



Vegetative propagation of *Solidago canadensis* – do fragment size and burial depth matter?

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Summary

Clonal species may benefit from human disturbance because their vegetative fragments may be distributed via soil. *Solidago canadensis* is an invasive rhizomatous perennial frequently found in ruderal environments. When creating new infrastructure, digging and cutting are two main factors that may influence the spread of *S. canadensis* into new areas. To have a better understanding of the invasive potential of *S. canadensis*, we investigated whether *S. canadensis* was able to survive and grow from stem cuttings as well as from rhizomes. Rhizomes and cuttings were collected from three populations in Eastern Norway. The rhizomes and cuttings were planted in a pot experiment to assess their vegetative ability to propagate. Rhizome fragments (5 and 10 cm long) were buried at 0.5, 10 and 30 cm depths. The cuttings

were planted as 15 cm stems, with the bottom 5 cm pushed into the soil. The results showed that rhizome length did not have an effect on survival. Although some sprouting occurred at all burial depths, increasing depth had a negative effect on rhizome survival. In general, development of the cuttings was good, but there were differences between population performance and survival. These results imply that care must be taken when (i) constructing new sites, because digging and transport of soil masses may spread *S. canadensis* into new areas by rhizomes or cuttings, and (ii) mowing road verges and other ruderal areas to prevent the spread of stem cuttings from one area to another.

Keywords: burying, resprouting, rhizomes, cuttings, inflorescence, populations, invasive, goldenrod, Canada goldenrod, Canadian goldenrod.

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Introduction

Areas invaded by alien species are often ruderal habitats, characterised by high levels of human disturbance, such as cutting, digging and relocation of soil masses from infrastructure and expansion areas (Parendes & Jones, 2000). Disturbance affects plants and may lead to the development of various sizes of fragments of roots and shoots. Clonal species may benefit from such disturbance, depending on burial depth, fragment size and sprouting ability (Li *et al.*,

2013). Fragments of plant species buried in soils at construction and waste dumping sites facilitate greater spread of invasive species into native habitats and gene flow between populations (e.g. Keller *et al.*, 2011). Different populations of the same species may respond differently to the same treatment, due to genetic variation, environmental conditions, age or time of year. Many invasive alien plants are spread by clonal fragments. Baker (1974) identified the ability to form clones and vegetative propagation combined with strong lateral growth as common traits among alien

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invasive species, even if clonal plants seem to be under-represented among this group of plants (Dietz *et al.*, 2002). To be able to manage the threat of vegetatively propagated alien species, we need a better understanding of their potential to establish and spread.

Solidago canadensis L. (Canadian goldenrod) is a rhizomatous perennial that originates from North America and has been introduced in Europe and temperate Asia (Weber & Schmid, 1998; Xu *et al.*, 2014); in Norway, it has been classified to the highest level of alien species impact ('severe') (Artsdatabanken, 2018), due to its rapid invasion and spread and negative effect on native species, habitats and ecosystems (Elven *et al.*, 2018). This species flowers in the second growth season (Bender *et al.*, 2000), and the small, wind-dispersed seeds ripen about 6 weeks after inflorescence (Pavek, 2011). It is often found at disturbed sites, such as industrial areas, alongside pavements and crop fields, as well as in transitional areas between forests and cultivated land, and in southern Norway, it is one of the most common alien species along road verges and on cultivated land, displacing native species and altering the cultural landscape (Elven *et al.*, 2018). The invasion success of *S. canadensis* is due to its rapid growth and prolific reproduction (both sexual and asexual) (Kabuce & Priede, 2010), rhizome survival in harsh conditions through the sharing of nutrients between ramets (Hartnett & Bazzaz, 1985) and allelopathy that outcompetes other plants (Dong *et al.*, 2006b); the formation of large colonies of *S. canadensis* may enhance nutrient cycling rates (e.g. Vanderhoeven *et al.*, 2006), inhibit microbiological activities (Deng *et al.*, 2015) and negatively affect biodiversity (Fenesi *et al.*, 2015). Environmental impacts of *S. canadensis* depend on local climate and recipient communities (Dong *et al.*, 2015b).

Management of *S. canadensis* in Norway includes application of herbicide during the early growth stage and mowing prior to flowering (cut material may lie on the ground, but not in contact with running water) (Fløistad, 2010). When creating new infrastructure, digging and cutting are two main factors that may lead to the spread of *S. canadensis* into new areas; however, Weber (2011) found that establishment of *S. canadensis* rhizomes was erratic. To obtain a greater understanding of the invasive potential of *S. canadensis*, we investigated population variation in rhizome and stem cutting establishment under contrasting burial regimes that mimicked disturbance conditions during construction work.

The research questions were as follows: (i) Do different rhizome lengths and burial depths affect the regrowth of *S. canadensis*? (ii) Do stem cuttings of

S. canadensis propagate? (iii) Do different populations of *S. canadensis* show different regeneration capacities?

Method and materials

Site selection

Three sites in eastern Norway (Ås and Røyken in Akershus County, and Drammen in Buskerud County) were selected for this study in which *S. canadensis* was the predominant species. All three sites are dispersed on both sides of the Oslo Fjord. Among the sites, annual normal temperatures are greatest at Drammen, and lowest temperatures and greatest amounts of precipitation are at Røyken; lowest levels of precipitation are at Ås (Table 1).

Sampling

Plant material from each population was collected on a single day (17, 18 and 19 June 2015), where five root clumps were removed from visually healthy plants that had large numbers of stems, and individual rhizomes were cut into 5 and 10 cm long pieces of approximately the same thickness (rhizome thickness was not measured). With existing roots still attached, five replicate single rhizomes (by size and population) were planted in square 25-L pots that were buried at one of three depths (0.5, 10 or 30 cm); the 90 rhizomes were randomly arranged in a grid of 6 × 15 pots (Fig. 1).

Three replicate stem cuttings (hereafter referred to as cuttings) were taken above the first pair of leaves on the same plants from which rhizomes were sampled and cut into 15 cm long pieces ($N = 45$). The cuttings were individually potted by inserting the lower 5 cm into the soil in the centre of each 2 L pot (Fig. 1).

The soil contained 85% sphagnum peat, 10% sand and 5% granulated clay, with 1 kg of multimix fertiliser (<http://www.horticoop.dk/index.php/godning/81-multimix-12-6-20-02-mo-npk-12-6-20-mg-mikro>) and 4.5 kg of chalk dolomite added per 20 kg of soil. The pH values were 5.5–6.5. All pots were randomised and placed outside to mimic a natural environment. To minimise edge effects from sun exposure, an extra row of pots filled with soil were placed along the border of the pots on the western side for the rhizome experiment. For the cutting experiment, pots filled with soil were placed around the outer edge of all experimental pots. All pots were watered as a group, usually about 15 min each day or as needed, using an overhead irrigation system with spray nozzles.

Table 1 Data from each of the study sites, temperatures and precipitations based on normal from 1960 to 1990 (eklima.met.no)

	Drammen	Røyken	Ås
Type of location	Untended flowerbed	Disturbed soil site, dumping ground	Roadside near highly trafficked road
Size of population	10 × 4 m	12 × 6 m	5 × 25 m
<i>S. canadensis</i> cover	40%	50%	80%
<i>S. canadensis</i> height	60–80 cm	60–80 cm	80–100 cm
Incline	27°	15°	25°
Exposure	Western sun exposure	South-eastern sun exposure	South-eastern sun exposure
Soil	Sandy clay	Varying texture, ranging from almost pure sand to sandy clay	Compacted silty and sandy clay
Altitude	8 m a.s.l.	135 m a.s.l.	66 m a.s.l.
Coordinates	N 59°44'50.218" E 10°11'07.851"	N 59°44'29.005" E 10°23'06.187"	N 59°42'34.520" E 10°43'29.277"
Annual mean temperature	5.5°C	5.2°C	5.3°C
Warmest month	July, 16.8°C	July, 15.9°C	July, 16.1°C
Coldest month	January, −5.6°C	January, −5.6°C	January, −4.9°C
Annual precipitation	830 mm	880 mm	785 mm
Wettest month	October, 100 mm	October, 113 mm	October, 110 mm
Driest month	April, 43 mm	February, 42 mm	February, 35 mm

**Fig. 1** Planted and randomly assigned pots with rhizomes and cuttings at the start of the experiment.

Measurements

For both the rhizome experiment and the cutting experiment, the height of the tallest shoot was recorded from the first sprouting, and subsequently, on average, every third day from 24 June until 12 August 2015. The termination of both experiments lasted 3 days, from 12 to 14 August 2015. All plants were carefully removed from the pots, keeping roots as intact as possible. The development of the root system was judged visually on two different scales, one for the rhizome experiment and one for the cutting experiment. Both scales ranged from 0 to 6, where 0 is dead and 6 is excellent root development (Table 2, Figs 2 and 3). All root systems were photographed upon termination.

In the rhizome experiment, the number of aerial shoots was recorded for all depths, and for the rhizomes buried at 10 and 30 cm, the number of shoots that did not reach the surface, their length (cm), and the extent of branching were also recorded. Shoots with inflorescence were also counted. For the cuttings, the number of shoots was counted, and the length of the longest shoot was recorded (cm).

Statistical analysis

We applied a Bayesian hierarchical model that allows experimental design with both effects associated with treatment and population-specific effects. The posterior distributions for the effects of interest were estimated using Integrated Nested Laplace Approximations

Table 2 Different root development stages for both experiments

Value	Cutting experiment	Rhizome experiment
0	Dead	Dead
1	Cutting is alive, but without callus	Living rhizomes, but no new root development
2	Cutting is alive, with developed callus	One to two new roots, but no root branching
3	One to two roots, without branching	More than two new roots, with root branching
4	More than two roots, with branching	Considerable root development with many new roots and root branching
5	Considerable root development, with many roots and significant branching	Excellent root development with the roots filling most of the pot, and some new rhizomes
6	Excellent root development, numerous long roots with significant branching	Excellent root development with the roots filling most of the pot, and development of thick rhizomes

(INLA) (Rue *et al.*, 2009). For all analyses, the mother plant was included as an independent and identically distributed random contribution, and population and treatments were considered as fixed effects. Root development and flowering (present or absent) assumed a binomial distribution, number of shoots assumed a negative binomial distribution and shoot length assumed a gamma distribution. Treatment effects on root development were analysed for living roots, where stages 1, 2 and 3 were classified as some root development and stages 4, 5 and 6 were classified as well-developed root system. The probability of inflorescence development in shoots was described as a function of aerial shoot length.

Statistical analyses were performed using R v. 3.2.3 (R Core Team, 2018).

Results

Rhizome survival

Survival of rhizomes from Ås was lower than those from Røyken and Drammen (Table 3); there was >50% mortality of rhizomes from Ås by the end of the experiment and rhizome survival was greatest from populations at Røyken (Table 4). There was no effect on survival of rhizome length for any of the populations (Table 3). There were minor differences in rhizome survival among the populations at 0.5 cm burial depth (Table 4); however, increasing burial depth had a negative effect on survival (Table 3).

Rhizome development

Rhizome development decreased with increasing burial depth for all populations, but this relationship appeared weaker for the Røyken and Drammen populations than the Ås population (Fig. 4). There were no effects of burial at 10 cm on root system development, although effects of burial at 30 cm were varied

(Table 5). Of rhizomes buried at 30 cm, 2 from the Ås population, 8 from the Røyken population and 2 from the Drammen population, developed shoots that did not reach the surface, with an average length of 16, 22 and 29 cm respectively.

Aerial shoots developed from 21 rhizomes from Røyken and Drammen and 11 from Ås, where there were fewer aerial shoots from rhizomes buried at 10 and 30 cm than from the other two populations. Mean length of the longest aerial shoot (500 mm) and number of aerial shoots per rhizome (4) for the Ås and Røyken populations were similar, and lower for the Drammen population (400 mm long; three shoots). Reaching the surface and starting to produce aerial shoots is a main factor on root system development (Fig. 5). The presence of two aerial shoots resulted in a 50% probability of a well-developed root system, while four aerial shoots increased this probability to >95%.

Inflorescence

None of the rhizome pieces buried at 30 cm developed inflorescence. However, the Ås population had three rhizomes with inflorescence, all from 0.5 cm burial depth. The Røyken population had 11 rhizomes with inflorescence and three from 10 cm burial depth. The Drammen population had nine rhizomes with inflorescence, eight from the 0.5 cm depth and only one from 10 cm burial depth. Estimated probability of inflorescence increased gradually with shoot height (Fig. 6). The largest increase in mean probability of development of inflorescence occurred when aerial shoot length increased from 500 to 600 mm (20–90%); at 660 mm, the mean probability of developing inflorescence was 98%.

Stem cutting development

Overall, survival and development of cuttings was high; mortality was observed only in 2 cuttings from

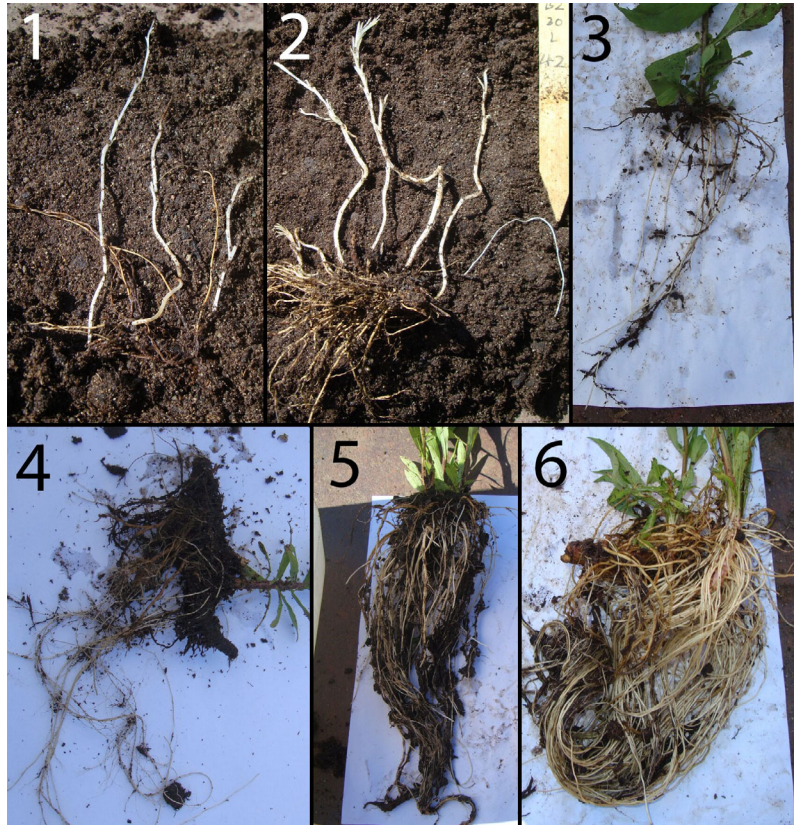


Fig. 2 Different root development stages for rhizomes. From top left is root development stage 1 (living rhizome) to 6 (excellent root development). Stages 1 and 2 have shoots that have not yet reached the surface.

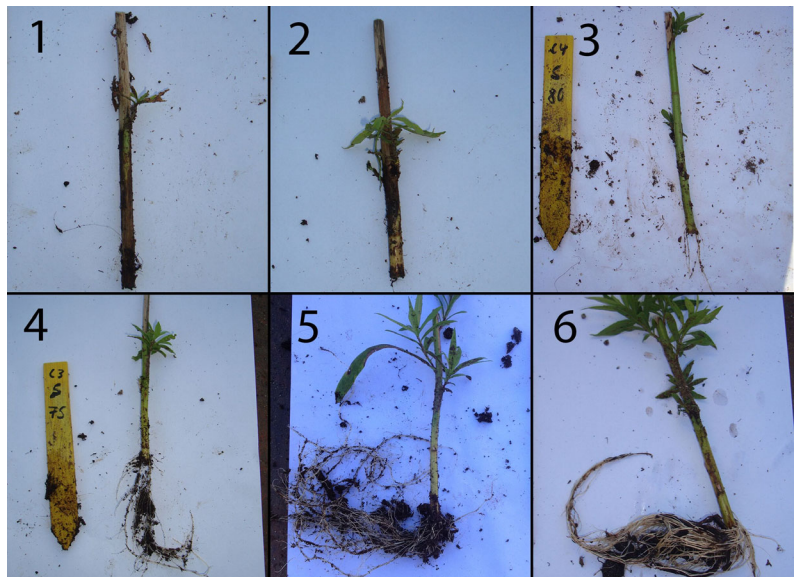


Fig. 3 Different root development stages for cuttings. From top left is root development stage 1 (living cutting) to 6 (excellent root development).

the Røyken population. There were no differences in root development (Fig. 4, Table 6), or number of shoots (Table 6) among the three populations; however, shoots were longer in the population from Ås than those from Røyken and Drammen (Table 6). None of the cuttings developed inflorescences, and we found that several leaves from the Ås population developed roots (14 August 2015; Fig. 7), unlike those of the other populations.

Discussion

Increasing burial depth had a negative effect on rhizome survival for all three populations. Decreasing survival or vigour of shoot growth from rhizomes with increasing burial depth is common for rhizomatous perennials, as their energy reserves are expended while growing towards the surface (Klimes *et al.*, 1993; Dalbato *et al.*, 2014). There was almost no difference in

Table 3 Intercepts of survival of rhizomes at contrasting burial depths. Intercept is 5 cm rhizomes buried at 0 cm from the Drammen population. Significant effects ($P = -0.05$) are shown in bold

	Low	High
(Intercept)	1.129	4.402
10 cm depth	-3.750	-0.511
30 cm depth	-4.473	-1.165
10 cm rhizome	-0.079	2.269
Røyken population	0.014	3.461
Ås population	-3.317	-0.715

Table 4 Predicted probability of surviving for different burial depths and populations

Burial depth	Population	0.025 quantile probability	Mean probability	0.975 quantile probability
0.5 cm	Drammen	0.831	0.942	0.991
10 cm	Drammen	0.502	0.732	0.906
30 cm	Drammen	0.357	0.605	0.824
0.5 cm	Røyken	0.949	0.977	0.999
10 cm	Røyken	0.771	0.919	0.989
30 cm	Røyken	0.660	0.862	0.976
0.5 cm	Ås	0.496	0.744	0.928
10 cm	Ås	0.133	0.335	0.578
30 cm	Ås	0.069	0.220	0.435

survival between the populations at 0.5 cm burial depth, most likely due to the rhizomes containing enough energy to grow new shoots and produce assimilates (Price *et al.*, 2001). However, at increasing burial depth, the number of dead rhizomes and differences in survival between the populations became evident; most

Table 5 Intercepts for degree of root development at 10 and 30 cm burial depths and shoot development, given survival of rhizomes. Intercept is 0 cm burial depth. Significant effects ($P = 0.05$) are shown in bold

	Low	High
(Intercept)	-3.334	1.931
10 cm burial depth	-3.326	0.311
30 cm burial depth	-29.707	8.307
Aerial shoot	0.119	2.107

of the rhizomes from Ås were dead, while most of the rhizomes from Røyken survived. Even though more stored energy is required to produce aerial shoots from a deeper burial, none of the burial treatments was fully effective in hindering sprouting for any of the populations. Rhizome length did not have a positive effect on survival. Still, the size of the rhizomes could have an effect, as the thickness of the rhizomes was not recorded for this experiment, and the biomass of the rhizomes might have given a more reliable result. Huang *et al.* (2015) found that thicker rhizomes of *Mikania micrantha* had more stored energy, but stolon thickness had a very limited role in the fragment survival. When looking at the underground shoot length of the rhizomes buried at 30 cm depth, there seems to be a threshold level of stored energy needed for rhizomes to reach the surface and survive. Beyond this burial depth threshold, new sprouts may fail to emerge because the carbohydrate reserves in the storage organs become completely depleted (Klimes *et al.*, 1993). This threshold level may also vary between seasons. In this study, the rhizomes were harvested in June and buried down to 30 cm. These rhizomes had a higher survival rate than the rhizomes in a study by

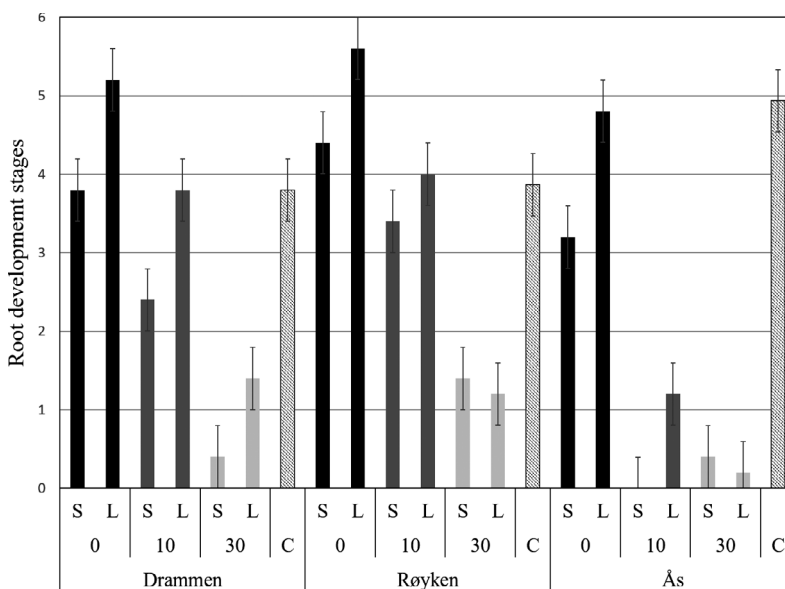


Fig. 4 Average root development for different populations (Drammen, Røyken and Ås), burial depths (0 cm, 10 cm and 30 cm) and rhizome piece lengths (S = 5 cm and L = 10 cm), and for stem cuttings (C), where 0 is dead and 6 is excellent root development (Table 2). Each category is an average from 5 pots for the rhizomes and average from 15 pots for the cuttings. Standard error bars are included.

Fig. 5 Estimated probability of attaining a well-developed root system with increasing numbers of aerial shoots. Quantile probabilities of 0.025 and 0.975 are included, while the red line is mean probability.

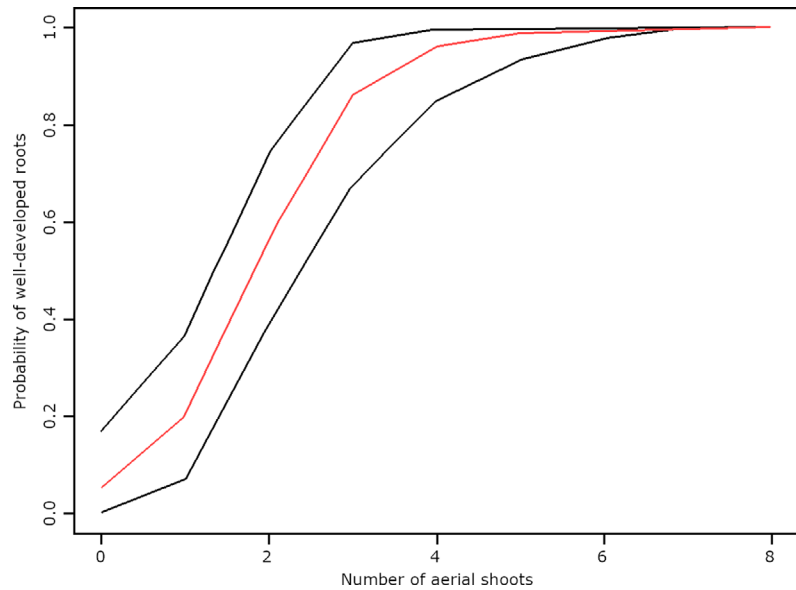
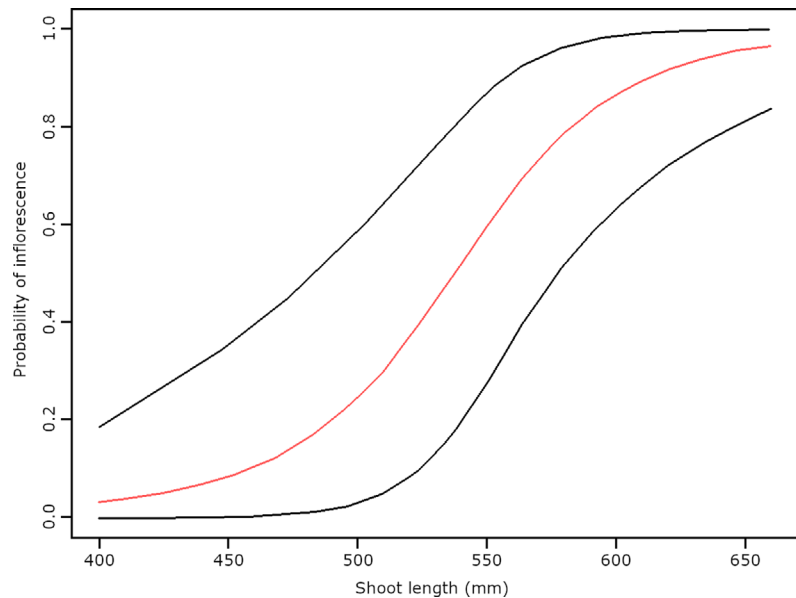


Fig. 6 Estimated probability of developing inflorescence with increasing aerial shoot length. Quantile probabilities of 0.025 and 0.975 are included, while the red line is mean probability.



Weber (2011), in which the rhizomes were harvested in early April and most of the rhizomes died at 5 cm burial depth. This may suggest that there are seasonal variations in stored energy of *S. canadensis* rhizomes. This is consistent with Bradbury and Hofstra (1977) who found lower carbohydrate levels in the rhizomes early in the growth cycle of *S. canadensis*. This means that the time of year for digging and burying may affect resprouting ability and the survival of the rhizomes, which is also found in other species (Nkurunziza & Streibig, 2011; Verwijst *et al.*, 2018).

To attain a well-developed root system, development of above-ground shoots is important; the probability of attaining a well-developed root system is over 95% when the rhizome has four aerial shoots. Above-

ground shoots give the photosynthetic capacity to support respiration and growth and develop root systems (Luo & Zhao, 2015). *Solidago canadensis* shoots grow rapidly and produce a great number of leaves early in their life cycle (Schmid *et al.*, 1988). This suggests that once a rhizome has shoot growth that reaches the soil surface, it performs well. However, at 30 cm burial depth, this effect is not as obvious, as most of the rhizomes from Røyken and Drammen had not developed aerial shoots even though the rhizomes were still alive. Nonetheless, the rhizomes from Røyken and Drammen had underground shoots that were growing towards the surface. If the experiment had been terminated later, underground shoots may have reached the surface, and these rhizomes may also have attained well-

Table 6 Cuttings analysed with respect to root development. Roots were considered good (classes 4–6) or bad (classes 1–3), number of shoots protruding, and the length of the shoots protruding. The population at Ås was the intercept

	Mean	SD	0.025 quant	0.5 quant	0.975 quant
(Intercept)	1.872	0.758	0.548	1.812	3.522
Røyken	−0.502	0.995	−2.531	−0.475	1.377
Drammen	−0.889	0.956	−2.875	−0.851	0.882
(Intercept)	1.511	0.122	1.264	1.514	1.742
Røyken	−0.159	0.179	−0.512	−0.158	0.192
Drammen	−0.307	0.187	−0.677	−0.306	0.056
(Intercept)	64.753	5.300	54.231	64.778	75.126
Røyken	−17.826	7.437	−32.386	−17.860	−3.089
Drammen	−24.300	7.440	−38.852	−24.339	−9.547

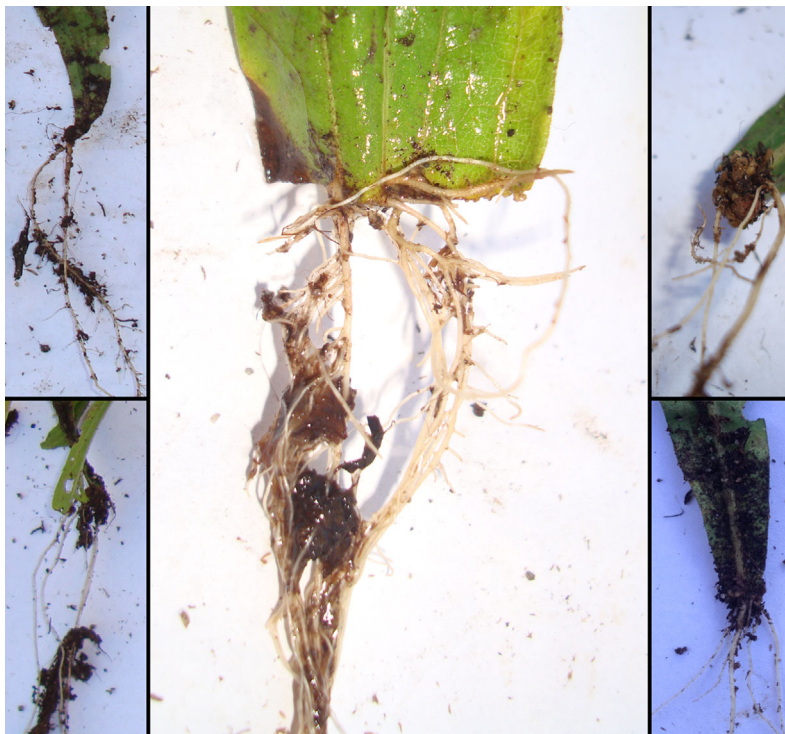


Fig. 7 Leaves with root development, from the population at Ås.

developed root systems. For *Mischantus sacchariflorus*, a rhizomatous grass that has ramet growth like *S. canadensis*, fragmentation and burial at 20 cm was shown to delay sprouting and subsequent growth, although it still managed to sprout (Chen *et al.*, 2015). Similarly, burial depth may delay sprouting of *S. canadensis* rhizomes, which could lower their competitive ability as they have less time to develop shoots and store assimilates. The probability of inflorescence increases gradually between 400 mm and 650 mm, indicating that the height of inflorescence is not absolute. Schmid and Weiner (1993) and Schmid *et al.* (1995) did find that *S. canadensis* flowers, after reaching a certain size. *Solidago canadensis* normally flowers in its second year of growth when propagated from

seeds (Bender *et al.*, 2000). Many of the plants grown from rhizomes in this experiment flowered in their first growth season, indicating that the rhizomes were more than 2 years old.

The Ås population had rhizomes with the lowest survival, but developed longer shoots on the cuttings than the two other populations. The difference in survival and growth between the rhizomes and cuttings from Røyken, Drammen and Ås is associated with inherent differences among the populations, as the soil used in the experiment was homogenous and similar for all pots. *Solidago canadensis* is known to be a species with large genetic variance between populations in Europe (Weber, 1997). The difference in height and longer shoot lengths of the cuttings as

well as the poor performance of the rhizomes of the Ås population could indicate a different subspecies, although it is uncertain how much genetic variance there is between the different populations in this experiment. There might also be trade-offs between above-ground and below-ground biomass allocation in this experiment. The Ås population may have a trade-off where the aerial shoots store more energy and have a stronger regenerative ability than the rhizomes, while the opposite may be the case for the Røyken and Drammen populations. This is not in accordance with Schmid and Weiner (1993) and Schmid *et al.* (1995) who described a linear relationship between allocation of resources to sexual and vegetative growth in *Solidago* species. However, Werner *et al.* (1980) found that *S. canadensis* tends to invest more biomass in sexual reproduction than vegetative reproduction as the plant ages. The Ås population is probably older than the two other populations and might therefore allocate more energy for inflorescence while storing less in its rhizomes. The younger populations in Røyken and Drammen, in contrast, may have stored more energy in their rhizomes. Also, plants growing on nutrient-rich soil often allocate more energy to above-ground growth (Aerts *et al.*, 1991). The Ås population likely grows on a slightly more nutrient-rich soil than the other two populations which favours resource allocation towards more stored energy in above-ground biomass. This could help explain why among the cuttings the Ås population was the tallest, had the longest shoots and was the only population to develop vegetative roots from leaves. *Solidago canadensis* do affect abiotic and biotic soil composition (Dong *et al.*, 2015a, 2017); however, neither soil nutrients nor the nutrients in the plants were analysed in this study. Differences in nutrient content in both soil and tissue might have explained some of the differences in establishment between populations.

Implications for management

Although the mortality was higher with increasing burial depth, none of the burial depths were sufficient to completely stop the rhizomes from sprouting. If they manage to sprout, the rhizomes have a high likelihood of re-establishing themselves. A 30 cm burial depth may delay growth and stop development of inflorescence similar to the effect of mowing (Fløistad, 2010), although this is uncertain given the experiment's short timeframe. However, care should be taken at construction sites. Digging and transport of soil masses may spread *S. canadensis* into new areas by rhizomes or cuttings, as both have shown a capacity to re-establish

themselves. Burying does not seem to prevent sprouting. Although our results indicate burying early in the season and at more than 30 cm may delay or hinder sprouting from rhizomes, this must be investigated further. When mowing road verges and other areas, care must be taken to ensure that cuttings are not moved from one area to another. Finally, it is important to manage the spread of *S. canadensis* by seeds, as sexual reproduction also may enable establishment of new populations (Dong *et al.*, 2006a). Because *S. canadensis* is a common invasive species in road verges in Norway (Elven *et al.*, 2018), the undertow from passing cars might also contribute to wind dispersal of its seeds.

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