Scandinavica, Section B – Soil & Plant Science.* In press. DOI: 10.1080/09064710.2015.1064540.

III S Anbari, A Lundkvist, J Forkman & T Verwijst. Generative reproduction of *Sonchus arvensis* in relation to initial root size (submitted manuscript).

IV B Torssell, H Eckersten, S Anbari, A Lundkvist & T Verwijst (2015). Modelling belowground shoot elongation and emergence time of *Sonchus arvensis* shoots. *Acta Agriculturae Scandinavica, Section B – Soil & Plant Science* 65(7), 582-588.

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The contribution of Saghi Anbari to the papers included in this thesis was as follows:

I Planned the study in collaboration with the co-authors, performed parts of the experimental work, analysed and interpreted results, and wrote part of the manuscript.

II Planned the study in collaboration with the co-authors, formulated the hypotheses, performed main part of the experimental work, analysed and interpreted results, and wrote the main part of the manuscript.

III Planned the study in collaboration with the co-authors, formulated the hypotheses, performed the main part of experimental work, analysed and interpreted results, and wrote the main part of the manuscript.

IV Planned the study in collaboration with the co-authors, performed the main part of experimental work, analysed and interpreted results, and wrote part of the manuscript.

1 *Sonchus arvensis* L.

Sonchus arvensis L. (perennial sow-thistle) is a vigorous, deep-rooted perennial herb which is regarded as a troublesome weed in the Nordic region (Eckersten *et al*., 2010). It often occurs in annual crops and may cause substantial yield losses. It reproduces both sexually and vegetatively. Sexual reproduction via seeds enables this weed species to colonise new habitats. Vegetative proliferation of *S. arvensis* occurs via buds on the roots and on underground aerial stems and is the main reason for its expansion and persistence (Lemna & Messersmith, 1990).

Sonchus arvensis is usually controlled by herbicides, often combined with mechanical measures. The Swedish government implemented legislation in 1981 on reduction of herbicide use to remove or diminish unsafe products from the marketplace and to reduce the development rate of herbicide resistance. As a result, in *e.g.* cereal fields, the rate of herbicide use was reduced from 1.5 kg active ingredient (a.i.) ha^{-1} in 1981 to 0.8 kg a.i. ha^{-1} in 1991 (Bellinder *et al*., 1994). Similar programmes were introduced in other Scandinavian countries to reduce the negative side-effects of pesticides on the environment and human health (Haas & Streibig, 1994). In recent years, the European Union has issued a directive on sustainable use of pesticides which states that all member countries should implement integrated pest management (IPM). This means that farmers must prioritise low pesticide input management regimes wherever possible (Anonymous, 2009). Withdrawal of herbicides from the market, the use of lower herbicide doses and an increase in reduced tillage have influenced the composition of the weed flora in the Nordic countries (Andreasen & Streibig, 2011). The frequency of several weed species has increased in cereal cropping systems, with *S. arvensis* being one species that has become more abundant (Hyvönen & Salonen, 2002; Salonen *et al*., 2001b).

A similar trend regarding changes in weed flora has been observed within organic farming. During recent decades, the area of land under organic farming has increased in the Nordic countries. Organic farming aims at developing more sustainable cropping systems with less negative effects on the agroecosystem and its surrounding environment, such as preventing decreases in soil organic matter content, development of herbicide resistance and declines in species diversity and abundance. In association with the increase in weed diversity in organic farming, the frequency of some perennial weeds such as *S. arvensis*, *Cirsium arvense* (L.) Scop. and *Elymus repens* (L.) Gould has also increased (Riesinger & Hyvönen, 2006; Salonen *et al*., 2001a).

In Sweden, the area of organically farmed land increased from 1% of all arable land in 1991 to 9% in 1998 (Anonymous, 1998), and reached about 16.5% in 2013 (Statistics Sweden, 2014; Jordbruksverket, 1999). Although improved soil cultivation technology during recent years has reduced infestation by perennial weeds on organic farms in Sweden (Rydberg & Milberg, 2000), these weeds still pose a threat to the future of Swedish organic cereal production (Gustafsson, 2008). The relative success of *S. arvensis* as a weed, especially in organic farming, is most likely due to traits such as its fast-growing, vegetatively reproducing root system, abundant seed production (Lemna & Messersmith, 1990) and effective nitrogen uptake during early spring (Eckersten *et al*., 2010). These traits give this weed species a competitive advantage over crops under current Scandinavian conditions.

Physical and cultural control measures are major components of weed management strategies in organic crop production. Knowledge regarding the response of *S. arvensis* to various physical and cultural control measures and the resulting changes in resource acquisition patterns is essential for designing more efficient control strategies for *S. arvensis*.

1.1 Origin and history

The area of origin of *S. arvensis* was Europe and Western Asia (Shumovich & Montgomery, 1955). The weed species was then introduced to North America, probably as a seed contaminant, and spread by railroads and threshing machines or in contaminated crop seeds and packing material and hay (Long, 1922). *Sonchus arvensis* var. *arvensis* was first reported in North America in 1814, in Pennsylvania (Shumovich & Montgomery, 1955). It had become a serious weed problem in Eastern Canada by 1910 (Harrison, 1916).

In Sweden, *Sonchus arvensis* was first reported as a common weed in eastern parts of the country. It then expanded its range to southern and central parts and eventually it was reported even in the northernmost part of Sweden (Håkansson, 1969; Granström, 1962; Hultèn, 1950; Bolin, 1922).

1.2 Geographical distribution and habitat

Sonchus arvensis ecotypes grown in different geographical areas may vary in growth characteristics. Brandsæter *et al.* (2010) showed that ecotypes of *S. arvensis* vegetative buds of *S. arvensis* root fragments collected from different Nordic countries varied in bud sprouting ability and the innate bud dormancy considerably (Brandsæter *et al.*, 2010). Liew *et al.* (2013) found that one population of *S. arvensis* from the northern part of Sweden developed fewer buds on the roots than the other studied populations. Also, the root surface of one of the populations from the northern parts was smoother than the root surface of the populations from southern Sweden. *S.arvensis* from the northern parts also developed different number of vegetative buds on the roots. In addition, different ecotype populations of *S. arvensis* may respond differently to mechanical control. Hence, knowledge on the geographical distribution, habitat and ecotype characteristics of the weed species might enable us to design the most efficient control methods for a specific region.

Sonchus arvensis is widely distributed in temperate regions and is found through most of the United States, Canada, northern and eastern Asia, Australia and South America (Lemna & Messersmith, 1990; Peschken, 1982; Pegtel, 1973). According to Boulos (1973), it occurs at high frequency in north-west Europe and at lower frequency in central Europe, but its occurrence is rare in southern Europe.

Sonchus arvensis is found in a wide range of habitats, ranging from disturbed areas such as wasteland, meadows, sloughs, woods, lawns and along roadsides to fields under small grain and row crops (Shumovich & Montgomery, 1955; Stevens, 1924). It occurs more frequently in non-compacted loam soils (moderately fine to moderately coarse-textured) due to better spread of the roots. Alkaline or neutral soils provide a suitable environment for growth of *S. arvensis* plants. The species is adapted to non-saline or moderately saline soil with water potential from -0.5 to -0.2 MPa (Lemna & Messersmith, 1990).

Sonchus arvensis is also found in dryland saline areas of central Saskatchewan, Manitoba, central Alberta and southern Alberta, in association with species such as *Aster brachyactis* Blake, *Atriplex patula* var. *subspicata* (Nutt.) S. Wats., *Grindelia squarrosa* (Pursh) Dunal, *Kochia scoparia* (L.) Schrad., *Puccinellia nuttalliana* (Schulte) Hitche., *Salicornia rubra* Nels. and *Suaeda calceoliformis* (Hook.) Torr. (Braidek *et al.*, 1984).

1.3 Biology

Studies of plant characteristics that are associated with growth and development of weed populations are regarded prerequisite to develop economically and environmentally sustainable weed management systems (Bhowmik, 1997). In perennial weeds such as *S. arvensis*, sexual reproduction contributes to the maintenance of a high genetic variability and enables the weed species to colonize new habitats by means of long distance dispersal of seeds (Heimann & Cussans, 1996; Dong *et al.*, 2006).Vegetative reproduction plays a vital role for the persistence of the weed species. Knowledge on the growth and development of reproductive and vegetative plant parts may give the opportunity to predict at which time the weed species is most susceptible to e.g. mechanical disturbance.

Sonchus arvensis is a deep-rooted perennial herb belonging to the family Asteraceae. Erect stems of *S. arvensis* are hollow and branched (Lemna & Messersmith, 1990). Crowded leaves on the lower section of the stems form rosettes at an early stage of development, which provides a large photosynthetic area (Pegtel, 1973). Upper leaves on the stems are reduced in size and sparse. The entire plant is filled with milky latex. Flower heads (capitulae) are arranged in loose, terminal cymose-type clusters and contain 150-240 perfect and self-incompatible flowers which typically produce an average of 30 achenes after pollination by insects, *e.g*. honeybees, hoverflies and blister beetles (Stevens, 1924). Great resistance of the thin, soft and flexible white pappus hairs to air attached to the achenes provides great wind dispersal potential (Lemna & Messersmith, 1990). Spreading roots originate from short, spindle-shaped fairy primary roots, which are often found 5-12 cm below the soil surface. Vertical roots can penetrate to 2 m depth and can produce vegetative buds even at a depth of 50 cm below the soil surface (Steven, 1924).

1.4 Control methods

1.4.1 Cultural control

The purpose of cultural control is to strengthen the competitiveness of the crop and to reduce the growth and development of the weed species.

Weed -crop competition

Competition has been defined as: "*An interaction between individuals brought about by a shared requirement for a resource in limited supply and leading to a reduction in the survivorship, growth and/or reproduction of the individuals* *concerned*" (Harper, 1977). Weeds compete with a crop for nutrients, water and light. The aim of weed control is to strengthen the competitiveness of the crop by reducing and delaying growth and development of the weeds, thereby making it possible for the crop to obtain a larger share of the limited resources. The competitiveness of a plant is affected by plant size, differences in plant physiological characteristics and the relationship between size and establishment time, *i.e.* plants that establish before other plants probably grow larger.

Eckersten *et al.* (2010) showed that *S. arvensis* had higher nitrogen uptake in spring compared with spring barley (*Hordeum distichon* L.) at low nitrogen fertilisation rates, while the reverse was found at high nitrogen fertilisation rates. Since nitrogen levels are usually rather low in organically managed soils in the spring, this might be one explanation for the increase of *S. arvensis* in organic farming. Early and uniform establishment of the crop, which can be accomplished by providing a uniform distribution of crop seeds at optimal soil depth, will therefore increase the competitiveness of the crop. Crop plants which emerge early have a better ability to acquire limited resources compared with weed plants. Eckersten *et al.* (2011) showed that in mixed plant stands of *S. arvensis* and spring barley, early emerging spring barley plants strongly suppressed *S. arvensis* and considerably reduced its biomass as a proportion of total aboveground biomass. In the thesis, I have addressed how the time of shoot emergence of *S. arvensis* populations was influenced by different degree of root fragmentation. This information can then be used to evaluate to what degree root fragmentation may delay weed emergence, and give the crop a competitive advantage against the weed.

Crops

Strongly competitive crop species with early vigour, such as cereals, are more competitive than oilseed rape, peas and potato/vegetables (Teasdale *et al.*, 2007; Håkansson, 2003). *Sonchus arvensis* can be found in most types of crops, but is more common in spring-sown crops such as cereals, oilseed crops, peas, potatoes *etc*. Pilipavičius *et al.* (2006) showed that the density of *S. arvensis* was reduced at the heading stage of spring barley as a result of competition with barley.

Cover crops

Cover crops can take the form of living plants or plant residues. Live cover crops have a greater suppressive effect on weeds than dead cover crop residues. The weed control effects of cover crops depend on the growth characteristics of the cover crop species used and the traits of the weed species. Because of the larger nutritional reserves and faster establishment rate of perennial weeds, their control by means of a cover crop may be less efficient than control of annual weeds (Teasdale *et al.*, 2007).

In Scandinavia and Finland, cover crops are usually sown either as a catch crop into/within a main crop or as green manure. Undersowing of clover or clover-grass as green manure during the growing season is carried out with the aim of reducing soil erosion, nutrient leaching and controlling perennial weeds (Teasdale *et al.*, 2007; Torstensson & Aronsson, 2000). Brandsæter *et al.* (2012) found that dense stands of red clover (*Trifolium pratense* L.) undersown as a cover crop on the same date as spring oats (*Avena sativa* L.) significantly reduced the number of shoots produced by *S. arvensis* root fragments, but the aboveground biomass increased linearly with increasing weight of the cover crop. A similar reduction in the number of *S. arvensis* shoots was observed by Sepp *et al.* (2009) in spring barley undersown with red clover-timothy (*Phleum pratense* L.). Residues of yellow sweet clover (*Melilotus officinalis* L.) grown with Indian mustard (*Brassica juncea* (L.) Czern.), field peas (*Pisum sativum* L.) and flax (*Linum usitatissimum* L.), and either incorporated or left on the soil surface, reduced *S. arvensis* density in the fallow year (Blackshaw *et al.*, 2001).

However, cover crops can be used as an efficient strategy to manage the deleterious effects of perennial weeds in cereal-dominated rotations in the Scandinavian region, if their competitive effect is strengthened with the suppressive effect of mechanical disturbance (Håkansson, 2003).

Crop rotation

Weed species tend to grow together with crops that have a similar life cycle as the weed species. Including crops with different life cycles in the crop rotation can impede weed-crop association. Choice of crop and the sequence in which crops are grown can markedly affect the composition of weed flora (Ba'rberi & Cascio, 2001). Vanhala *et al.* (2006) showed that a red clover-timothy ley in rotation with spring barley reduced *S. arvensis* biomass, but had no effect on the plant density. Similarly, Lundkvist *et al.* (2011) found that perennial ley crops in sequences with annual crops were able to control *S. arvensis* effectively. Blackshaw *et al.* (2001) found that *S. arvensis* was abundant when winter wheat (*Triticum aestivum* L.) was rotated with (i) spring oilseed rape (*Brassica rapa* L.) or (ii) flax combined with zero tillage, but was absent in the continuous wheat and wheat-fallow rotations.

1.4.2 Mechanical control

Physical removal of weeds by soil disturbance is undoubtedly the oldest measure of weed control. Weeds are affected by tillage and cultivation in different ways: (i) Growing weeds and penetrating organs are uprooted, dismembered and buried; (ii) the soil environment is altered in such a way that germination and establishment of weeds is promoted; and (iii) weed seeds are moved vertically and horizontally, affecting the emergence, survival and competitiveness of the weeds (Mohler, 2001).

Ploughing

Ploughing cuts up the belowground parts of perennial weeds and buries the fragmented roots or rhizomes rather deep in the soil. Shoots developing from these fragments consume more resources to reach the soil surface than shoots arising from fragments buried at shallow depth. Boström & Fogelfors. (1999) found that the weight and shoot density of *S. arvensis* were lower in late-ploughed plots than in stubble-cultivated plots. Similarly, Deveikytė *et al.* (2006) found that ploughing effectively reduced both the density and air-dry weight of perennial weeds, including *S. arvensis*, in spring wheat and spring oilseed rape. Seibutis & Feiza. (2008) found that autumn ploughing in combination with a compactor reduced the abundance of *S. arvensis* in spring barley.

Stubble cultivation

Stubble cultivation is considered an efficient way to control perennial weeds (Håkansson, 2003). New shoots which develop from fragmented roots and rhizomes following stubble cultivation may deplete the nutrient reserves in these fragments. In Sweden, autumn stubble cultivation to a depth of 10-15 cm is usually performed after harvest using a tine or disc cultivator (Lundkvist & Fogelfors, 2004). Stubble cultivation has a good control effect on *S. arvensis*. Brandsæter *et al.* (2012) found that the density of *S. arvensis* aboveground shoots and their biomass was somewhat lower in plots that were shallow-ploughed followed by harrowing. Melander *et al.* (2012) reported that autumn stubble cultivation reduced shoot numbers of *S. arvensis*, while Sepp *et al.* (2009) found that deep ploughing following stubble cultivation resulted in low emergence of *S. arvensis*, with the effect being more pronounced in spring wheat and spring barley fields than in pea fields. Soil cultivation with either a shallow plough or rototiller has the potential to reduce *S. arvensis* and other perennials such as *Cirsium arvense* (L.) Scop., *Rumex crispus* L., *Tussilago farfara* L. and *Stachys palustris* L. (Pekrun & Claupein, 2006).

Mowing, weed harrowing and hoeing

Mowing disturbs the growth and development of weeds by cutting off their aboveground parts. In comparison with tillage operations, mowing requires less energy and causes less soil erosion and nutrient leaching (Mitchell *et al*., 2000). Mowing may be an appropriate way to control perennial weeds, *e.g*. Holmøy & Teslo. (2000) found that mowing just after harvest and 4 weeks later had a good control effect on annual and perennial weeds in cereals. Brandsæter *et al*. (2012) found that mowing in autumn seemed to suppress *S. arvensis*.

Weed harrowing destroys weeds by uprooting them and covering them with soil. The efficiency of weed harrowing in controlling weeds may vary depending on weed species and their development stages and on the harrowing technique used. Auškalnis & Auškalnienė. (2009) found that early harrowing and harrowing two or three times was rather effective in controlling weeds in barley fields where *S. arvensis* was the dominant weed species. In contrast, Gawęda *et al*. (2014) found that harrowing at the cracking and 3-4 leaf stage was not effective in reducing the density of *S. arvensis* in spring barley.

The thesis focus mechanisms of interest for evaluating measures of mechanical control, and choosing the proper size of propagules and planting depth was one of the challenges in the experiments. The results of earlier experiment with *Sonchus arvensis* showed that shoots could develop from root fragments with a length of 5, 10 and 20 cm (Grauzdev& Tulikov, 1966). The largest width reported for thickened young roots of *S.arvensis* is 4-5 mm (Håkansson, 1969). In the thesis root fragments with thickness lower than 2.5 mm were regarded to have less chance to reach the soil surface, and thicknesses of about 2.5 to 4 mm were used in the experiments (Paper I-IV). Håkansson & Wallgren. (1972b) showed that the numbers of produced shoots on *S.arvensis* root fragments decreased with increasing planting depth. Root fragments placed at the depth of 2.5, 10 and 17.5 cm produced many living shoots, whereas those buried deeper (at 25 and 30 cm depth) had lower shoot production capacity. To evaluate any effects of depth, but still provide the root fragments a reasonable chance to emerge, planting depths of 3, 10 and 17 cm were used in the experiments of the thesis.

1.4.3 Chemical control

Synthetic auxin herbicides are the primary chemicals used to control *S. arvensis*. This weed species is moderately susceptible to phenoxy acetic acid herbicides such as 2,4-D, 2,4-DB and MCPA while in the seedling stage and moderately resistant when the stand has established (Fogelfors & Lundkvist, 2008; Lemna & Messersmith, 1990). Auxin-type herbicides achieve more efficient control of *S. arvensis* when applied at the late rosette stage (Vidme, 1961). Pyridine carboxylic acid herbicides such as picloram, clopyralid and triclopyr, used in combination with phenoxy acetic acid herbicides, are considered to be effective against *S. arvensi*s. The ready-to-use herbicide mixture of 2,4-D 140.2 g L^{-1} + triclopyr 144 g L^{-1} at a dose of 3552 mL ha^{-1} at the weed stage of early stem formation reduces the population density of *S. arvensis* considerably (Dimitrova & Marinov-Serafimov, 2008).

Branched-chain amino acid (ALS) inhibitors such as sulfosulfuron, chlorsulfuron, metsulfuron-methyl, tribenuron-methyl and thifensulfuron-methyl are also used to control *S. arvensis*. Pilipavičius *et al.* (2010) showed that autumn application of Monitor 75% (sulfosulfuron 750 g kg^{-1}) could effectively destroy *S. arvensis* in a winter wheat crop. Darwent *et al.* (1998) suggested application of clopyralid at 0.1 or 0.2 kg a.i. ha^{-1} followed by application of metsulfuron in the second year and dicamba plus MCPA in the third year under zero tillage as an option for gradual reduction of *S. arvensis* in a 4-year oilseed rape-barley rotation.

In Sweden, to achieve a sufficient control effect against *S. arvensis* and other dicotyledonous weeds in the field, synthetic auxin herbicides are usually combined in different ways with ALS inhibitors. In spring cereals, the following mixtures of active ingredients are often used: chlorpyralid + fluroxypyr, MCPA + chlorpyralid + fluroxypyr, tribenuron-methyl + fluroxypyr, and tribenuron-methyl + tifensulfuron-methyl + fluroxypyr. In winter cereals, MCPA + fluroxypyr are often used, while rimsulfuron may be used in potatoes and rimsulfuron + mesotrion and rimsulfuron + fluroxypyr in maize. In pastures and grass leys, fluroxypyr may sometimes be used (Jordbruksverket, 2015).

1.4.4 Biological control

Microbially produced herbicidal compounds which possess characteristics such as relatively short life time, activity in small quantities and non-toxic residues in the environment have advantages over synthetic chemical structures (Saxena & Pandey, 2001). Several microbial phytotoxins or their synthetic analogues can be utilised for the development of new agrochemicals against *S. arvensis*. Cimmino *et al.* (2008) found that the phytotoxin deoxaphomin, produced by the fungus *Phoma exigua* var. *exigula* (strains C177 and S-9), had a high level of toxicity on the leaves of *S. arvensis*.

A survey of potential insect biological control agents of *Sonchus* spp. resulted in the introduction of three insect species, *Tephritis dilacerata* Lw. (Diptera: Tephritidae), *Cystiphora sonchi* (Bremi) (Diptera: Cecidomyiidae) and *Lyriomyza sonchi* Hendel (Diptera: Agromyzidae), into Canada (Lemna &

Messersmith, 1990; Peschken, 1984). *Tephritis dilacerata* occurs throughout northern and central Europe and the button-like floral galls which develop due to its larvae feeding on the developing plant ovaries hamper seed production in infested buds. *Lyriomyza sonchi* comes from Europe and forms blotch mines within the leaf tissue. However, both these species proved unsuccessful as biological control agents because of their inability to establish after release in Canada (Lemna & Messermith, 1990; Peschken, 1984). *Cystiphora sonchi* is native to Europe and its larvae form galls on the leaves (DeClerck-Floate & Steeves, 1995). Although the introduction of this insect species into Canada was successful, it was only able to cause limited damage to *Sonchus* spp. weeds (McClay & Peschken, 2001).

2 Population dynamics of *Sonchus arvensis* L.

Plant population dynamics is an area of plant science dealing with changes in the density, size and fecundity of the individual plants that make up the population and factors affecting their germination, growth, development, reproduction and death rate (Crawley, 2007).

2.1 Life cycle

In central Sweden, the life cycle of *S. arvensis* may be described as follows (Håkansson, 1969). When soil temperature in the upper soil layer increases in early April, belowground shoots start to grow from vegetative buds on the root surface. In late April, the shoots are still under the soil surface and the first new thin and unbranched roots are being produced at this stage. Belowground shoots reach the soil surface about a month after initial growth and the roots have become slightly branched at this time. Initial thickening of the roots takes place at the 3-7 leaf stage in the end of May. The increase in thickness of new roots proceeds and the thickness of new roots reaches 3-5 mm by the end of June (Håkansson, 1969). Thickened roots are usually found at a soil depth of 5-12 cm, but can penetrate to a depth of 2 m and produce vegetative buds as deep as 50 cm below the soil surface (Stevens, 1924). New roots developing from thickened roots and adventitious roots originating from belowground stem parts of aerial shoots are the main sources of infestation in new areas. The number of shoots increases rapidly in May, remains stagnant in the beginning of June and then starts to decrease during August (Brandsæter *et al.*, 2012). Aerial shoots develop flowering stalks and inflorescence buds in the latter part of July. The time required for seeds to become mature is about 10 days. Most of the flowering is completed by the end of August and seeds are dispersed until the end of September. In the autumn, bud dormancy in root buds is induced due to lower temperature and shorter photoperiod. This causes a decrease in the development of shoots between mid-September and early October. However, a further decrease in soil temperature can break this innate dormancy and the development of shoots begins again if the temperature permits (Liew *et al.*, 2013; Andersson *et al.*, 2013; Brandsæter *et al.*, 2010). Aerial shoots and the majority of thin roots finally die and thickened roots with a width of 4-5 mm remain as overwintering organs to support the regrowth of new shoots in the next growing season (Håkansson, 1969; Stevens, 1924).

Successful establishment of *S. arvensis* from seeds depends on the depth at which the seeds are buried and the orientation of the seeds in the soil. Håkansson & Wallgren. (1972a) found that *S. arvensis* seeds buried at a depth of 0.5 cm established seedlings which developed thickened horizontal and vertical roots with considerable regenerative ability. Bosy & Aarssen. (1995) also found that *S. arvensis* seeds with horizontal radical emergence had higher germination rates than seeds with either vertical upward or downward emergence.

Håkansson. (1969) showed that *S. arvensis* reached a minimum dry weight in belowground plant parts at 5-7 leaf stage, due to retranslation of stored reserves to the growing aboveground parts, respiration of the old roots and development of fine roots. At this stage, *i.e.* the compensation point, the plants showed minimum regenerative capacity and were most susceptible to mechanical disturbance.

However, studies by Tavaziva. (2012) and Verwijst *et al.* (2014) have shown that the compensation point occurred earlier, at leaf stages 4 and 5; little earlier for plants without competition than plants growing in competition with a crop.

Studies on the population dynamics of as may rise many questions needed to investigate.

- ✓ Is there any difference in the ability of proliferation between *S.arvensis* roots with different sizes?
- ✓ To which extent does the depth at which the roots develop influence the emergence time of shoots and their growth?
- ✓ How does temperature affect emergence time and development of shoots from roots of *S.arvensis*, and how large are the effects of variable climatic conditions?
- ✓ Does dormancy in the vegetative buds break at the same time in *S.arvensis* roots with different initial weights?
- ✓ Does compensation point take place in the same time in *S.arvensis* roots with different initial weights?

- ✓ Is the rate of shoot emergence higher for thickened roots than for thin roots?
- ✓ Does the position of buds on the roots affect their release from dormancy, and growth and development of the shoots arisen from the buds?

In the thesis some of these questions have been addressed. The regenerative capacities of *S. arvensis* root fragments with different initial sizes are compared. Also, the impacts of temperature and soil depth on emergence are examined.

2.1.1 Environmental factors

A single plant of *S. arvensis* is able to establish a large patch of shoots through vegetative proliferation. Soil properties such as pH, soil type, water content and soil depth at which root fragments are placed and the light intensity are environmental factors that strongly affect the establishment, growth and development of *S. arvensis* plants. For instance, Zollinger & Kells. (1991) found that *S. arvensis* plants grown in a soil with pH 5.2 had lower total biomass than plants grown at higher soil pH levels. Those authors also showed that an increase in soil water content to (full saturation) was associated with an increase in plant height, number of leaves and number of capitula. Decreasing the light intensity from 580 to 285 µE m^{-2} s^{-1} resulted in production of fewer leaves with smaller size, as a result of greater growth of stems and leaves at the expense of root growth.

Belowground shoots that originate from vegetative buds on deeply buried root fragments need a longer time to reach the soil surface and consequently use larger amounts of nutrient reserves from the roots. Therefore *S. arvensis* root fragments placed in deeper layers of the soil produce fewer shoots than root fragments placed at shallower depth in soil (Brandsæter *et al.*, 2011).

In perennial weeds, early establishment of bud sprouting by vegetative reproductive structures at the beginning of growing season is regarded as a critical factor for weed survival (Ghersa *et al.*, 1990). Stored carbohydrate reserves in overwintering belowground vegetative structures provide resources for growth of the new developing sprouts. Sprouting and growth are under the control of many factors, among which temperature plays an important role (Satorre *et al.*, 1985).

Travlos *et al.* (2009) found that the sprouting rate and percentage of purple nutsedge (*Cyperus rotundus* L.) was highest at temperatures between 34 and 38 °C and lowest at temperatures between 18 and 22 °C. Elevated temperature (29-38 °C) not only increased the sprouting rate of *Cyperus esculentus* (L.), but also enhanced the growth of sprouts, so that the length and dry weight of shoots increased parabolically with increasing temperature (Li *et al*., 2000). Spencer & Ksander. (2006) found that the emergence rate of giant cane (*Arundo donax*) ramets and their weight were under the control of temperature. Holshouser *et al*. (1996) found that the bud break rate of *Sorghum halepense* (L.) increased with temperature within the range 28-36 °C, while a further increase in temperature resulted in a reduction in the rate of rhizome bud break.

A better understanding of the impact of increasing temperature on sprouting and prediction of time of emergence in a changing climate would enable the capacity of existing weed management strategies to be improved and new strategies to be designed. In the thesis, these questions were addressed by letting roots grow under three constant temperature conditions, from which a relation between emergence and temperature was developed, and thereafter applied to observed variations in weather.

2.1.2 Pre-emergence variation

Pre-emergence traits such as growth rate, duration of growth and initial plant size not only determine the seedling performance at the beginning of the growing period, but also affect the fitness of adult plants (growth, survival and fecundity) and consequently their mode of competition (Weiner & Damgaard, 2006; Benjamin & Hardwick, 1986). Variation in size is considered to be an important factor resulting in the development of size hierarchies in plant populations. Several studies have shown the significant role of size variation for growth and development of weed species. For example, in comparison with late-emerging seedlings originating from small seeds of *Ericameria nauseosa*, seedlings from larger seeds emerged earlier at a higher rate and produced a larger percentage of total biomass, from which a high proportion was allocated to longer taproots (Benard & Toft, 2007). Susko & Lovett-Doust. (2000) concluded that low-weight seeds developed seedlings with larger height and lower weight.

Dalbato *et al.* (2014) found that longer fragments of the rhizomatous herbaceous perennial coltsfoot (*Tussilago farfara* L.) produced more aboveground shoots and developed more leaves than shorter fragments. Song *et al.* (2013) found that removing proximal and distal internodes from single-node fragments reduced their reproductive capacity in terms of ramet numbers and biomass compared with fragments on which the internodes remained attached to the nodes in 15 stoloniferous species. Highly fragmented rhizomes of *Alternanthera philoxeroides* (Mart.) produced more new ramets which had a lower biomass and leaf area (Dong *et al*., 2012). In the creeping perennial weed *Cirsium arvense* (L.) Scop., the probability of emergence increased with increasing initial weight of root fragments and more shoot and root dry biomass was produced at harvest (Sciegienka *et al.*, 2011). Abdullahi & Cavers . (1997) found that the total percentage of regeneration was higher in 10 cm long root fragments of clammy ground-cherry (*Physalis heterophylla* Nees) than in shorter root fragments.

The significant role of initial size on growth and development of clonal aquatic plants has been also documented in several studies. For instance, Lin *et al.* (2012) showed that larger fragments of *Ipomea aquatic* with a larger number of nodes produced more dry biomass and developed a higher leaf area due to a higher growth rate. Riss *et al.* (2009) found that two-node stem pieces of *Potamogeton perfoliatus* (L.) regenerated better than one-node stem pieces. A study on the impact of fragmentation on growth of *Elodea canadensis* by Mielecki & Peiczynska. (2005) showed that the number of lateral shoots produced by fragments from the middle and the bottom (4-5 cm) of the plant was 50% less than the number arising from apical fragments (3 cm). In the current thesis, the role of initial size on emergence was examined by dividing roots into classes with significantly different initial size and weight at planting.

2.2 Resource allocation

The success of plants in natural ecosystems depends upon traits related to resources acquisition. Plants respond to variations in the environment by apportioning biomass among various plant organs in order to optimise the capture of nutrients, light, water and carbon dioxide in a way to maximises plant growth rate and maintains fitness (Mc Connaughay & Coleman, 1999).

The patterns of biomass partitioning to various organs are under the influence of environmental factors, either biotic agents such as insect herbivores (Orians *et al.*, 2011) and pathogens (Kluth *et al.*, 2003) or abiotic agents such as soil nutrient availability, light intensity (Geng *et al.*, 2007), soil water content (Acciaresi & Guiamet, 2010), competition (Blank, 2010), plant density and propagule fragmentation (Wang *et al.*, 2014) and habitant and disturbance (Shadel & Molofsky, 2002). Life history traits such as plant size and relative growth rate are other factors affecting biomass allocation pattern. Within a population of herbaceous perennials, large plants allocate disproportionately more resources to female functions than smaller plants (Zhang & Jiang, 2002). Three native varieties of *Alternanthera philoxeroides* which differ in growth vigour were found to have different biomass allocation patterns (Jia *et al.*, 2010).

Biomass allocation affects the competitive ability of plants (Gaudet & Keddy, 1988). Drenovsky *et al.* (2008) found that a larger root system, arising as a result of more allocation of biomass to belowground parts, enabled invasive species to capture more resources and to outcompete native species. Holt & Orcutt. (1991) found that Johnsongrass (*Sorghum halepense* L.) was superior in competition to cotton (*Gossypium hirsutum* L.) due to a better developed root system, which resulted from greater biomass allocation to the roots.

Among nutrient resources, nitrogen plays a major role in the balance in biomass allocated to roots and shoots. There is a near linear relationship between plant nitrogen concentration and relative growth rate (Hilbert, 1990). For example, cheat grass (*Bromus tectorum*) plants grown in an N-enriched environment had increased root and shoot biomass relative to the native perennial as a consequence of greater growth rate (Vasquez *et al.*, 2008).

In this thesis, biomass production and its partitioning among different plant components of *S. arvensis* populations were studied as treatment effects of root fragments with different initial length. Also nitrogen allocation pattern and its dynamic during the autumn were evaluated.

3 Overall objectives and specific hypotheses

The overall objective of this thesis is to increase the knowledge on the suppressive effect of mechanical control measures on the abundance/growth/competitiveness of *S. arvensis* in terms of its population dynamics. The other aim is to develop relations for the impact of temperature on sprouting of *S. arvensis*, and to make predictions for variable climatic conditions. The findings were intended to contribute to theory development and to lead to recommendations for practical weed control, especially in organic farming.

The aim in Papers I-IV was to determine the impact of pre-emergence variation traits (initial root size) on sprouting, shoot emergence time, shoot numbers, rosette size, shoot height, biomass production, nitrogen content and recycling.

3.1 Paper I

The specific objective in Paper I was to assess the impact of pre-emergence variation on emergence, growth and development of aboveground plant parts of *S. arvensis*. The hypotheses tested were that: (1) shoots on longer roots emerge earlier than shoots on shorter roots; (2) longer roots produce more shoots per root; (3) longer roots produce larger rosettes; and (4) longer roots produce more flowers and mature seeds.

3.2 Paper II

The specific objective in Paper II was to quantify how the lengths of *S. arvensis* root fragments affect shoot development, biomass production and nitrogen allocation. The hypotheses tested were that: (1) shoot height frequency distributions become bimodal later in the season due to variations in shoot emergence time, regardless of degree of fragmentation; (2) longer root fragments produce larger plants with a higher amount of nitrogen per plant; (3) for a given total root length per m^2, total biomass production and total amount of nitrogen per m^2 are the same regardless of degree of fragmentation; (4) longer root fragments produce plants with a higher proportion of biomass and nitrogen in the roots compared with the shoots; and (5) the amount of nitrogen is higher in roots compared with buds for all root lengths.

3.3 Paper III

The specific objective in Paper III was to assess the impact of root fragmentation on seed production in *S. arvensis*. The hypotheses tested were that: (1) longer root fragments produce plants with a higher number of flower receptacles, each containing more seeds; (2) for a given total root length, the number of mature flower receptacles and number of seeds produced is not affected by root fragmentation; (3) the first cohort of shoots contributes more to generative reproduction than the second cohort of shoots; (4) average seed weight does not differ between plants originating from different root lengths or between shoot cohorts; and (5) number of seeds per flower receptacle and average weight per shed seed are constant over time.

3.4 Paper IV

The specific objectives in Paper IV were to compare simulated time of emergence with observed emergence in practical experiments and to use a model to predict the time when belowground shoots of *S. arvensis* reach the soil surface and start producing aboveground shoots in spring under variable climate conditions. The hypotheses tested were that: (1) soil temperature is the driving force for the processes which determine the elongation rate of belowground shoots from the roots of *S. arvensis*; (2) the time of emergence is determined by an accumulated temperature sum specific for each root-weight class.

4 Material and methods

4.1 Site

The experiments were conducted in (1) boxes placed in an outdoor net enclosure or (2) in buckets placed in dark chambers, with permanently controlled temperatures at Ultuna, close to Uppsala in Sweden (59º48'N, 17º39'E). A sandy soil was used in the outdoor box experiment (Papers I-III), while in the bucket experiment (Paper IV) a mixture of moderately decomposed peat and sand was used.

4.2 Plant material

Root fragments of *S. arvensis* with a length of 5, 10 and 20 cm and of differing thickness (fine, medium or thick) constituted the plant material for the experiments (Papers I-IV). The root fragments were obtained by cutting up *S. arvensis* roots harvested from a plant bank stored over winter in buckets with a soil volume of 10 L from October to June in a dark cold store at +2-4ºC.

4.3 Experimental designs

In the outdoor box experiment (Papers I-III), the roots in each box were selected in such a way that the thickness categories were represented in as equal numbers as possible to generate uniform weed stands (Håkansson, 1969). Depending on the specific aims of the subsequent analyses and on the data available, specific parts of the box experiment were used as follows:

In the experiment described in Paper I, the fully randomised experiment comprised boxes with four length traits or combinations (all with a total root length of 1 m): 20 roots of 5 cm, 10 roots of 10 cm, 20 roots of 5 cm and with 4 × 20 cm + 4 × 5 cm roots, each in six replicates, *i.e.* 24 boxes in total.

The experiment described in Paper II used a completely randomised design involving five replicates of three length traits (all with a total root length of 1 m): 5 root pieces of 20 cm, 10 root pieces of 10 cm, and 20 root pieces of 5 cm, giving 15 boxes in total.

In the experiment described in Paper III, two root length traits (both with a total length of 1 m): 5 root pieces of 20 cm and 20 root pieces of 5 cm, were used in a completely randomised design with four replicates for each trait, *i.e.* 8 boxes in total.

The impact of three factors, initial root length with two levels (5 and 10 cm), temperature with three levels (4, 8 and 18 °C) and planting depth with three levels (3, 10 and 17 cm), on belowground shoot elongation and emergence time of *S. arvensis* shoots was assessed in the experiment described in Paper IV. For each temperature level and root length, 81 roots were planted, so that three roots (one root for each thickness category) were present in each layer at a depth of 3, 10 or 17 cm below the soil surface (in total 27 roots × 3 replicates = 81 roots per temperature level and root length, or 486 roots in total). These 486 roots were ranked according to their initial weight and separated into three non-overlapping weight classes, each containing 162 roots. This gave three classes with mean root dry weight of 0.044, 0.079 and 0.163 g, respectively.

4.4 Measurements

In the outdoor box experiment (Papers I-III), shoot emergence time was monitored continuously during the growing season (Papers I and II). Before the first occurrence of shoot elongation, the diameter of each *S. arvensis* rosette was measured and rosette area was calculated (Paper I). Emerging shoots were classified according to their origin, *i.e.* whether they originated from the originally planted roots or from roots developed during the season, defined here as the first and second shoot generation (Paper II) or cohort (Paper III), respectively. Shoot numbers either per root fragment (Paper I) or per box (for each of the generation and root length traits) (Paper II) and their height (Paper II) were recorded. One of the replicates was harvested before any of the leaves turned yellow (early August) and aboveground dry weight of plant components was recorded after oven drying of samples at 50 °C for 24 h (Paper II). One replicate was harvested after the onset of flowering (early September) and the number of flower receptacles per shoots was counted (Paper I).

For two of the root length traits (5 and 20 cm) and shoot cohorts, the number of mature seeds and seed weight were recorded at harvest and seed samples were taken on three occasions (8, 17 and 26 September) (Paper III).

Four replicates were harvested in the beginning of October. Number of flower buds per shoot on each root fragment (Paper II), dry weight of leaves, stems, roots and flower buds (Paper II), number of flower receptacles that had produced mature seeds per box (for each of the generation and root length classes) (Paper III), number of living plants (Papers II and III), and length of the roots produced were measured (Paper II). Nitrogen concentration (%) in the plant components was quantified (Paper II).

In the experiment described in Paper IV, harvest was performed per temperature level and replicate (consisting of three buckets) just after the initial emergence of the first shoot per temperature level and replicate, and the length of the longest shoot per root was measured. Time (days) from planting until harvest was recorded for each of the buckets. This resulted in five harvest occasions per temperature treatment (Table 1 in Paper IV).

4.5 Statistical analyses

The MIXED procedure (SAS Institute, 2011) was used to assess the effect of initial root length (Papers I-III), initial root weight (Paper I), shoot cohort and sampling time (Paper III) on shoot emergence time, number of shoots, rosette area, number of flowers, maturity of buds (Paper I), number of flower receptacles per plant and unit area, number of seeds at harvest per flower receptacle, average seed weight at harvest, and seed number and seed weight per unit area and per plant (Paper III). This procedure fits mixed models, *i.e.* models including both fixed and random effects. The MIXED procedure was also used to perform linear regression analyses. A linear mixed model was used to establish the relationships between initial root weight within roots of different lengths and shoot emergence time, number of shoots, rosette area, and number of flowers and maturity of buds (Paper I). Similarly, a linear mixed model was used to establish the relationship between the number of seeds per flower receptacle and average seed weight, taking into account the effects of initial root length and sampling time (Paper III).

The relationship between shoot emergence time and sprouting order of shoots within roots of different root lengths, and rosette diameter, rosette age and root length were evaluated by non-linear regression analyses performed in Statistica (Statsoft, 2009) (Paper I).

The MODECLUS procedure of the SAS system was used to test bimodality in shoot height frequency distribution and to calculate the bimodality coefficient (BC) (Paper II).

One-way analysis of variance was used to assess the effect of initial root length on total and plant dry weight of plant parts and shoots, relative proportion of plant components, root:shoot ratio, total and plant root length, total and plant nitrogen content in plant and root:bud nitrogen ratio (Paper II).

Repeated measurements analyses, accounting for intra-box correlation, were performed using mixed models (the MIXED procedure, SAS). These models evaluated changes over time in total nitrogen and nitrogen concentration in plant parts (Paper II) and effects on the number of seeds per flower receptacle and average seed weight (Paper III). The models included main effects of initial root length (Papers II and III), shoot cohort (Paper III), harvest or sampling time (Papers II and III), plant component (Paper II), and all their interactions as fixed effects, and plant component (Paper II) and sampling time (Paper III) as repeated factors.

5 Results and discussion

5.1 Shoot sprouting and emergence (Papers I and IV)

Root length (Paper I), root weight (Papers I and IV) and temperature (Paper IV) had a strong influence on the emergence time of the shoots (Table 2 in Paper I; Table 1 in Paper IV).

The higher amount of stored reserves in heavier root fragment shorten the time of emergence, due to a higher elongation rate of the first belowground (bg-) shoots (i.e. the one that first reach the soil surface), than for lighter roots. As a consequence of this the temperature sum requirement to reach to the soil surface was lower for the higher roots (Paper IV).

The higher the content of stored nutrients, the higher the depletion rate (Guncan, 1973; Paper I). Large depletion of nutrient reserves in heavier root fragments due to a relatively larger amount of stored carbohydrates and protein relative to lignified tissue is likely to be the reasons for faster bg-shoot elongation rate and consequently earlier emergence time in heavier roots.

An increase in soil temperature was associated with an increase in elongation rate of the first bg-shoot. The difference in the rate of shoot elongation between the first shoot from the heaviest root fragments and the first shoot from the lightest root fragments increased with increasing soil temperature. At 18 °C, the rate of bg-shoot elongation in heavier root fragments was 5.34 mm day^{-1} more than in lighter root fragments, while this difference was reduced to 0.64 mm day^{-1} at 4 °C (Table 2 in Paper IV).

However, the accumulated temperature sum that was required for bg-shoots to reach the soil surface, for a specific root weight class, was found to be independent by the temperature level, assuming a threshold of 2 - 2.5 ^{o}C below which no bg-shoot elongation occurred.

In heavier root fragments, the first bg-shoot required a higher temperature base (0. 5 °C higher) than in lighter root fragments to start the growth, but had a lower temperature sum requirement for emergence (103 d°C lower) (Figure 2b in Paper IV).

Using the temperature sum requirement as a predictor, the emergence of shoots from the largest root fragments buried at a depth of 10 cm took place 2 weeks earlier in the earliest spring (2007) at Ultuna than in the latest spring (2005 and 2006), due to differences in observed soil temperature between the years (Figure 4 in Paper IV). In spring 2005 in Uppsala, the difference in emergence time between the heavy roots and the light roots was 9 days, which was 4 days less than the differences caused by different temperature conditions between the years 2004 - 2010 (Figure 3, Paper IV); i.e. the variation in emergence time between years was larger than the variation due to difference in initial root weights. (Table 2, Paper IV).

Increasing the daily soil temperature (as recorded in 2008) by 2, 4 and 6 °C, to roughly mimic potential temperature changes in a range corresponding to alternative future projected climate change scenarios (e.g. IPCC, 2014), shortened the calculated emergence time by 8, 19 and 30 days, respectively, for the lightest roots and by 1-2 days for the heavy roots (Table 3 in Paper IV).

A similar positive effect of temperature on sprouting of rhizome buds of torpedograss (*Pannicum repens* L.) was observed by Hossain *et al.* (2001), who found that increasing the temperature from 10 to 20 °C increased rhizome buds sprouting from 50 to 96 %. Satorre *et al.* (1996) also found that the rate of sprouting increased with temperature within the range 11-33 °C in rhizomes and stolons of *Cynodon dactylon* (L.). High temperature probably causes activation of the enzymatic and physiological function of rhizome buds and increases the rate of mobilisation of nutrient reserves to the growing belowground shoots.

The first shoot from long roots broke the soil surface on average about 6 days earlier than the first shoots from short roots (Fig. 1 in Paper I, temperature was 15.6 ^{0}C). In shorter and lighter root fragments, a lower amount of stored nutrients (<1 g) not only exerted an influence on the emergence time of the first shoot, but also postponed the emergence of later shoot cohorts arising on the root fragments (Paper I).

Similarly, Scieginka *et al.* (2011) found that both initial root diameter and root length of *Cirsium arvense* (L.) Scop. were positively related to the probability of emergence, but root diameter was of higher relative importance than root length. In the rhizomateous perennial shrub *Calligonum arborescens* (Litv.), increasing diameter of the rhizome fragments markedly increased the emergence rate, while the emergence time was decreased (Luo & Zhao, 2015).

Faulkner & Young. (2006) also found that the first shoot on 10-cm rhizome fragments of *Physalis viscosa* (L.) took a shorter time to emerge than the first shoot on 1.5-cm rhizome fragments.

5.2 Shoot density and shoot height frequency distribution (Papers I and II)

Initial root length (Papers I and II), root weight (Paper I) and shoot generation (Paper II) significantly affected aboveground shoot production. The number of (ag-) shoots produced per root fragment was larger from long root fragments than from short root fragments. However, fewer ag-shoots were produced per cm on long root fragments compared with short root fragments (Table 5 in Paper I). Differences in the number of ag-shoots between different generations from short and long root fragments were only observed in the first generation at area level (Table 1 in Paper II). However, the number of ag-shoots increased with increasing root weight and this increase was faster in 5 cm roots than in 20 cm roots. Long roots within an equal weight range of 0 to about 2.4 g had more shoots than 5 cm long roots of the same weight, which led to a significant interaction of root length and root weight (Figure 2 in Paper I).

In a previous study, Dalbato *et al.* (2014) found that the number of emerged shoots increased per fragment and decreased per cm fragment with increasing initial length of *Tussilago farfara* L. rhizome fragments. Edwards & Oliver. (2004) also found that the density of trumpet creeper (*Campsis radicans* (L.) Seem) shoots was greater in longer and heavier pieces.

In long root fragments, mean shoot height was higher in the first and second generations compared with the shoot generations from short root fragments (Table 1 in Paper II). A lower amount of stored nutrient reserves in short root fragments may be the reason for lower shoot height from short root fragments and an increase in the variation in shoot height between early and late emerging shoots in short root fragments (Paper II). Similarly, West *et al.* (2012) found that the height of *Cayratia* shoots originating from root fragments of 5 and 7 cm was higher than for 1-3 cm root fragments.

In all the populations with different initial root lengths, shoots from the first generation were taller than shoots from the second generation (Table 1 in Paper II). On long root fragments, the first shoot emerged earlier and seemed to impede sprouting of the other buds (apical dominance). Delay in activation of buds not only reduced the number of shoots produced, but also delayed the emergence of the later shoot cohorts. This difference between the emergence of the first and later shoots finally resulted in the development of a shoot bimodal frequency distribution in the first generation of shoots. Bimodality in shoot height frequency distribution was also observed in the whole population consisting of both the first and second generation, which could be ascribed to differences in shoot numbers and shoot height between the first and second generations as a result of differences in shoot emergence time (Figure 1 in Paper II).

Similar effects of emergence time on the development of a size hierarchy in populations of cocksfoot (*Dactylis glomerata* L.) were reported by Ross & Harper. (1972). Differences in relative growth rate of early and late emerging individuals caused the development of a size hierarchy.

5.3 Biomass production (Paper II)

5.3.1 Plant level

Biomass production per plant was strongly affected by initial root length fragment (Table 2 in Paper II). Plants originating from long root fragments had larger total biomass than plants originating from short root fragments. These differences in biomass production between plants originating from short and long root fragments might be a result of differences in the leaf area per plant. Early emerging first shoot cohorts on long root fragments had larger rosette diameter than first shoot cohorts from short root fragments (Figure 3 and Table 6 in Paper I) and developed a larger total rosette area 5 weeks after planting (Table 5 in Paper I).

West *et al.* (2012) also reported a similar increase in dry weight with increasing length of initial root fragments in *Solidago canadensis* and *Solidago gigantea*. Sciegienka *et al.* (2011) observed a positive relationship between the initial weights of *Cirsium arvense* (L.) Scop root fragments and plant dry shoot and root biomass at harvest, although this varied with water regime and soil depth of the root fragment. More biomass was produced by plants on long root fragments of trumpet creeper (*Campsis radicans* (L.) Seem) than by plants from short root fragments (Edward & Oliver, 2004).

5.3.2 Population level

Total dry weight per m^2 and the relative proportion of dry weight of leaves, stems, buds and roots at harvest were not affected by initial root length (Paper II).

Root: shoot ratio did not differ between the populations with initially different root lengths.

These results are in agreement with findings by Pan *et al.* (2009) that fragment size had no impact on biomass partitioning between roots and shoots of alligator weed (*Alternanthera philoxwroides* (Mart.) Griseb.

5.4 Nitrogen allocation (Paper II)

5.4.1 Plant level

Total nitrogen content per plant was larger in plants from long root fragments, due to their higher dry weight. Of the total nitrogen content found in roots and buds, 80% was allocated to the roots while about 20% was found in the buds.

Nitrogen concentration (%) did not differ between plants originating from initially different root fragments, but varied significantly in the different parts of the plants on two harvest occasions in August and October, respectively (Table 2 in Paper II).

The pattern of change in nitrogen concentration during autumn varied among the plant components. While the nitrogen concentration in the roots did not change between August-October, the concentration of nitrogen was considerably reduced in the leaves due to translocation to the roots (Figure 2a in Paper II). Similarly, Bausenwein *et al.* (2001) found that the nitrogen concentration in leaves of *Rumex acetosa* L. was reduced as a result of redistribution of nitrogen to reproductive parts later in the season.

5.4.2 Population level

Total nitrogen content (g m^{-2}) was significantly different between plant components, but did not differ between the three populations (Paper II). A decrease in total nitrogen content in leaves and stems between August and October coincided with an increase in total nitrogen content in the roots (Figure 2b in Paper II).

Increased biomass in the belowground parts of *S. arvensis* functioned as a sink for nitrogen withdrawn from senescing shoots in late autumn (Paper II; Limami *et al.*, 1993). The increase in nitrogen content in the belowground organs of *S. arvensis* was most likely due to a highly effective maintenance system, which not only ensures the survival of overwintering roots in harsh condition during the winter period, but also increases the probability of successful proliferation from vegetative buds in the next growing season by reducing the dormancy of vegetative buds. Translocation of nitrogen to the roots is an important strategy for reducing dormancy in rhizome buds due to nitrogen deficiency (Chancellor, 1974).

Internal cycling of nitrogenous compounds in the plant system and its significant role in the survival of belowground vegetative plant parts over winter and regenerative capacity in the next growing season in herbaceous perennials have been well documented (*e.g.* Omezine & Skhiri-Harzallah, 2011; Emily *et al.*, 2009; Cordazzo & Seeliger, 2003).

5.5 Reproduction

5.5.1 Vegetative reproduction (Paper II)

Initial root length had a strong influence on the length of newly developed roots and their weight. Longer root fragments produced plants with heavier and longer roots compared with shorter root fragments (Table 2 in Paper II).

In a previous study, Weber. (2011) found that plants originating from long rhizome fragments of *Solidago gigantea* buried in the soil at a depth of 5 cm produced longer rhizomes than plants from shorter root fragments. Rask & Andreasen. (2007) found that longer rhizome fragments of *Calystegia sepium* produced more rhizomes than shorter rhizome fragments. Moreover, Klingeman *et al.* (2004) found that the length of the roots produced was larger when 0.5 and 1 cm long sections of *Artemisia* rhizome fragments included a leaf scale.

The total root length per m^2 and the relative proportion of dry weight of roots were not significantly affected by initial root fragment length (Paper II).

5.5.2 Generative reproduction (Papers I, II and III)

The number of flower receptacles per plant was affected by initial root fragment length (Table 2 in Paper I; Table 1 in Paper II), initial root weight (Table 3 in Paper I) and shoot cohort (Table 1 in Paper III).

The shoot cohorts from plants originating from 20-cm root fragments produced more flower receptacles that the shoot cohorts from plants originating from 5-cm root fragments (Table 5 in Paper I; Figure 1 in Paper III). An increase in the total number of flower receptacles per plant with increasing root weight was observed in the shorter root fragments, but not in the long root fragments (Table 3 in Paper I).

The proportion of flower receptacles that gave rise to mature seeds among total number of flowers either per unit root length or whole fragment increased with initial root fragment length, but the initial weight of root fragments had no significant effects (Table 5 in Paper I).

Shoots from the first cohort produced significantly more seeds per flower receptacle at harvest than shoots from the second cohort, but the average weight of seeds was similar in the two shoot cohorts (Paper III). A possible explanation for fewer seeds per receptacle could be shortened flowering duration due to delayed emergence time of the second generation shoots. This is in line with observations on *Agilinis strictifolia* (Benth.) by Dieringer .(1991), who found that large shoots flowered longer and produced more flowers than those of late emerging and small shoots which had their peak flowering later in the season. Another explanation could be a resource restriction or pollination restriction. In *S. arvensis*, average shoot height of the second cohort was much lower (Paper II) and therefore the flower receptacles had a lower position in the canopy. This is in line with observations by Lortie & Aarssen. (1999), who found that taller plants of *Verbascum thapsus* L. had more opening flowers and attracted more pollinators.

Seed number per plant was significantly higher for plants from long root fragments than for plants from short root fragments. The number of seeds per plant was significantly higher in shoots from the first cohort compared with the second cohort. Shoot cohort had also a significant effect on seed number per unit area, the first cohort producing one order of magnitude more seeds than the second. No significant effects were observed for initial root length or its interaction with shoot cohort on the number of seeds per unit area (Table 1 in Paper III).

There were some variations in individual seed weight and number of seeds per flower receptacle over the seed shedding time. While the first cohorts of shoots had their maximum number of seeds per flower receptacle at the middle of September, the number of seeds per flower receptacle of the second shoot cohort was constant over time. The highest average seed weights were observed in the first shoot cohort at the first sampling time (Figure 2a, b in Paper III).

A negative relationship between the number of seeds per receptacle and the weight of seeds produced in early September was observed at the first sampling time (Figure 3 in Paper III). A similar observation was made by Primack. (1978), who found a negative correlation between weight per seed and seed number per capsule in the genus *Plantago*. The disappearance of the trade-off between seed weight and number of seeds per receptacle at the second and third sampling times is most likely the result of a higher number of pollinated flowers per receptacle due to attraction of more pollinators.

While the number of flower receptacles per m^2 was higher for the first shoot cohort compared with the second shoot cohort (Paper III), shoots from root fragments with different initial lengths produced similar numbers of flower receptacles per m^2 (Paper II; Table 1 in Paper III).

Shoots from the first cohort produced on average 30 391 seeds m^{-2}, whereas shoots from the second cohort produced 2307 seeds m^{-2}. Our observed seed production per m^2 was in the same order of magnitude as found by Dorph-Petersen. (1924) and number of seeds per flower receptacle was in the same order of magnitude as reported by Derscheid & Schultz. (1960). The difference in the number of seeds produced per unit area was ultimately reflected in higher seed weight per unit area (Paper III).

6 Conclusions and further research

- *Emergence:* The degree of root fragmentation strongly influenced aboveground plant performance in terms of shoot emergence time, shoot numbers, rosette size, flowering and seed production. Compared with larger root fragments, small root fragments of *S. arvensis* produced more numerous but smaller-sized shoots, which emerged later in the beginning of the growing season. Shoot emergence time is considered to be crucial for weed perpetuation, and early establishment of weed plants increases their chances of competing with crops. In competition with a crop, *S. arvensis* is known to be sensitive with regard to emergence time relative to the emergence time of cereals. Delayed emergence time from fragmented roots of *S. arvensis* gives the crop the opportunity to establish and increase its competitive potential. Soil cultivation during autumn, in spite of the lower sprouting readiness of *S. arvensis* due to innate bud dormancy, weakens shoot development during the next growing season through root fragmentation. Hence, autumn cultivation may contribute to more sustainable agricultural practice, as part of an integrated pest management (IPM) strategy.

- *Aboveground shoots:* Root fragmentation resulted in a change not only in the frequency of aboveground shoots originating from *S. arvensis* root fragments, but also in the height of these shoots. Shoot height is an important trait which determines the final outcome of competition for light. Light competition is the probable reason for the sensitivity of *S. arvensis* to emergence time relative to crop emergence time. For this reason, fragmenting *S. arvensis* roots into smaller pieces may reduce the ability of weeds to compete with the crop, thus lowering the viability of the weed population.

- *Seed production*: Highly fragmented roots of *S. arvensis* produced plants which had a lower generative capacity in terms of seed production compared with plants produced on roots with a lower degree of fragmentation. However, the generative output of short and long root fragments per unit area was similar. When *S. arvensis* plants are grown with a crop in the field at the onset of a cropping season, small shoots from short root fragments will probably suffer more from competition with the crop due to their small size and will produce fewer regenerative modules as a consequence of delay in their growth. Furthermore, a higher intensity of root fragmentation in combination with competition from the crop is likely to be an efficient way to decrease seed production by *S. arvensis.* Further studies are required to assess the interaction of root fragmentation and crop competition on the generative production of *S. arvensis.*

- *Climate impact:* Temperature significantly affected sprouting and emergence time of *S. arvensis*. An increase in temperature caused an increase in the rate of *S. arvensis* belowground shoot elongation. Variations in temperature between years under field conditions (in central Sweden) resulted in larger variations in emergence time than differences in root fragment weight. An average increase in mean air temperature by about 3 °C would cause earlier emergence, approximately equal to the difference between the earliest and latest year in the present climate.

  The onset of decreased sprouting capacity caused by low temperatures is expected to occur even later in the autumn, thereby counteracting the effects of cultivation methods that promote depletion of roots during autumn. Further, weed control operations over longer periods might be needed to control this perennial weed prior to sowing crops under a changed climate in the future. Higher temperature levels are likely to also affect other aspects of growth and development of *S. arvensis*, as well as cropping. Therefore further studies are needed to evaluate the impact of an increase in temperature on the dynamics of *S. arvensis* populations with different degrees of root fragmentation, and the relation to the competition with the crop in a future changing climate.

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