

Seasonal restrictions of bud growth on roots of *Cirsium arvense* and *Sonchus arvensis* and rhizomes of *Elymus repens*

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Summary

The success of weed management aimed at depleting the regenerative structures of perennial weeds depends largely on the sprouting activity of rhizome and root buds. Seasonal variation in sprouting of these buds on *Cirsium arvense*, *Sonchus arvensis* and *Elymus repens* was studied for plants collected from Denmark, Finland, Norway and Sweden. At 2-week intervals from July to October, 5-cm fragments of roots or rhizomes were cut from plants grown in buckets and planted into soil in pots, half of which were placed immediately into growth chambers at 18°C for 4 weeks. The other half of the pots were initially placed in a dark room at 2°C for 4 weeks before being transferred to the same growth chamber, also for 4 weeks. During the

growth chamber period, the numbers of emerged shoots in each pot were counted weekly. The sprouting activity of *C. arvense* and *E. repens* was relatively uniform during this period and bud dormancy was not apparent. In all ecotypes of *S. arvensis*, innate bud dormancy developed during the latter part of the growing season. For all three species, differences in sprouting readiness were found among ecotypes. The results imply that *C. arvense* and *E. repens* are more likely to be controlled by mechanical measures in autumn than *S. arvensis*.

Keywords: perennial weeds, couch grass, creeping thistle, perennial sowthistle, dormancy, vegetative buds, rhizomes, roots, regenerative structures.

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Introduction

Creeping perennial weeds, such as *Elymus repens* (L.) Gould, *Cirsium arvense* (L.) Scop. and *Sonchus arvensis* L., are of major concern in many cropping systems, especially in organic systems that have a high proportion of cereals in the rotation (Bacher *et al.*, 1997; Cormack, 1999; Salonen *et al.*, 2001). Effective management of

E. repens, *C. arvense* and *S. arvensis* by non-chemical means requires an extensive understanding of their shoot growth behaviour, especially after fragmentation. The sprouting readiness of vegetative buds on roots (*C. arvense* and *S. arvensis*) and rhizomes (*E. repens*) differs among the three species and changes during the growing season. Physical weed management of these species aimed at weakening the regenerative ability

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needs to be timed according to bud activity and subsequent shoot growth. However, the phenology of bud dormancy may vary among species and among clones and ecotypes within a species. To deplete the root and rhizome reserves and thereby achieve better control effects, physical weed management tactics need to be applied when the buds are ready to sprout after physical disturbance and fragmentation. Effects of herbicides are also reduced or impeded during periods of restricted growth of buds, which also largely applies to situations when other plant parts grow slowly.

New shoots and plants develop from buds formed by differentiation of meristematic cells in the regenerative structures. Restrictions in bud activity were categorised by Håkansson (2003) into four classes: (i) Enforced (imposed) dormancy, caused by unsatisfactory environmental conditions, such as low temperature or water deficiency, (ii) shortage of food reserves, caused by extensive energy consumption in the early period of new shoot growth in spring or during regrowth after physical disturbance, (iii) apical dominance caused by hormones produced near actively growing apices and (iv) all-embracing innate dormancy, which is similar to apical dormancy and is caused by certain concentrations and proportions of hormones. In contrast with apical dominance, however, innate dormancy does not immediately cease or become reduced by fragmentation of the regenerative structures. In experiments with *S. arvensis*, such all-embracing innate dormancy of the buds has been observed at the end of the growing season (e.g. Håkansson, 1969b; Fykse, 1974, 1977). The readiness of fragmented *C. arvensis* roots to produce new shoots in

late summer or autumn is not well documented, and innate dormancy does not appear to be responsible for any growth restrictions (Henson, 1969; Fykse, 1974, 1977). Buds on fragmented *E. repens* rhizomes normally demonstrate high germinability throughout the year during frost-free periods and any restrictions in bud growth cannot be ascribed to an all-embracing innate dormancy (Håkansson, 1967, 2003).

Despite what is known generally about shoot growth from root and rhizome buds on *E. repens*, *C. arvensis* and *S. arvensis*, few reports related to timing and nature of shoot emergence are available. The objective of this study was therefore to achieve a better understanding of seasonal variations in the bud activity of roots and rhizomes after fragmentation, as a base for improving non-chemical weed control methods against the three perennials. In addition, the study was designed to indicate variation in the readiness to produce new shoots after fragmentation among species originating from different Nordic countries and/or among different ecotypes within each country.

Materials and methods

First phase: propagation of test material in 2001

Fragments of roots of *C. arvensis* and *S. arvensis* and rhizomes of *E. repens* were collected in the spring 2001, late April or early May, in arable fields, mostly sown to cereals (Table 1). To get some information about the variability in terms of sprouting ability within the species, the propagation material was randomly

Table 1 Origin of the plant material studied in the experiment

Country	Species	Ecotype	Location	Latitude	Soil type	Farming system
Denmark	<i>C. arvensis</i>	1	Slagelse	55°29'N 11°21'E	Sandy loam	Organic
		2	Jyndevad	54°53'N 09°08'E	Sandy	Organic
	<i>S. arvensis</i>	1	Årre	55°34'N 08°40'E	Sandy	Organic
		2	Brenderup	55°29'N 09°58'E	Loamy sand	Conventional
Finland	<i>C. arvensis</i>	1	Jokioinen	60°51'N 23°26'E	Organic soil	Wasteland close to field
		2	Juva	61°48'N 27°50'E	Fine sandy till	Wasteland growing wild hay
	<i>S. arvensis</i>	1	Jokioinen	60°51'N 23°26'E	Sandy clay	Conventional, Cereal farm
		2	Juva	61°48'N 27°50'E	Fine sandy till	Organic, cabbage in previous year
	<i>E. repens</i>	1	Jokioinen	60°51'N 23°26'E	Clay	Cereal farm
		2	Juva	61°48'N 27°50'E	Sandy till	Organic field, legume-grass, rhizomes from headland
Sweden	<i>C. arvensis</i>	1	Offer	63°80'N 17°45'E	Loam	Organic
		2	Värmdö	59°23'N 18°41'E	Sandy loam	Organic
	<i>S. arvensis</i>	1	Offer	63°80'N 17°45'E	Loam	Organic
		2	Ekenäs	58°56'N 16°34'E	Clay loam	Organic
	<i>E. repens</i>	1	Ultuna	59°48'N 17°39'E	Heavy clay	Conventional-
2		Ultuna	59°48'N 17°39'E	Heavy clay	Conventional	
Norway	<i>C. arvensis</i>	1	Kvithamar	63°30'N, 10°52'E	Sandy loam	Organic, cereal
		2	Øsaker	59°15'N 10°58'E	Loam	Organic, clover-grass
	<i>S. arvensis</i>	1	Kvithamar	63°30'N, 10°52'E	Sandy loam	Organic, cereal
		2	Øsaker	59°15'N 10°58'E	Loam	Organic, clover-grass

collected in two different locations in each country and marked ecotype 1 and 2 (Table 1). *Elymus repens* was only collected in Finland and Sweden. After collection, the fragments were stored for 30 days in a cooling chamber at 2–5°C until the start of the propagation period. Then about 25 groups of eight 10 cm long root or rhizome fragments per ecotype were planted at 2 cm depth in buckets (8–12 L in size). The buckets were filled with limed peat enriched with nutrients [e.g. Norway: L.O.G. 'Gartnerjord', Mixture 840 g kg⁻¹ sphagnum peat, 100 g kg⁻¹ fine sand, 60 g kg⁻¹ clay, 5.5 kg dolomite lime m⁻³, 1.2 kg fertiliser (NPK 15–4–12), 0.2 kg F.T.E. no.36 (micronutrients), pH 5.5–6.5, and density: 270 kg m⁻³ (applied volume)] and then embedded into the soil in a nearby field to normalise the temperature conditions surrounding them. In mid-July, the pots were given additional NPK fertiliser corresponding to 70 kg N ha⁻¹, except for sample pots in Denmark. Just before winter storage in mid-October, aboveground shoots were cut at the soil surface, and the buckets containing belowground plant material were taken into a cooling chamber with a constant temperature of 1–2°C and stored in darkness until mid-April 2002.

Second phase: propagation of test material in 2002

After the winter storage, pieces of roots and rhizomes were harvested from the plant material produced the previous year and the same number and size planted into

the same type of buckets and soil as described for 2001. To secure enough material for the planned dormancy, tests 24 buckets were used, eight more than strictly needed. The buckets were placed randomly outdoors in a nearby field and embedded into the soil. In order to minimise loss of moisture and ensure as equal conditions for shoot emergence as possible, the buckets were covered for 2–3 weeks with a white polypropylene fibre textile, except in Denmark. The cover was removed when shoots had emerged evenly. During summer and autumn, the buckets were irrigated in accordance with common agricultural practise when needed and fertilised on 25th–30th June, with a 15–4–12 NPK fertiliser at a rate providing 70 kg N ha⁻¹. Weather data for the 2002 growing season is shown in Table 2 for weather stations that were as close to the propagation field in each country as possible.

Third phase: the dormancy tests

Starting on 2 July 2002 (Sweden 30 July) and at 2 week intervals until 22 October, two buckets of each ecotype were selected at random for testing bud dormancy in roots and rhizomes. The roots and rhizomes were cut into 5-cm fragments and in groups of 10 pieces planted into 3 L pots to a depth of 2 cm in a similar soil as the one used in phases 1 and 2. Only roots and rhizomes that had developed during 2002 were used. These were distinguished from the older roots and rhizomes by their lighter colour and different structure. In addition, we

Table 2 Meteorological data (monthly means) at the experimental stations for the period of bud activity tests in 2002

Factor	April	May	June	July	August	September	October
Denmark, Flakkebjerg (55°20'N, 11°23'E)							
DM, °C	7.4	13.2	15.9	17.7	20.1	14.8	7.5
Max, °C	17.1	23.3	28.4	31.3	28.1	25.0	18.2
Min, °C	-3.0	4.6	8.8	10.7	12.8	2.2	-1.7
R, MJ m ⁻²	369	538	646	520	505	388	187
Finland, Jokioinen (60°51'N/23°26'E)							
DM, °C	5.2	11.3	15.4	18.2	17.9	10.1	-0.4
Max, °C	11.3	17.4	20.6	23.0	24.8	16.0	3.0
Min, °C	-0.9	4.0	9.9	13.4	10.7	4.9	-3.2
R, MJ m ⁻²	454	629	576	568	545	328	138
Sweden, Uppsala (59°48'N/17°39'E)							
DM, °C	6.3	11.8	16.5	18.5	19.3	11.7	2.7
Max, °C	12.5	18.1	22.5	23.5	26.4	18.1	6.2
Min, °C	-0.6	4.3	9.8	13.0	11.3	4.9	-1.1
R, MJ m ⁻²	422	639	627	591	559	356	127
Norway, Ås (59°40'N/10°46'E)							
DM, °C	6.1	11.9	15.2	16.4	18.6	12.2	3.2
Max, °C	21.3	22.4	25.9	26.7	27.4	25.8	13.1
Min, °C	-4.3	0.4	3.7	6.9	8.4	-2.7	-6.6
R, MJ m ⁻²	340	542	662	536	522	348	114

DM, daily mean air temperature; Max, max. daily air temperature; Min, min. daily air temperature; R, daily global radiation. R: Calculation from Wm⁻² to MJ m⁻²: Wm⁻²*0.0036 = MJ m⁻² as a sum for all hours in each month.

only used fragments that were at least 2–3 mm in diameter, preferably 3–4 mm.

From each bucket, six small pots per test date were established, yielding 12 pots per ecotype altogether. Of these 12 pots, six pots, three from each of the two buckets, were placed in a growth chamber with constant temperature of 18°C for 4 weeks, and with 18 h day and 6 h night. The pots were covered with fibre textile to ensure optimal moisture content in the soil, until new shoots started to emerge. The photon flux in the growth chambers varied between the countries, from 175 $\mu\text{mol s}^{-1}\text{m}^{-2}$ in Norway and Sweden, to somewhat lower values, between 140 and 150 $\mu\text{mol s}^{-1}\text{m}^{-2}$, in Denmark and Finland. To equalise variations in light levels at different spatial positions in the growth chambers, the location of the pots was rotated twice a week. The other six pots were initially placed in a dark chamber with a constant temperature of 2°C for 4 weeks to break any bud dormancy. After that period, the pots were transferred to a growth chamber with the same conditions as those not receiving any darkness and pre-chilling.

Statistical analyses

Shoots that emerged in the 18°C growth chamber were counted in each pot 7, 14, 21 and 28 days after placing the pots into the chamber. The results were analysed by means of Proc Catmod of SAS 9.1 (SAS Institute, 2002–2003). To reveal any significant effects of the three main factors: ecotypes, the starting date of the dormancy tests and the temperature treatment, as well as interactions during the test period, only the recordings made on the 28th day after start of the tests were used. However, in tests of the rates with which the shoots emerged in the pots during the 4 weeks after start of each dormancy test, the shoot numbers at all four recording times were used (repeated measure analysis). In all tests, the effects were considered significant when $P \leq 0.05$. To obtain sufficiently large samples for the analyses, the observations from the six pots related to a specific date, ecotype and treatment were pooled. In the figures presenting the shoot numbers at each test date, however, the results are expressed as number of shoots per pot. Due to strong interactions between country and other factors (ecotype and date), the results were analysed and are presented by country separately.

Results

Shoot emergence

Significant variation in sprouting of buds during the growing season among *C. arvense*, *S. arvensis* and *E. repens*, as well as differences between countries, was found (Figs 1 and 2).

Cirsium arvense

Significant differences in the sprouting ability were observed between the two ecotypes collected in Finland and between those collected in Sweden ($P = 0.02$ and $P = 0.001$ respectively), but not among the Danish and Norwegian ecotypes ($P = 0.17$ and $P = 0.50$ respectively). In all countries, the starting date of the dormancy test significantly influenced the number of shoots produced ($P < 0.001$) and a significant interaction was detected between the starting date and the ecotypes ($P < 0.001$). As revealed in Fig. 1, however, this interaction does not work in the same direction in all countries. In Denmark, there was a marked drop in the sprouting ability in ecotype 1 at the end of the test period, which did not occur for the ecotypes from the other countries. For ecotype 1 from Sweden, there was a conspicuous increase in the middle of the period. The Finnish ecotypes exhibited a markedly different pattern of behaviour. Both ecotypes went into a period with reduced sprouting activity, but ecotype 1 entered this stage 1½ months before the other and recovered correspondingly earlier.

The four-week cold treatment of the roots prior to planting into pots did not influence significantly the sprouting ability of the ecotypes from any country, except Sweden, where the cold treatment in general reduced the number of emerged shoots ($P < 0.001$).

Sonchus arvensis

The two ecotypes from each country, except those from Finland, differed significantly from each other in terms of number of shoots produced ($P < 0.001$) and, as with *C. arvense*, the starting date of the dormancy test had a significant influence on the number of shoots emerging from the root fragments in all countries ($P < 0.001$). The dormancy test also revealed a significant interaction between the starting date and the ecotypes ($P < 0.001$). In all countries, a marked decrease in the sprouting ability was detected, but the onset of this behaviour differed amount countries (Fig. 1). The ecotypes from Norway entered the dormant period earlier than the ecotypes from Denmark and, to some extent, earlier than those from Sweden. The Finnish ecotypes showed a fairly steady and significant decrease with time from the first test, 2 July, until September–October. Thereafter, the emergence increased. At the end of the test period, all ecotypes showed a distinct recovery in sprouting ability.

The cold treatment of the roots prior to planting influenced significantly the sprouting ability of the ecotypes from all countries ($P < 0.001$), except those from Denmark ($P = 0.28$). In all countries a significant interaction between the cold treatment and the starting date of the dormancy test was detected ($P < 0.001$).

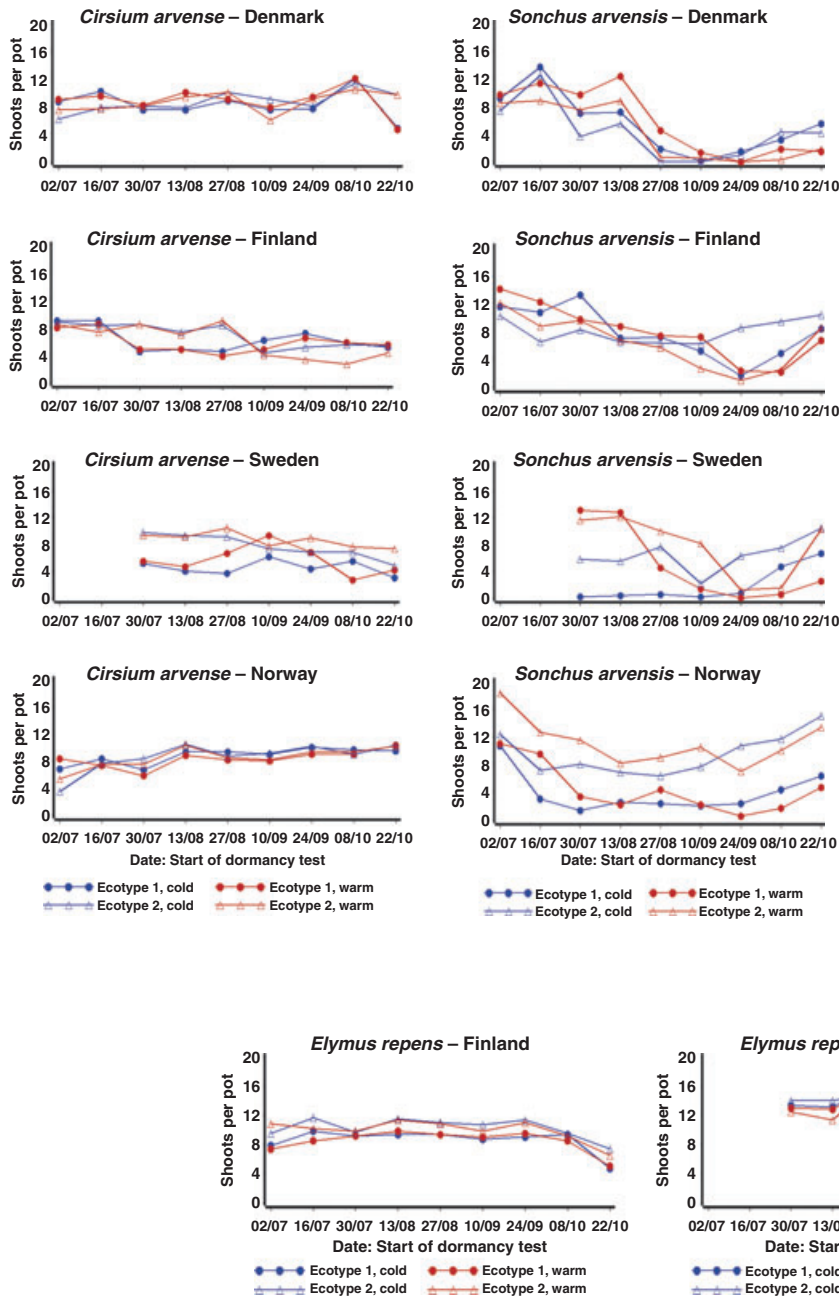


Fig. 1 Emergence of shoots from two randomly chosen ecotypes of *Cirsium arvense* and *Sonchus arvensis*, collected in Denmark, Finland, Norway and Sweden, for simplicity called ‘Ecotype 1’ and ‘Ecotype 2’ of each species and country. At regular intervals from mid-summer to late autumn 2002, root fragments were planted in pots located in a growth chamber at 18°C and the number of emerged shoots counted 4 weeks after planting. ‘Warm’: Pots placed into the growth chamber immediately after planting. ‘Cold’: Pots stored 4 weeks in darkness at 2°C before moving to the growth chamber. To facilitate comparison of emergence, the ‘Cold’ figures are adjusted to the starting date of the dormancy test, i.e. omitting the time in cold storage.

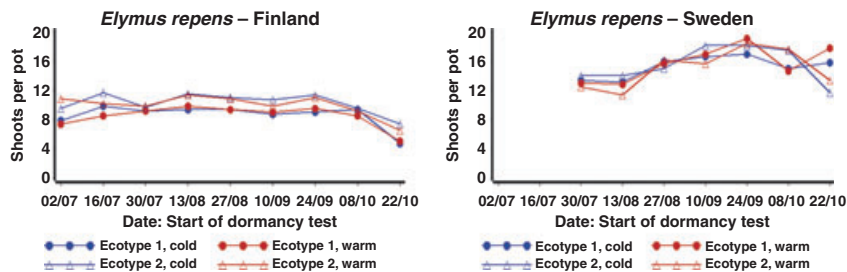


Fig. 2 Emergence of shoots from two randomly chosen ecotypes, ‘Ecotype 1’ and ‘Ecotype 2’, of *Elymus repens* collected in Finland and Sweden. At regular intervals from mid-summer to late autumn 2002, root fragments were planted in pots located in a growth chamber at 18°C, and the number of emerged shoots counted 4 weeks after planting. For further details, see Fig. 1.

The cold-treated ecotypes from Norway and Sweden revealed a more rapid onset of dormancy and a corresponding earlier recovery. In Finland, cold treatment before planting reduced the emergence of shoots from ecotype 2 during the first part of the test period, resulting in the ecotype with the lowest number of shoots. During the last part of the test period, however, this ecotype yielded the highest shoot number, while ecotype 1 was less influenced by the cold treatment.

Elymus repens

In Finland, the two ecotypes developed significantly different shoot numbers ($P < 0.001$) (Fig. 2). The starting date of the dormancy test significantly influenced the sprouting activity ($P < 0.001$), with a marked drop at the end of the test period. However, no significant effect of cold treatment prior to planting, or interactions between treatment and ecotypes, between ecotypes and test date, or between treatment and test

date, were detected. The Swedish ecotypes were very similar ($P = 0.94$) and did not respond in a significantly different manner to any of the test variables.

Rate of shoot emergence

The speed with which shoots develop may serve as an additional indicator of the dormancy status of the vegetative reproductive organs. Figure 3 shows the number of shoots at the end of each of the four weeks following planting of cold-treated roots of ecotype 2 of *C. arvense* and *S. arvensis* from Finland and Norway during the dormancy test period. Results from the other ecotypes were similar but less remarkable and were not presented.

Cirsium arvense

For the early dates of the onset of the dormancy test, there was fairly rapid shoot emergence from both the Finnish and Norwegian ecotypes (Fig. 3). However, for later dormancy test onset dates, the Finnish ecotype had little emergence after 1 week. In fact, by the August 27 onset date, there was no emergence at all after 1 week. For these later onset dates, there was rapid significant emergence only after the second week ($P < 0.001$), with little further shoot emergence in weeks 3 and 4.

For the Norwegian ecotype (for which there was no data collected for the first dormancy testing onset date), there was significant shoot emergence after one week, regardless of dormancy test onset date (Fig. 3). For the onset dates from the 13th of August until the 22nd October, there continued to be substantive emergence between the first and second weeks, but very little further emergence in weeks 3 and 4.

Differences in emergence between weeks 1 and 2 were only significant ($P = 0.046$) for the October 8 onset date. A change in rate of shoot emergence, from rapid emergence for early dormancy onset dates to more protracted emergence for later onset dates indicates development of dormancy in the roots of both ecotypes, and more so in the Finnish versus the Norwegian ecotype.

Sonchus arvensis

The Finnish ecotype of this species behaved very much in the same way as the Finnish ecotype of *C. arvense*, revealing some sprouting ability in the first week after the start of the test, for the earliest onset date of the dormancy test and very little shoot emergence in subsequent weeks (Fig. 3). For the later onset dates, there was almost no emergence in the first week, with most emergence occurring after 2 weeks. There were significant differences in shoot emergence between weeks 1 and 2 ($P < 0.005$), but no significant differences between weeks 2 and 3, and 3 and 4.

As with *C. arvense*, the Norwegian ecotype responded differently with high emergence after one week for the first two dormancy test onset dates and for the last one (October 22) as well (Fig. 3). For the interim onset dates, there was almost no shoot emergence after one week, with almost all of the shoot emergence occurring after two weeks. For these interim onset dates, the differences between weeks 1 and 2 were significant ($P < 0.001$). This result suggests that the Finnish ecotype had a similar dormancy status, regardless of test onset date, while for the Norwegian ecotype, bud dormancy was very much affected by test onset date.

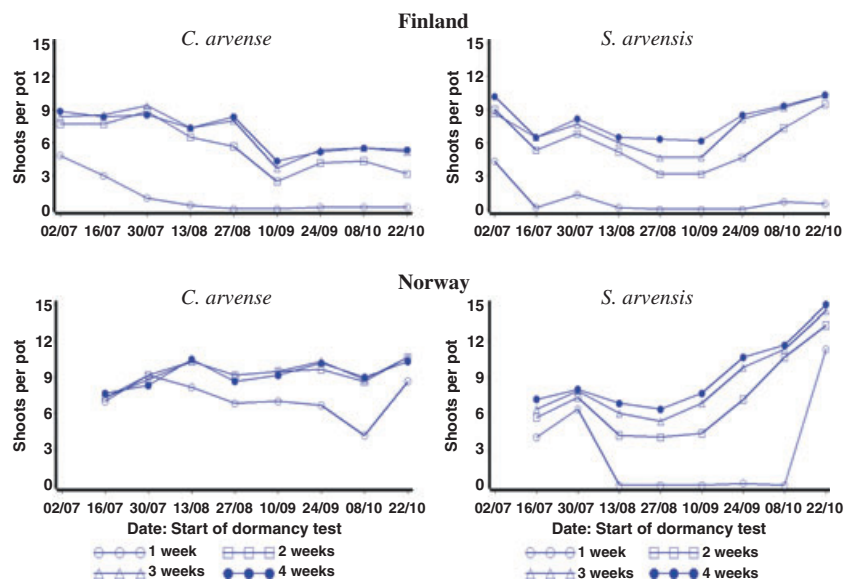


Fig. 3 Rate of emergence of the pre-chilled ecotype 2 of *Cirsium arvense* and *Sonchus arvensis* from Finland and Norway, measured as number of shoots per pot, 1, 2, 3 and 4 weeks after the day of moving the pots from 4 weeks cold storage at 2°C, to a growth chamber at 18°C. For further details, see Fig. 1.

Discussion

Cirsium arvense

The readiness to sprout of this species was relatively uniform during the experimental period and bud dormancy was generally not present. However, slight reductions in sprouting readiness and subsequent shoot growth were seen in some cases, which was also observed by Henson (1969) and Fykse (1974, 1977). Thind (1975) and Kvist and Håkansson (1985) suggested that this phenomenon could be caused by low food reserves in young roots, which is common in young roots in the autumn. However, this was unlikely the case in our study, where small and light root pieces were excluded. A review by McAllister and Haderlie (1981) concluded that root buds of *C. arvense* showed no restrictions in growth at any time of the year, as long as environmental conditions were not limiting. Variation in the ability of less developed buds to produce shoots might be caused by competition for internal resources in young roots, relative to older shoots. Based on field experiments, Nadeau and Vanden Born (1990) concluded that nitrogen fertilisation leads to a greater number of shoots by increasing the total number of buds, due to a greater quantity of regenerative roots, rather than by increasing the relative number of activated buds. Even if no great restrictions in bud activity were observed between ecotypes from different countries or between ecotypes from the same country, some differences seem to exist. This is demonstrated by the two ecotypes from Finland, where ecotype 1 entered mild dormancy only one month after the onset of the test, while ecotype 2 did not enter mild dormancy until 1½ months later. Similar differences in ecotype may well occur in agricultural fields and may partly explain the variability in management efficacy.

Sonchus arvensis

This species revealed greater variability than *C. arvense* with respect to sprouting activity during the test period. Shoot emergence was greatest in the early part of the test period (July) decreased after some time and increased again towards the end of the experimental period (October). This was a common feature of the ecotypes from all of the countries, but in spite of this general trend, the development of new shoots differed both between ecotypes and countries. One very clear and important difference was the time of onset of the decline of sprouting in late summer (for example, 1½ months earlier in Norway versus Denmark). This difference in behaviour was most likely caused by differences in innate bud dormancy, which is consistent with the findings of other researchers (Håkansson, 1969b; Henson, 1969).

The low temperature treatment decreased or increased early and late dormancy test onset dates respectively. For late dormancy test onset dates, the low temperature treatment seemed to have the same effect as winter (breaking innate dormancy). One may speculate whether this effect was caused by the low temperature itself, or by the fact that the root pieces, because of the cold treatment, were four weeks older. If age were a factor, then the shoot numbers for the warm temperature treatments four weeks on should have been similar to the shoot numbers for the cold-treated pieces. Our results showed this to seldom be the case. Nevertheless, age cannot totally be excluded, as a contributing factor. Low outdoor temperatures in the autumn of the second phase were, presumably, the reason why sprouting generally increased considerably from September to October, even for non-pre-chilled root pieces brought into the 18°C growth chamber. This result suggests a gradual relief of innate dormancy.

Elymus repens

As for *C. arvense*, our study did not reveal any clear period of innate dormancy for *E. repens* and this result is consistent with other studies. It is, however, worth noting that the Finnish ecotypes expressed a significant decline in sprouting readiness at the end of the test period. Håkansson (1967) also found no discrete period where there was significant growth restriction on all the buds of fragmented rhizomes of *E. repens*. Moreover, further fragmentation of the rhizomes always triggered increased proportional sprouting, indicating no innate dormancy. The most convincing evidence to conclude that *E. repens* has no discrete and complete bud dormancy is that bud activity is immediately stimulated by rhizome fragmentation at any time of the growing season. Variation in sprouting readiness, even in spring, is thus interpreted to be caused primarily by variations in the amount of food reserves in the rhizomes (Håkansson, 1967, 1969a; Leakey & Chancellor, 1977a,b).

The results of this study support the idea that to make clear distinctions between physiological dormancy caused by shortage of food reserves, apical dominance or an innate dormancy, the amounts of available food reserves (mainly carbohydrates and nitrogen), as well as hormone concentrations, should be determined. An important question driving our study was whether any of the three species developed innate dormancy and, if so, could it be broken by a simulated winter. The cold treatment we used seemed to have some effect in breaking dormancy and so it acted to some extent like a winter period. Using lower temperatures may have produced a more pronounced result. However, our methodology was adequate for revealing the existence of innate dormancy because: (i) all environmental factors

in the growth chamber, including temperature, soil moisture and light were kept at levels that do not give rise to sprouting restrictions, (ii) food reserves were not limiting, illustrated by the fact that the sprouting level was generally highest at the start of the experimental period, and (iii) apical dominance was removed.

In terms of practical management, a control campaign based on weakening the regenerative structures by means of fragmentation and regrowth, is likely to have very different effects on the different species we studied. With evidence of strong innate dormancy in the reproductive roots of *S. arvensis*, it is unlikely that this control strategy will be effective on this species, if performed during the late summer and early autumn. However, with little evidence of innate bud dormancy in either *C. arvensis* or *E. repens* in the late summer-autumn period, this strategy should be effective on these species. Unpubl. obs. from Norway (K. S. Tørresen) showed *E. repens* growing temperatures as low as 5°C, much lower than *C. arvensis*, which required around 10°C for similar growth. Therefore, in relation to propensity for innate dormancy of regenerative structure buds, a ranking of the potential for obtaining good results, in terms of bud exhaustion via mechanical control in late summer-early autumn, would be *E. repens*, then *C. arvensis*. One classical experiment in Denmark (Permin, 1961) showed that shallow post-harvest cultivation had greatest effect on *E. repens*, followed by *S. arvensis* and then *C. arvensis*. The reason for *S. arvensis* being more strongly controlled than *C. arvensis*, in spite of its autumn dormancy, is presumably its shallow root growth. The greater difficulty in controlling *S. arvensis* than *E. repens* is probably primarily due to the innate dormancy in the former species. On the basis of effects of the regenerative buds and the propensity for these buds to be dormant in late summer-early fall, the results of our study would suggest that autumn mechanical control would provide greatest efficacy on *E. repens*, followed by *C. arvensis* and then *S. arvensis*.

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