

Cirsium arvense differs from *Tussilago farfara* in regrowth from intact and fragmented below-ground systems

U. Boström¹  | L. O. Brandsæter^{2,3}  | L. Andersson¹ 

¹Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

²Faculty of Biosciences, Department of Plant Sciences, Norwegian University of Life Sciences (NMBU), Ås, Norway

³Division of Biotechnology and Plant Health, Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway

Correspondence

L. O. Brandsæter, Faculty of Biosciences, Department of Plant Sciences, Norwegian University of Life Sciences (NMBU), Post Box 5003, 1432 Ås, Norway.
Email: lars.olav.brandsaeter@nmbu.no

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Abstract

Fast regrowth from deep roots and rhizomes makes it difficult to mechanically control the perennials *Cirsium arvense* and *Tussilago farfara* respectively. It is, however, not clear whether new shoots originate mainly from fragments of roots/rhizomes in upper soil layers or from an intact system below depth of soil cultivation. Here we present results from three experiments with natural infestations of *C. arvense*, and two with both *C. arvense* and *T. farfara*. Plots of 1 m² were excavated to different depths (13–25 cm), all below-ground plant parts in the topsoil were collected and thereafter fragments were either returned to or removed from the plots. Regrowth from disturbed plots with removed or returned fragments was compared. The origin of regrown shoots, that is, whether they originated from seeds, intact below-ground root/rhizome systems or returned fragments, was examined. More *C. arvense* shoots originated from the intact root system (48%–84%) than from root fragments (16%–52%). The final aboveground biomass was not affected by removal of the top-soil fragments. For *T. farfara*, a small proportion (3%) of new shoots originated from the intact rhizome system, and the rest from fragments. We conclude that the intact root system of *C. arvense* contributes at least as much as root fragments to regrowth after soil cultivation, which might imply that time of treatment and depth of cultivation are crucial for the effect of mechanical control. For *T. farfara*, the results suggest that tillage equipment with high capacity to fragment the rhizome system will contribute to efficient control.

KEYWORDS

Canada thistle, coltsfoot, creeping thistle, mechanical weed control, perennial weed, soil cultivation

1 | INTRODUCTION

The herbaceous *Cirsium arvense* (L.) Scop. and *Tussilago farfara* L. are both among the most troublesome perennial weeds in Scandinavia. While *T. farfara* mainly occurs on organically cultivated land (Roschewitz et al., 2005), *C. arvense* is problematic also in conventional agriculture and was listed as one of the world's worst weeds by

Holm et al. (1977). Non-chemical control strategies often include different types of soil tillage aiming to fragment the below-ground system, thereby initiating depletion of stored carbohydrate reserves by stimulating bud burst and shoot regrowth. The challenge of such strategies is that both species proliferate by an extensive and deep, below-ground root (*C. arvense*) or rhizome (*T. farfara*) system. For successful control, there is a general perception that repeated tillage is required,

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which is energy consuming and environmentally unsustainable. Thus, there is a significant need for more resource efficient control measures. We argue that such measures must be based on an increased understanding of the species' regenerative biology. This can improve control efficiency by choice of, for example, appropriate weed management equipment, soil tillage depth and timing of weed control.

Cirsium arvense and *T. farfara* reproduce sexually by seeds, but vegetative reproduction is considered to be more important and the main factor explaining their success as agricultural weeds. Fresh seeds of *C. arvense* germinate readily, but may show primary dormancy (Hodgson, 1964) and persistence in undisturbed soil (James et al., 2010). The seeds of *T. farfara* have limited persistence in soil, and according to Korsmo (1954), they do not form a soil seedbank. In *C. arvense*, new shoots sprout from adventitious buds formed on plagiotropic roots, while the vegetative production of new shoots and roots in *T. farfara* is from axillary buds on rhizomes. In both cases, roots and rhizomes, respectively, are distributed to a large depth. In a 2-year old stand of *C. arvense*, 84% of the roots were above a depth of 40 cm (Hodgson, 1968) and it was suggested that a greater percentage of roots might have reached deeper in older stands. In a 10-year old stand, the vertical roots had reached almost 2 m, with the major part of the total root system located within a soil depth of 20–40 cm (Nadeau & Vanden Born, 1989). Hayden (1934) observed that the depth of the longest roots seemed to be determined by the depth of the soil water table. According to Håkansson (1982), *T. farfara* produces large parts of its regenerative system below ploughing depth. In contrast, a fact sheet mentioned that most rhizomes grow in the upper 5–20 cm soil profile, but can be found to a depth of 3 m.

After soil disturbance, regeneration is possible from buds on the fragmented roots or rhizomes as well as from the intact system below disturbance depth, which has been suggested to explain the species' tolerance to soil cultivation (e.g., Moore, 1975). The relative importance of fragments compared to the intact root system for regrowth is, however, not well understood. Thomsen et al. (2013) showed that removal of all fragments of *C. arvense* in the topsoil did not influence the final aboveground biomass, leading them to conclude that regrowth from the intact root system below ploughing depth was larger than from root fragments. However, the actual origin (i.e., from the intact root system, from root fragments or from seeds) of the aboveground shoots was not investigated in their study.

Several studies have addressed the regrowth capacity of different weed species from buds on fragmented roots or rhizomes in relation to, for example, fragment length, diameter, weight, burial depth, nutrient content and soil type (e.g., Dalbato et al., 2014; Dock Gustavsson, 1997; Hamdoun, 1972; Sciegienka et al., 2011; Thomsen et al., 2011). Although both *C. arvense* and *T. farfara* can regenerate from small fragments that have been buried deeply, the number of shoots decreases with increasing burial depth. In addition, deep burial has been shown to delay the time of emergence as compared to shoots from buds at shallower depths (Dalbato et al., 2014; Dock Gustavsson, 1997).

Date of tillage may affect the regrowth from roots and rhizomes, as for example, shown by Brandsæter et al. (2017), who found that

spring tillage had a stronger control effect than autumn tillage on *C. arvense*. In both *C. arvense* and *T. farfara*, the regeneration capacity from the undisturbed root/rhizome system is reduced during a period in the autumn (Andersson et al., 2013; Boström et al., 2013). In addition, reduced sprouting from fragmented *T. farfara* rhizomes in autumn was noted by Liew et al. (2013), but in a study presented by Fykse (1977) the reduction was small. None of the authors found a similar reduction of regeneration capacity from fragmented *C. arvense* roots.

The objective of the presented experiments was to compare shoot regrowth capacity from intact root and rhizome systems below depth of disturbance with regrowth from fragmented root or rhizome pieces within the upper disturbed fraction after simulated soil cultivation. We analysed, separately, three semi-field experiments in Norway and two in Sweden, with slightly differing experimental design. The experiments consisted of excavation to specific depths, and returning soil with or without root/rhizome fragments. This was done in two species differing in reproductive biology and type of perennating organ. Each experiment was designed to test hypothesis (i) shoot regrowth after soil disturbance is higher from the intact system than from the fragmented roots or rhizomes. In addition, two of the experiments were designed to test the hypothesis (ii) that shoot regrowth capacity depends on date of cultivation, and two experiments were designed to test the hypothesis (iii) that deep soil disturbance results in less shoot emergence.

2 | MATERIALS AND METHODS

Experiments in three annually cropped agricultural fields with natural infestation of *C. arvense*, and in two fields infested with both *C. arvense* and *T. farfara*, were established in Norway and Sweden (Table 1). Three experiments were established in Norway: *C. arvense* in 2013 (hereafter referred to as Ca₂₀₁₃), *T. farfara* + *C. arvense* in 2013 (TfCa₂₀₁₃), and *T. farfara* + *C. arvense* in 2014 (TfCa₂₀₁₄). In 2014, two additional experiments were conducted in Sweden: *C. arvense*, started in May (Ca_{2014_May}) and in August (Ca_{2014_Aug}) respectively.

In all experiments, plots of 1 m² were excavated to different depths, all roots/rhizomes in the topsoil were collected and thereafter either returned to the plots as fragments of maximum 10 cm or discarded. To assess the relative importance of intact root/rhizome systems below topsoil versus fragmented roots/rhizomes within the topsoil layer, regrowth from disturbed plots with removed or returned fragments was compared. Also, in four of the experiments, the origin of regrown shoots was examined by checking whether the shoots originated from seeds, from the intact root/rhizome systems or from the returned fragments. The background competing vegetation (i.e., the crop surrounding the experimental plots) was spring- and autumn sown wheat in Ca_{2014_May} and Ca_{2014_Aug} respectively. The area surrounding the experimental plots in Norway were used for growing spring cereals.

TABLE 1 Overview of the design of five semi-field experiments situated in Norway (Ås) and in Sweden (Uppsala) with natural infestations of *Cirsium arvense* (Ca) and *Tussilago farfara* (Tf).

Experiment	Species	Site and year	Number of replicates	Treatments
Ca ₂₀₁₃	Ca	Ås 2013	3 ^a per starting date	Fragments removed/returned, 2 starting dates
Ca _{2014_May}	Ca	Uppsala 2014	8 until check of shoot origin, 4 thereafter	Fragments removed/returned
Ca _{2014_Aug}	Ca	Uppsala 2014–2015	8	Fragments removed/returned
TfCa ₂₀₁₃	Tf, Ca	Ås 2013	3 per starting date and depth	Fragments removed/returned, 2 starting dates, 2 depths
TfCa ₂₀₁₄	Tf, Ca	Ås 2014	3 ^a per depth	Fragments removed/returned, 2 depths

^aAll treatments with returned fragments were represented by two replicates in each of three blocks.

TABLE 2 Overview of experimental details for five semi-field experiments with natural infestations of *Cirsium arvense* (Ca) and *Tussilago farfara* (Tf), in which plots were excavated to different soil depths and the fragmented roots/rhizomes were removed or returned.

Treatment	Ca ₂₀₁₃	TfCa ₂₀₁₃	TfCa ₂₀₁₄	Ca _{2014_May}	Ca _{2014_Aug}
Start of experiment	May 24	Jun 3	May 15	May 15	Aug 21
	Jun 19	Jun 19			
Soil depth (cm)	25	13	13	20	20
		25	25		
Check of shoot origin	Jul 10, Aug 30	–	Jul 16–17	Jul 21–22	Jun 8–9*
End of experiment	Aug 5	–	Sep 30	Aug 20	Jun 8–9*
	Aug 30	Aug 30		–	

Note: ×, treatment implemented; –, treatment not performed; *, after overwintering.

2.1 | Experiments Ca₂₀₁₃, TfCa₂₀₁₃ and TfCa₂₀₁₄ in Norway

In 2013, excavations were conducted in one experiment with *C. arvense* (Ca₂₀₁₃), and one with *T. farfara* + *C. arvense* (TfCa₂₀₁₃) in late May and early June, respectively, about 50 m from each other (Table 2). In addition, a second excavation, hereafter referred to as late disturbance, was done in both experiments 2½–3½ weeks later. The TfCa₂₀₁₄ experiment, consisting of only one excavation date, was initiated in mid-May 2014, ca. 300 m from the site of the 2013 experiments. All three experiments were located at the Norwegian University of Life Sciences (NMBU), Ås (59°40' N, 10°47' E, 75 m above sea level). The soil is described as silty clay loam with poor natural drainage (Bakken et al., 2006) and classified as Epistagnic Albeluvisol (Siltic) (IUSS Working Group WRB, 2006).

All three Norwegian experiments were laid out in a randomised complete block design with three replicates. Experiment Ca₂₀₁₃ encompassed four treatments with excavated plots, in a full two factorial design consisting of: (i) root fragments (removed and returned) and (ii) starting time (early and late). TfCa₂₀₁₃ had eight treatments with excavated plots, in a full three factorial design consisting of (i) rhizome/root fragments (removed and returned), (ii) digging depth (13 and 25 cm) and (iii) starting time (early and late). TfCa₂₀₁₄ consisted of four treatments with excavated plots, in a full two factorial design of: (i) root fragments (removed and returned) and (ii) digging depth (13 and 25 cm). To enable destructive harvesting for checking of shoot origin in Ca₂₀₁₃ and TfCa₂₀₁₄, all treatments with returned fragments were represented by two replicates in each block while one replicate was used in each block where fragments were removed. In TfCa₂₀₁₃, all treatments were represented by one replicate per block.

In all three experiments, the experimental plots were placed at a distance of 1–2 m from each other within each of three blocks. To prevent *C. arvense* and *T. farfara* in the surrounding area from growing into the experimental plots later in the season, the adjacent area was frequently mown to 2–4 cm stubble height throughout the season. To prevent roots from penetrating the walls of excavated plots, a thick, plastic membrane was placed along the walls down to the digging depth before the soil was returned.

The soil in TfCa₂₀₁₃ and TfCa₂₀₁₄ was excavated to depths of 13 or 25 cm, and to 25 cm in Ca₂₀₁₃. At excavation, all roots and rhizomes were carefully separated from the soil, and subsequently either kept for reburial or discarded. For plots on which fragments were to be returned, long roots/rhizomes were cut into 10 cm lengths before burial. To avoid the dehydration of the fragments between excavation and reburial, they were wrapped in wet paper in a cooler. In plots with 13 cm digging depth, 50% of the root/rhizome fragments were placed at the bottom level (13 cm) and the other 50% at 6.5 cm depth. In plots with 25 cm digging depth, the fragments were evenly divided between depths of 6.5, 13, 19 and 25 cm.

2.2 | Experiments Ca_{2014_May} and Ca_{2014_Aug} in Sweden

In 2014, one experiment with *C. arvense* was initiated in May (Ca_{2014_May}) and one in August (Ca_{2014_Aug}) in an agricultural field outside of Uppsala, Sweden (59°50' N, 17°34' E, 27 m above sea level). The two experiments were located about 30 m from each other and had, apart from different starting dates, identical design. The soil was a heavy clay, and since there was a risk that the hard soil would make

it impossible to correctly determine shoot origin, the clay in all plots was excavated and replaced with a sandy soil.

The experiments encompassed 16 plots in a completely randomised design, with two treatments: (i) excavation of eight plots to a depth of 20 cm, return of fragments, and (ii) excavation of eight plots to a depth of 20 cm, fragments removed. In Ca_{2014_May} , registration of shoot origin was conducted 1 month before final harvesting to enable a correct identification of origin. Thus, only four plots per treatment were used for this registration, as compared to eight plots per treatment for Ca_{2014_Aug} .

In each experiment, 16 1 m^2 -plots were marked in each corner with wood sticks. The plots were thereafter roughly dug out to a depth of about 18 cm using an excavator. The size and depth of the plots was manually adjusted to $1 \times 1 \times 0.2\text{ m}$ by using a spade.

The soil from eight of the plots was carefully hand-sorted and all visible roots of *C. arvensis* were collected, rinsed in water and long roots were cut to a length of 10 cm for subsequent reburial. The soil from these, and from the remaining eight excavated plots, was rejected and removed from the field. All excavated plots were refilled with a 10 cm layer of sandy soil, and for the reburial treatment the fragmented roots were returned to their eight original plots and evenly spread over the surface. All plots were watered with 5 L of tap water (i.e., corresponding to 5 mm precipitation), whereafter the excavated plots were filled with an additional 10 cm layer of the sandy soil. All plots were then watered once again with 5 L of tap water, and thereafter regularly watered throughout the experimental period to avoid drought. All other weed species, growing inside the plots or within the nearest 20 cm zone, were regularly removed, as were also shoots of *C. arvensis* emerging within a 50 cm zone outside the plots.

At the start of the experiment, the mean number of leaves on the two most developed shoots in each plot was 10 leaves in Ca_{2014_May} and the mean length of the five longest shoots in two randomly chosen plots was 78 cm in Ca_{2014_Aug} .

2.3 | Assessments

In the Norwegian experiments Ca_{2013} and $TfCa_{2013}$, the numbers of emerged shoots were counted regularly during the growing season, while in $TfCa_{2014}$ the number of shoots was counted solely at the termination of the experiments. In all three experiments, the above-ground biomass of *C. arvensis* and *T. farfara* was harvested at the end of the experimental period, dried at 70°C for 72 h, and its dry weight determined (by mistake not done for *Cirsium* in $TfCa_{2013}$). The origins of shoots were checked in Ca_{2013} and $TfCa_{2014}$, but not in $TfCa_{2013}$.

At the termination of the Swedish experiments Ca_{2014_May} and Ca_{2014_Aug} (Table 2), the above-ground shoots of *C. arvensis* in each plot were cut at soil surface, counted, dried at 105°C until constant weight and weighed. The regrowth of *C. arvensis* was followed by regularly counting emerged shoots until August in Ca_{2014_May} and until the following June in Ca_{2014_Aug} . At the termination of Ca_{2014_May} the mean length of the five longest shoots in the experimental plots was determined.

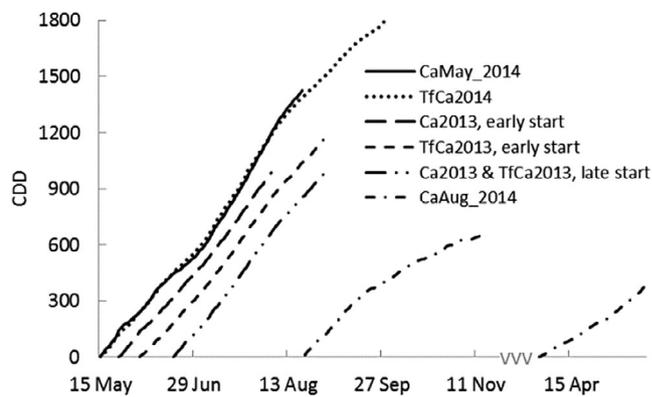


FIGURE 1 Cumulative growing degree-days (CDD) are the sums of daily degree-days in the five field experiments from start to end. Note that the x-axis is broken between December 2014 and April 2015.

In July 2014 (Ca_{2014_May}) and June 2015 (Ca_{2014_Aug}), the origins of the *C. arvensis* shoots in plots with and without reburied root fragments were determined by carefully uncovering the plant bases and roots from the sandy soil. Shoots were categorized as originating either from (i) beneath 20 cm (i.e., from vertical roots on the intact root system), (ii) 10 cm depth (i.e., from the returned root fragments), (iii) roots growing in from the sides (walls) of the plots (i.e., from horizontal roots outside the plots within the upper 20 cm soil profile) or (iv) seeds. The above-ground shoots were counted, cut at soil surface, dried and weighed. For each type of origin (fragment, intact, side or seed), the numbers of below-ground shoots were counted as well.

Shoot origins were checked in Ca_{2014_May} when the emerged shoots were in the early bud stage, in four excavated plots where fragments had been removed and in four plots with returned fragments. In Ca_{2014_Aug} , shoot origins were checked in all 16 excavated plots at the time of stem-elongation start.

2.4 | Weather conditions

The hourly mean air temperatures were measured at 2 m above ground level; 800 m from the Swedish experimental sites and 1500 m from the Norwegian sites.

Daily growing degree-days (DD) were calculated as:

$$DD = ((T_{\max} + T_{\min})/2) - T_{\text{base}}, \quad (1)$$

where T_{\max} is the daily maximum air temperature ($^\circ\text{C}$), T_{\min} is the daily minimum air temperature and T_{base} is 2°C . If the mean of the minimum and maximum air temperatures was below the base temperature, then DD was set at 0. Cumulative growing degree-days (CDD) are the sums of daily degree-days (Figure 1). Weekly precipitation was measured at the Norwegian experimental sites (Figure S1). The Swedish experiments were regularly watered so that drought was avoided.

TABLE 3 Results of the analysis of variance (p -values) for number of emerged shoots (no m^{-2}) in five semi-field experiments with *C. arvensis* (Ca) and *T. farfara* (Tf).

	TfCa ₂₀₁₃			Ca ₂₀₁₃		TfCa ₂₀₁₄			Ca _{2014_May}		Ca _{2014_Aug}				
	Jul 11–Aug 30			Jul 11–Aug 5		Sep 30			Jun 11–Aug 20		Sep 30– Nov 17			May 5–Jun 8	
	df	T. <i>farfara</i>	C. <i>arvensis</i>	df	C. <i>arvensis</i>	df	T. <i>farfara</i>	C. <i>arvensis</i>	df	C. <i>arvensis</i>	df	C. <i>arvensis</i>	df	C. <i>arvensis</i>	
Fragment	16.0	<0.001	0.983	20.8	0.886	12	0.001	0.673	15.7	0.012	15.5	0.036	14.1	0.833	
Time of disturbance (TD)	16.0	<0.001	0.005	20.8	0.007	–	–	–	–	–	–	–	–	–	
Fragment × TD	16.0	0.175	0.745	20.8	0.526	–	–	–	–	–	–	–	–	–	
Soil depth (SD)	16.0	0.746	0.627	–	–	12	0.500	0.203	–	–	–	–	–	–	
Fragment × SD	16.0	0.364	0.850	–	–	12	0.459	0.271	–	–	–	–	–	–	
TD × SD	16.0	0.600	0.138	–	–	–	–	–	–	–	–	–	–	–	
Fragment × TD × SD	16.0	0.445	0.521	–	–	–	–	–	–	–	–	–	–	–	
Sampling date (D)	47.1	<0.001	0.002	34.4	<0.001	–	–	–	91.6	<0.001	41.5	<0.001	69.5	<0.001	
Fragment × D	47.1	0.031	0.724	34.4	0.872	–	–	–	91.6	0.164	41.5	0.288	69.5	0.960	
TD × D	47.1	<0.001	0.019	34.4	0.0013	–	–	–	–	–	–	–	–	–	
Fragment × TD × D	47.1	0.018	0.866	34.4	0.808	–	–	–	–	–	–	–	–	–	
SD × D	47.1	0.448	0.598	–	–	–	–	–	–	–	–	–	–	–	
Fragment × SD × D	47.1	0.593	0.166	–	–	–	–	–	–	–	–	–	–	–	
TD × SD × D	47.1	0.669	0.445	–	–	–	–	–	–	–	–	–	–	–	
Fragment × TD × SD × D	47.1	0.551	0.253	–	–	–	–	–	–	–	–	–	–	–	

Note: Before the statistical analysis, data for *T. farfara* in TfCa₂₀₁₃ were transformed as $\log_{10}(x + 1)$, in TfCa₂₀₁₄ as $\log_{10}(x)$ and data for *C. arvensis* were square-root transformed. Bold type indicates $p < 0.05$.

2.5 | Statistical analyses

Data were analysed by the Mixed procedure in SAS software (SAS Institute, Cary, North Carolina, USA). Sampling dates were analysed as repeated measurements with plots as subject, blocks and replicates were considered as random effects, while other factors were considered fixed. Means separation was done using PDIF when treatment effects were significant ($p < 0.05$).

To fulfil the requirement of homoscedasticity, numbers of *T. farfara* shoots in TfCa₂₀₁₃ were transformed as $\log_{10}(x + 1)$, in TfCa₂₀₁₄ as $\log_{10}(x)$ and data for numbers of *C. arvensis* shoots were square-root transformed. Biomasses were transformed as $\log_{10}(x)$. Data were back transformed before presentation.

3 | RESULTS

3.1 | Shoot emergence and biomass

There was no difference in the final number of emerged *C. arvensis* shoots between plots with removed and returned fragments in the Norwegian experiments Ca₂₀₁₃, TfCa₂₀₁₃, and TfCa₂₀₁₄ (Table 3, Figures 2 and 3). In addition, measurements of total or individual biomass in Ca₂₀₁₃ (data not shown) and total (Figure 3) or individual (data not

shown) biomass in TfCa₂₀₁₄ did not reveal any differences among fragment treatments.

Treatments had a larger impact in the Swedish experiments, especially in the early started Ca_{2014_May}. In this experiment, the number of shoots was reduced by 44% at the first registration date where fragments had been removed ($p < 0.001$, Figure 4). However, the difference seemed to decrease over time, and was small at the termination of the experiment in August (Figure 4). The biomass of the above-ground shoots was not significantly affected by fragment treatments, neither in July (mean 75 g DM m^{-2}), nor in August (mean 370 g DM m^{-2} , 73 cm shoot length) (Figure S2). In Ca_{2014_Aug}, fewer shoots emerged during autumn in plots where root fragments had been removed than in those where they had been returned ($p = 0.036$) (Figure 5A). The shoots remained in the rosette stage until late November, when all shoots died. In the following spring, no influence of fragment removal was found on shoot emergence. At the time of the last sampling, that is, early June, a mean of 44.9 shoots m^{-2} (Figure 5B) with a total biomass of 28 g DM m^{-2} had emerged (Figure S2).

The effect of the time of soil disturbance (removal and return of fragments) was tested in two experiments. Late soil disturbance, as compared to early disturbance, reduced the number of *C. arvensis* shoots in TfCa₂₀₁₃ during July and early August by 95% ($p = 0.001$) (Figure 2). The corresponding reduction in Ca₂₀₁₃ in early July was 76% ($p = 0.028$), but 1 month later the effect was no longer

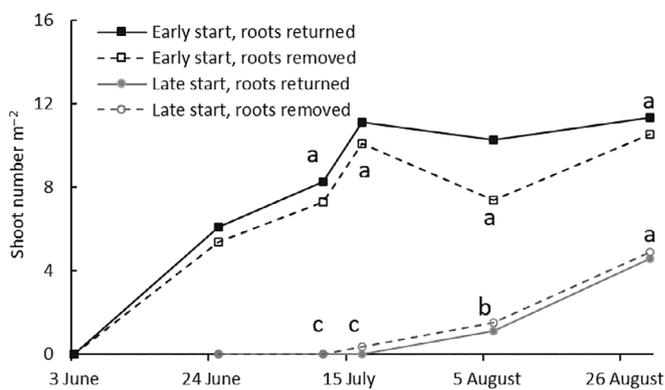
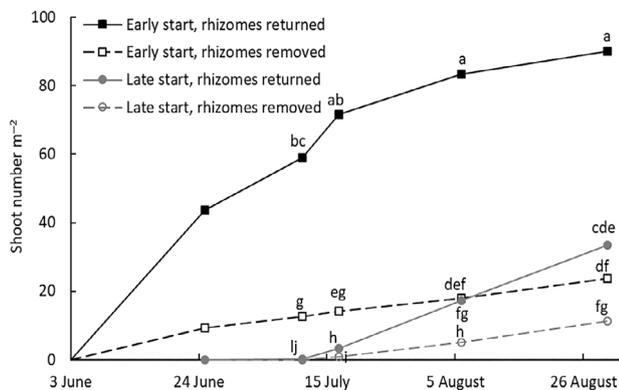


FIGURE 2 Shoot regrowth in *T. farfara* (left) and *C. arvense* (right) following soil disturbance on two occasions in TfCa₂₀₁₃. Means over two treatments comprising soil disturbance to a depth of 13 or 25 cm. Within species significant differences ($p < 0.05$) between treatments are indicated by different letters. Fragment treatment (removed or returned) is not significant ($p > 0.05$) for *C. arvense* (see Table 3).

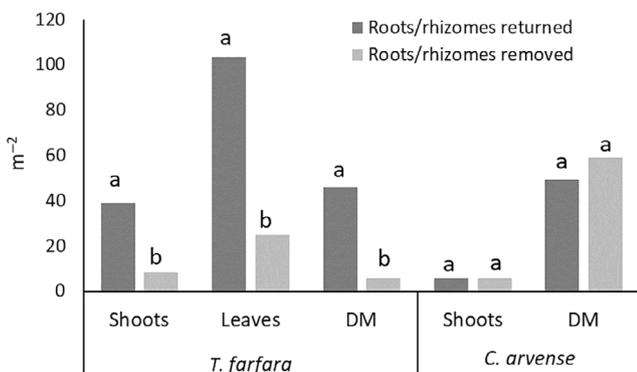


FIGURE 3 Numbers of aboveground shoots or leaves (no. m^{-2}) and biomass (g DM m^{-2}) of aboveground shoots in plots where roots/rhizomes had either been removed or returned to the top soil layer in TfCa₂₀₁₄. Means over two treatments comprising soil disturbance to a depth of (1) 13 cm or (2) 25 cm. Within response variable and species, significant differences ($p < 0.05$) between treatments are indicated by different letters.

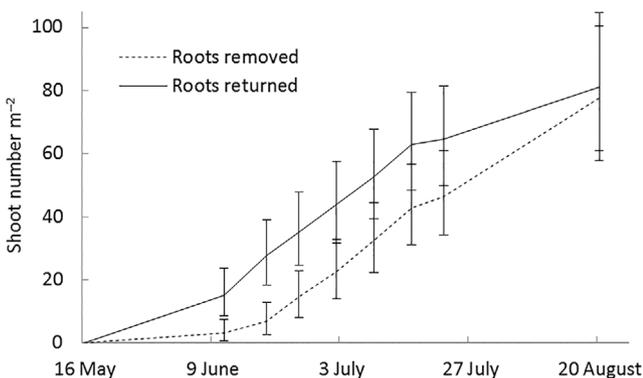


FIGURE 4 Shoot regrowth in *C. arvense* following soil disturbance to a depth of 20 cm in Ca_{2014_May}. Error bars represent 95% confidence intervals.

significant (Figure 6). As a mean over fragment treatment in Ca₂₀₁₃, both total and individual shoot biomass were five times higher after late than after early disturbance ($p < 0.014$) (late disturbance: 86.5 g DM m^{-2} ; 5.7 g DM ind^{-1}) (data not shown).

For *T. farfara*, removal of rhizome fragments had a large effect on number of emerged shoots. In TfCa₂₀₁₃, removal of fragments reduced the number of shoots during July and August by 68% and 78% after late and early soil disturbance respectively ($p = 0.018$) (Figure 2). Importance of rhizome fragments for regrowth became even more pronounced at the termination of the experiment; the number of shoots was higher (97.6 shoots m^{-2}), and the individual shoot biomass lower (0.1 g ind^{-1}) in early disturbed plots with rhizomes returned, than in all other treatments (mean 24.3 shoots m^{-2} and 0.7 g ind^{-1}) ($p < 0.05$). The total biomass of shoots (mean 12.6 g DM m^{-2}) was, however, not significantly influenced by treatments (data not shown).

At the termination of TfCa₂₀₁₄, removal of fragments had reduced the number of *T. farfara* shoots by 79% ($p = 0.005$), the number of leaves by 76% ($p = 0.007$) and shoot biomass by 88% ($p = 0.002$) (Figure 3). None of these response variables were influenced by the depth of soil disturbance ($p > 0.05$). When fragments were removed in TfCa₂₀₁₄, the individual shoot weight was reduced at 25 cm soil disturbance (0.6 compared to 1.8 g shoot⁻¹ when fragments were returned; $p < 0.05$), while no effect was found at 13 cm.

3.2 | Origin of shoots

The origin of *C. arvense* shoots was checked in all experiments, except in TfCa₂₀₁₃. As a mean over treatments (i.e., soil depth and/or time of disturbance) in each experiment, 16%–52% of the emerged shoots regenerated from the returned fragments and 48%–84% from the intact root system below the depth of soil disturbance (calculated from Table 4, excluding shoots emerging from roots outside the sample plots [i.e., from the side]). The origin of *T. farfara* shoots was

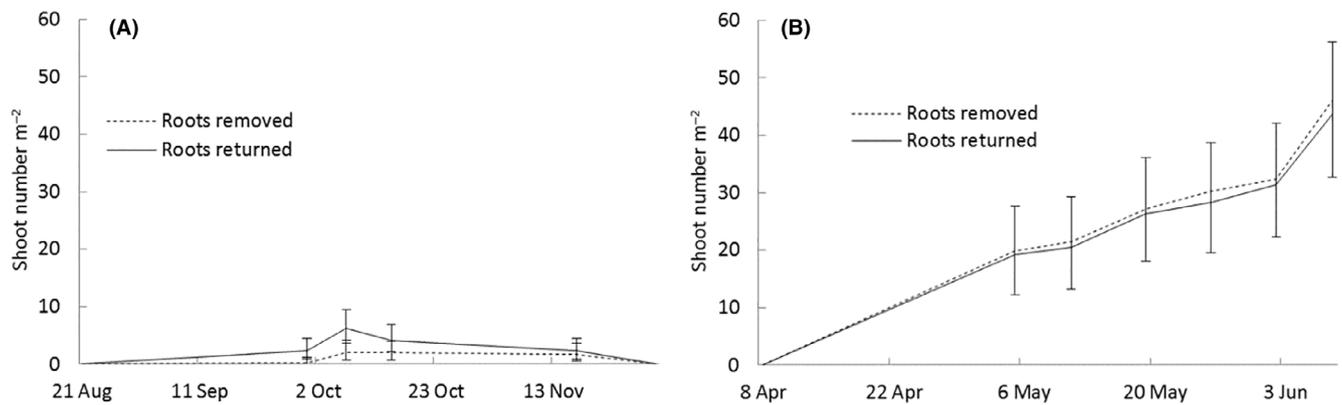


FIGURE 5 Shoot regrowth in *C. arvensis* during (A) autumn 2014 and (B) spring 2015 following soil disturbance to a depth of 20 cm in Ca_{2014_Aug}. Error bars represent 95% confidence intervals.

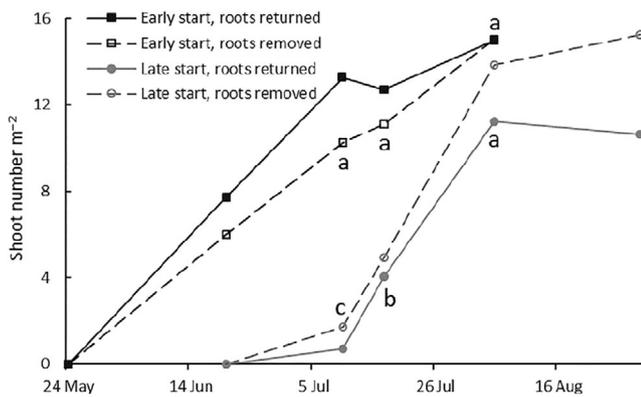


FIGURE 6 Shoot regrowth in *C. arvensis* following soil disturbance on two occasions in Ca₂₀₁₃. Significant differences ($p < 0.05$) between treatments are indicated by different letters. Fragment treatment (removed or returned) is not significant ($p > 0.05$) (see Table 3).

checked in one experiment. In this, as a mean over two depths, 97% regenerated from the fragments and 3% from the intact rhizome system (Table 4). For *C. arvensis*, shoot regrowth from the intact below-ground system was similar or higher than from fragments while for *T. farfara* significantly more shoots originated from the fragments (Figure 7).

In both Ca₂₀₁₃ and TfCa₂₀₁₄, the origins of shoots were checked in two of the plots in each block where fragments had been returned. Since plastic sheets prevented lateral growth through the plot wall, no check was made in plots where fragments had been removed. In these plots, it was assumed that all shoots originated from the below-ground system beneath the depth of soil disturbance or from seeds. No influence of depth of soil disturbance on the number of shoots from the intact root system was found for any of the two species ($p > 0.05$).

In Ca_{2014_May} and Ca_{2014_Aug}, the shoot origins were checked both in plots where fragments had been returned and where they had been removed. Shoots originating from outside the plot (i.e., from the side) constituted 26.5% of all emerged shoots in Ca_{2014_May} and 5.6% in Ca_{2014_Aug} (Table 4).

4 | DISCUSSION

Results presented here are based on five experiments, all designed to test the effect of removing fragments of roots/rhizomes from a disturbed soil layer. By making use of experiments with somewhat differing experimental design, hence separately analysed, we were able to draw more general conclusions regarding the relative importance of intact root/rhizome system versus fragments for emergence and biomass production.

Our first hypothesis, that is, that shoot regrowth after soil disturbance is higher from the intact below-ground system than from fragments, was partly confirmed for *C. arvensis*. When excluding shoots emerging from roots outside the sample plots, between 48% and 84% of the emerged *C. arvensis* shoots originated from the intact root system below the depth of soil disturbance, while 16%–52% of the shoots originated from the returned fragments. High regeneration capacity from the intact root system of *C. arvensis* has earlier been observed by Thomsen et al. (2013) and Thomsen and Brandsæter (2014), who noticed that the final aboveground biomass was not influenced by the removal of root fragments from the topsoil. This was also the outcome in all our experiments with *C. arvensis*. Although shoot emergence in some cases was influenced by the handling of fragments (removed vs. returned), no effect was found on the final biomass of *C. arvensis* in any of the experiments, or on shoot length in Ca_{2014_May}. Thus, aboveground biomass from the intact root system seemed to fully compensate for loss of emergence from removed fragments. It should, however, be noted that the experiments were conducted without competition from other species. The delay in emergence from intact root systems as compared to emergence from fragments in the upper soil layer, shown as difference in number of shoots m⁻² at earlier dates (Figure 4) would have been a disadvantage in a situation with interspecific competition.

In clear contrast to *C. arvensis*, the regenerating capacity of *T. farfara*, measured as number of emerged shoots, was 70%–80% lower when rhizome fragments were removed than when they were returned, and also the number of leaves and shoot biomass were reduced.

TABLE 4 Origin of emerged or below-ground shoots in excavated and refilled plots in which the roots/rhizomes in the topsoil had been removed or returned.

Experiment and species	Shoot status	Time of start	Excavated soil depth (cm)	Roots or rhizomes	Number of plots	Shoots (no. m ⁻²)	Origin of shoots (%)		
							Fragment	Intact root or rhizome	From the side
<i>C. arvense</i>									
Ca _{2014_Aug}	Emerged	Late	20	–	8	48.1 ^a (5.37)	0 (0)	90.1 (1.58)	6.8 (1.23)
				+	8	45.5 ^b (6.08)	15.3 (2.93)	78.9 (4.23)	4.4 (2.03)
Ca _{2014_May}	Below	Late	20	–	8	9.3 (1.93)	0 (0)	94.6 (2.7)	5.4 (2.7)
				+	8	12.3 (2.8)	16 (6.47)	82.8 (6.15)	1.2 (1.19)
				–	4	54.8 (14.81)	1.4 (1.4)	70.3 (12.04)	28.3 (11.51)
Ca ₂₀₁₃	Emerged	Early	20	–	4	63.3 (1.65)	39.1 (6.06)	36.1 (5.63)	24.8 (4.54)
				+	4	9.8 (4.96)	32.3 (13.65)	58.7 (16.5)	9 (5.93)
				–	4	10 (3.49)	0 (0)	87.5 (12.5)	12.5 (12.5)
Ca ₂₀₁₃	Emerged	Early	25	+	3	13.7 ^c (5.7)	41.1 (2.59)	51.5 (4.31)	P
		Late	25	+	3	8.3 (1.86)	54 (12.7)	46 (12.7)	P
TfCa ₂₀₁₄	Emerged	Early	13	+	3	11 (4.16)	34.6 (12.29)	65.4 (12.29)	P
			25	+	3	2.3 (0.88)	66.7 (16.67)	33.3 (16.67)	P
<i>T. farfara</i>									
TfCa ₂₀₁₄	Emerged	Early	13	+	3	46.3 (17.84)	94.1 (3.14)	5.9 (3.14)	P
			25	+	3	55.3 (19.74)	100 (0)	0 (0)	P

Note: Mean values with SEM within brackets. –, roots/rhizomes removed; +, roots/rhizomes returned; P, prevented by plastic sheets; Below, below-ground.

^a3.1% originated from seeds.

^b1.4% originated from seeds.

^cNot possible to determine the origin of 1 shoot m⁻² (7.4%).

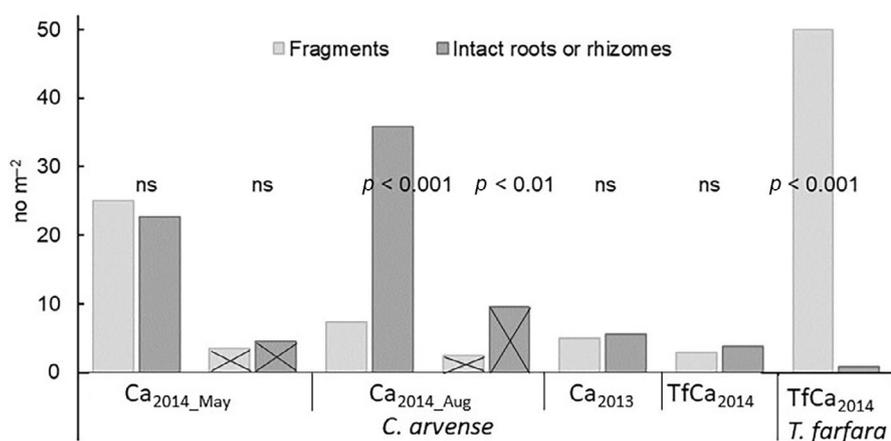


FIGURE 7 Origin of above- or below-ground shoots (no. m⁻²) of *C. arvense* and *T. farfara* in excavated plots where roots/rhizomes had been returned to the top soil layer. Means over treatments in five experiments. Crossed bars indicate below-ground shoots. *p*-values indicate significant differences between number of shoots originating from fragments or from intact roots/rhizomes; ns denotes no statistically significant difference (*p* > 0.05). Data for *T. farfara* in TfCa₂₀₁₄ were transformed as log₁₀(*x* + 1) before the statistical analysis.

Our results indicate that regrowth from fragmented roots is less important than commonly expected in *C. arvense*, considering the focus in numerous studies on shoot growth capacity of fragmented roots in relation to the effects of soil cultivation and environmental factors (e.g., Dock Gustavsson, 1997; Hamdoun, 1972; Thomsen

et al., 2011). It does, however, highly coincide with the results of Thomsen et al. (2013). Also, dispersal of root fragments via soil cultivation seems to be of limited importance for the growth of *C. arvense* field patches, as observed by Hettwer and Gerowitt (2004) in their study of the genetic variation in the species. Dispersal and regrowth

of fragments is perhaps an overrated explanation for the ability of the species to survive soil cultivation, and the importance of regrowth from the intact below-ground root system should not be underestimated. Our results, however, also clearly show the difference in shoot-regeneration strategies of creeping perennials with deep root/rhizome systems. *Tussilago farfara*, compared to *C. arvensis*, seems to have an opposite strategy; after soil tillage more shoots come from fragments than from the intact root/rhizome system.

There are several alternative explanations to the difference observed in these experiments, such as a relatively smaller proportion of total rhizomes below disturbance depth in *T. farfara* as compared to root distribution in *C. arvensis*. Since both species experienced the same agricultural influence during development this would be a species specific difference, which highlights the need for profound studies of the development and growth of the below-ground vegetative system of creeping perennial weeds. Also, other possible explanations would be experimental handling problems, consisting of drought stress, or too short fragments, which affected *C. arvensis* more than *T. farfara*. Based on earlier studies (e.g., Hamdoun, 1972; Liew et al., 2013), and careful handling, as described in Material and methods, we consider this unlikely.

The regrowth capacity of both species was highly dependent on the time of soil disturbance as suggested in hypothesis 2. Regrowth of shoots after early soil disturbance was often faster than after late disturbance, but differences in numbers of emerged shoots decreased with time. In Ca₂₀₁₃, both early and late soil disturbance were terminated 73 days after the start of the experiments, that is, with a time difference of 26 days. By then, the cumulative day-degrees (CDD) were almost the same in both treatments (985 and 978 CDD in early and late soil disturbance respectively), and no influence on number of emerged shoots was found anymore. The positive correlation between temperature and shoot emergence from adventitious root buds in spring was described in a degree-day model developed for *C. arvensis* by Donald (2000). Although the cumulative day-degrees were close to 980 CDD in both treatments at the termination of Ca₂₀₁₃, the shoots of *C. arvensis* had grown five times heavier after late than after early disturbance. The initially lower temperatures after early than after late disturbance possibly favoured assimilate translocation to roots. A greater root/shoot ratio when grown at 16°C than at 21°C has been reported in this species by Hunter and Smith (1972). This highlights the capacity of rapid shoot growth even when soil tillage is done rather late in the season.

In TfCa₂₀₁₃, both treatments were terminated the same day. The consequence of this was a difference of 182 CDD (i.e., CDD was higher in early than in late disturbance), which may have been the cause of the higher number of emerged shoots after early than after late disturbance in both species.

In the Swedish experiments, early shoot emergence was lower in Ca_{2014_Aug} than in Ca_{2014_May}. This may have been caused by somewhat lower temperatures in August than in May (a difference of 40 CDD during the first 30 days, Figure 1). The difference may also have been caused by an impaired sprouting capacity during September and October, which was found in the undisturbed root

systems of the species (Andersson et al., 2013) and in fragmented roots of two out of four populations (Liew et al., 2013). In Ca_{2014_Aug}, the emerged shoots during autumn remained in the rosette growth stage as a response to decreasing day-length. Hunter and Smith (1972) noted that *C. arvensis* plants remained in the rosette stage at 8 and 12-h photoperiods but tended to bolt at a 16-h photoperiod. In our study, the aboveground shoots died during late autumn, resulting in a large proportion of final shoots originating from the intact root system in Ca_{2014_Aug} (84% of shoots from within the plot as compared to 48% in Ca_{2014_May}).

The shown importance of deep roots for overwintering might explain the stronger control effect of spring cultivation compared to autumn cultivation in *C. arvensis*, as shown by Brandsæter et al. (2017). Autumn cultivation would kill emerged shoots, while enabling new shoots being produced from the intact root system, ready to emerge in spring from the upper soil layer. Spring cultivation, on the other hand, would force new shoots to emerge from below plough depth, thus meeting tougher interspecific competition. This is also in accordance with findings that deep ploughing in spring has a better control effect than shallow ploughing (Brandsæter et al., 2011). Also, a new study of Weigel et al. (2024) showed that cutting roots at ploughing depth in spring, without inverting the soil, was almost equally efficient in controlling *C. arvensis* as ploughing.

For *T. farfara*, emerged shoots originated mainly from the returned fragments. The number of shoots in TfCa₂₀₁₃ was considerably higher and the individual shoot biomass lower in early disturbed plots with rhizomes returned than in other treatments. According to Namura-Ochalska (1993), *T. farfara* benefits from systematic cultivation that eliminates potential competitors, and Thomsen et al. (2015) noted a tendency towards higher biomass of the species in treatments with low competition in spring. In our study, low individual shoot biomass at high shoot densities was most likely a response to high intra-specific competition.

The results for *T. farfara* partly supported the third hypothesis, that is, that shoot regrowth capacity depends on the depth of soil disturbance. At one site the individual shoot weight of *T. farfara* was reduced by 67% after 25 cm disturbance depth when compared to 13 cm. This result was found only in plots where the fragmented rhizomes had been removed, that is, where emerged shoots originated solely from the intact below-ground system. Regarding buried rhizome fragments, Dalbato et al. (2014) found a negative correlation between burial depth and time to emergence in *T. farfara*, while a decrease in dry-matter production by emerged shoots with increasing depth of fragment burial was noted in, for example, *Achillea millefolium* L. (Bourdôt, 1984) and *Elymus repens* (L.) Gould (Håkansson, 2003). Likewise, shoots generated from the intact below-ground system also require a longer time to emerge and at a higher energy cost when originating from greater soil depth. Together, this may result in lower dry mass per individual shoot.

Results from our experiments with *C. arvensis* show the ecological importance of emergence from the intact root system in frequently ploughed fields. For weed control, results indicate a need for deep soil cultivation to also reach deeper parts of the root system, thereby

delaying emergence. This might be especially effective if cultivation is conducted in early spring, shortly before sowing of the crop. For *T. farfara*, a species which mainly regenerates from the rhizome fragments, this study implies that management strategies should include repeated soil cultivation to stimulate bud growth, thereby exhausting carbohydrate reserves and when possible also increasing damage by desiccation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

U. Boström  <https://orcid.org/0000-0002-8632-457X>

L. O. Brandsæter  <https://orcid.org/0000-0002-0878-9128>

L. Andersson  <https://orcid.org/0000-0002-1676-5361>

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