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Vegetative propagation of *Solidago canadensis* from populations in Eastern Norway

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Master in Plant Sciences

Preface

This thesis concludes my master's degree at the Norwegian University of Life Sciences (NMBU), with the Department of Plant Sciences (IPV). The pot experiment was completed at NMBU's nursery in the summer of 2015.

I would like to extend my gratitude to the people who have shared their knowledge, motivated me and offered their assistance while working on this paper. Line Rosef (associate professor, IPV), my supervisor at NMBU, helped me find the right thesis and gave indispensable advice and support throughout the whole process. Einar Heegard (senior researcher), my supervisor at the Norwegian Institute of Bioeconomy Research (NIBIO), was instrumental in finding the suitable statistical and experimental method, and provided the support needed to implement it. Ellen Zakariassen (research technician) provided excellent advice, kept the plants healthy and helped with recordings during the pot experiment. I would also like to thank my friends, Ruben Møller Aas – for assisting me in identifying species compositions at the different population sites – and Benjamin Isaac Sellars for reading through this paper several times and pointing out grammatical failings.

Lastly I would like to thank my family for their interest and support, and my significant other, Frida, for keeping me level-headed while writing.

All pictures are taken by the author, unless otherwise stated.

Ås, May 13th, 2016

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Summary

Solidago canadensis is a well-established invasive alien plant species in the lowlands and coastal areas from Østfold to Agder in Norway, with an expanding range. It spreads with small wind-dispersed seeds, and rhizomes. It is commonly found on cultivated land and road verges, where it alters the landscape and displaces native species.

Rhizomes and cuttings from *S. canadensis* were collected from three populations in Eastern Norway. The rhizomes and cuttings were planted in a pot experiment to examine their ability to propagate vegetatively, and thereby use this knowledge in managing their spreading. The rhizomes were buried at 0, 10 and 30cm, at two fragment lengths: 5 and 10cm. The cuttings were planted as 15cm stems, where the bottom 5cm where pushed into the soil. The experiment lasted from June 17th to August 12th. The probability of surviving, attaining a well-developed root system and attaining inflorescence for rhizomes was estimated statistically using 'integrated nested Laplace approximations' (INLA).

The results showed that increasing burial depth has a significant negative effect on rhizome survivability, although sprouting occurred at all burial depths. In addition, there was a significant difference in survivability between the populations. However, rhizome length did not have a significant effect on survivability. The number of aerial shoots had a significant positive effect towards attaining a well-developed root system, and the height of the tallest shoot increased with increasing root development. Many of the tallest shoots developed inflorescence, and the probability of inflorescence was estimated to be 90% at 600mm shoot length. The results suggest that if the rhizomes manage to sprout, they have a high likelihood of attaining a well-developed root system and thereby develop inflorescence.

Sammendrag

Solidago canadensis er en godt etablert fremmed invaderende planteart i lavlandet og kystområder fra Østfold til Agder, med økende utbredelsesområde. Den spres med små vindspredte frø, samt rhizomer. Den vokser vanligvis i kulturmark og langs veikanter, hvor den endrer tilstanden i landskapet og fortrenger stedegne arter.

Rhizomer og stiklinger fra *S. canadensis* ble samlet fra tre populasjoner i Øst-Norge. Rhizomene og stiklingene ble plantet i et potteeksperiment for å undersøke deres evne til vegetativ formering, i det øyemed å bruke denne kunnskapen til å begrense dens spredning. Rhizomene ble begravet på 0, 10 og 30cm, med to fragmentlengder: 5 og 10 cm. Stiklingene ble plantet som 15cm lange stengler, hvor de nederste 5cm ble dyttet ned i jorda. Eksperimentet varte fra 17. juni til 14. august. Sannsynligheten for å overleve, å oppnå et velutviklet rotsystem samt å oppnå blomstring for rhizomene ble estimert statistisk ved hjelp av 'integrated nested Laplace approximations' (INLA).

Resultatene viste at økende jorddybde hadde en signifikant negativ effekt på rhizomenes overlevelse, selv om spiring forekom på alle jorddybdene. Det var også en signifikant forskjell i overlevelse mellom populasjonene. Rhizomenes fragmentlengde viste seg å ikke ha noen signifikant effekt på overlevelse. Antallet overflateskudd hadde en signifikant positiv effekt på oppnåelsen av et velutviklet rotsystem, og høyden på det høyeste skuddet økte med økende rotutvikling. Mange av de høyeste skuddene utviklet blomstring, og sannsynligheten for blomstring ble estimert til å være 90% ved 600mm skuddlengde. Resultatene tyder på at dersom rhizomene klarer å spire, har de en høy sannsynlighet for å få et velutviklet rotsystem og dermed utvikle blomstring.

Content

1. Introduction

1.1. Alien invasive plant species

The Norwegian Biodiversity Information Centre (2012) defines an alien species as "(...) a species, subspecies or lower taxon occurring outside of its natural range (past or present) and dispersal potential (...)". However, this excludes native Norwegian species that are spreading outside of their natural range within Norway (Gederaas et al. 2012). Particularly problematic alien species are considered 'invasive species', meaning that the plant is capable of spreading and has a negative impact on the native ecosystem (Gederaas et al. 2012).

Alien invasive species are an increasing threat to global biodiversity and ecosystem integrity (Keller et al. 2011). Generally, they can affect populations, community interactions, ecosystem processes and abiotic variables (Charles & Dukes 2007). Additionally, there is a correlation between their ecologic impact and their economic impact. The economic impact can stem from the invasive species disruption of an ecosystem service and the cost of managing the invasion. As of 2009, invasive species are estimated to have a yearly economic impact of 12.5 to 20 billion EUR in Europe, whereas plants account for at least 3.7 billion EUR (Keller et al. 2011). However, invasive plant species tend to have a larger ecological impact than economic impact (Vilà et al. 2010). According to Keller et al. (2011), 17 out of the 18 most damaging invasive plant species in Europe reduce the habitat of native species. Reduction of native habitat is more severe if the habitat in question is populated by rare or threatened species. The species affected by habitat reduction is not necessarily other plants, as the invading species can for instance reduce another species source of food or cover. Additionally an invading species can be a host for pathogens, and cause a loss of genetic diversity in native plants (Gederaas et al. 2012).

In an increasingly globalized world, introduction of alien species is ever more common. This introduction can happen as a by-product of commerce or the introduced species being the commodity in itself. Lambdon et al. (2008) has identified common intentional and unintentional pathways of introduction for alien plants in Europe. The intentional introduction pathways are usually forestry, amenity, ornamental, agricultural or horticultural. The common unintentional introduction pathways are seed contaminants, commodity contaminants and stowaways.

Almost two thirds of the established alien plant species in Europe have been introduced intentionally (Keller et al. 2011). Intentional introduction can be an advantage for the invading plant, as they are more likely to be better adapted to the conditions at their destination, because its ability to grow is necessary for it to be a commodity. Additionally, intentional introduction increases propagule pressure, particularly for popular plants.

The time since introduction has a positive correlation with invasiveness, as species that have been present longer have larger ranges. This is a result of the species fulfilling more life cycles and having the time to spread further. Species that have been present for extended periods of time also tend to have multiple introductions, which increases propagule pressure. Furthermore, alien species that have a large native range are more likely to be adapted to climate conditions where they are introduced (Keller et al. 2011).

However, not all introduced species become problematic. According to the ‘Tens rule’, only 10% of introduced species escape to the wild, while 10% of these go on to establish themselves and spread, and 10% of these are deemed ‘invasive’ (Henderson et al. 2006). Although the applicability of this rule is contextual, it illustrates the barriers an alien species has to overcome to become invasive. The species has to be able to grow beyond cultivation, spread and propagate in large enough numbers to sustain a population.

To infer common traits of alien invasive species Pyšek and Richardson (2007) examined 18 different comparative multispecies studies. Their findings suggest that invasive traits often are contextual, as many of the studies contradict each other or have ambiguous findings. However, some general traits were identified: The ability to form clones and vegetative propagation combined with good lateral growth. Additionally, Invasive species tend to have either shorter or longer life cycles than their native counterparts, as they either arrive early and mature rapidly or outperform and displace the native vegetation by growing old. Furthermore, short-lived species perform better in disturbed habitats while the long-lived species thrive in semi-natural vegetation. Smaller seeds also positively impact invasion success as this usually correlates with increased seed output, ease of dispersal with wind and long persistence in soil. Additionally, high specific leaf area is associated with invasiveness.

High levels of human disturbance are characteristic of invaded areas as this leads to loss of native species, enabling non-native species to establish themselves with less competition and with increased availability of resources. Furthermore, human disturbance increases propagule pressure and facilitates more pathways of introduction (Keller et al. 2011).

1.2. *Solidago canadensis*

Solidago canadensis, commonly known as 'Canadian goldenrod' in English and 'kanadagullris' in Norwegian, is a rhizomatous perennial native to North America. In its native region it is commonly found on abandoned farmland, infrequently grazed pastures, waste areas and tall-grass prairies. It forms 30-150 cm tall erect aerial stems that are spaced 5-12 cm apart, with a covering of fine hair on the apical part of the stem. The leaves are alternately arranged, three-nerved, and have an elliptical lancet shape. Additionally, the leaves can be toothed and covered with fine hair. Its flowers are 2-3 mm yellow heads that branch above the foliage in clusters (Werner et al. 1980).

Inflorescence is developed in its second growth season (Bender et al. 2000), although it can occur in the first growth season if grown in glasshouse conditions (Werner et al. 1980). Inflorescence lasts from August until October (Lid & Lid 2005; Mossberg & Stenberg 2012). The flowers are self-incompatible. A large range of insects can pollinate it, although honeybees, bumblebees, soldier beetles and syrphid flies are their main pollinators (Werner et al. 1980). It has small, wind-dispersed seeds that ripen about 6 weeks after inflorescence (Pavek 2011).

It is a hemicryptophyte, where its aerial stem dies down every winter. The rosette stage is brief, with shoot extension and formation of new roots happening in June. Rhizomes are normally formed at the base of the current year's aerial shoot, growing circularly outwards from a central area. New aerial stems grow from the apex of each rhizome the following spring and form a rosette of scale leaves by April (Werner et al. 1980). The new rhizomes with aerial stems are called ramets, which are interconnected clones that share nutrients and water. If a ramet has limited resources or is competing with a different species, the interconnecting ramets may reallocate resources to enable its continued growth. This enables the plant to expand its ramet network in tough conditions (Hartnett & Bazzaz 1985a). Ramets usually extend about 30 cm laterally from the mother plant every season, although it can increase this distance if growing in unfavorable conditions (Hartnett & Bazzaz 1985b). *Solidago canadensis* also utilizes allopathy to outcompete other plants (Dong et al. 2006b).

1.3. *Solidago canadensis'* impact in Norway

The Norwegian Biodiversity Information Centre has made a risk assessment of *S. canadensis* and deemed it an alien invasive species with "severe impact", the highest impact category. This position is mainly supported by its ability to invade and spread, whereas its effect on native species and nature types are more uncertain. It is able to reproduce sexually, and has a generation time of 5 years (Artsdatabanken 2012) .

According to Artsdatabanken (2012) *S. canadensis* has been present in Norway since 1762, imported as an ornamental plant in gardens. Additionally, unintentional introduction through ballast earth, grain import and as a stowaway in other types of commerce is likely. The first report of it escaping and establishing in nature was in

Ås in 1883, although its point of origin is unknown. However, granted that there may be unrecorded findings, the extent of its spread seems to be negligible until 1940 (Figure 1). From 1940 onwards it has spread north to Nordland and to the southern coast of Norway, although it is uncommon in Western- and Mid-Norway. Its main range is the lowlands and coastal areas from Østfold to Agder. It is expected to expand from its main range, although it has mostly filled its ecological and geographical range in Eastern-Norway. Unintentional spread of *S. canadensis* from private gardens is common, with several recorded cases a year (Artsdatabanken 2012).

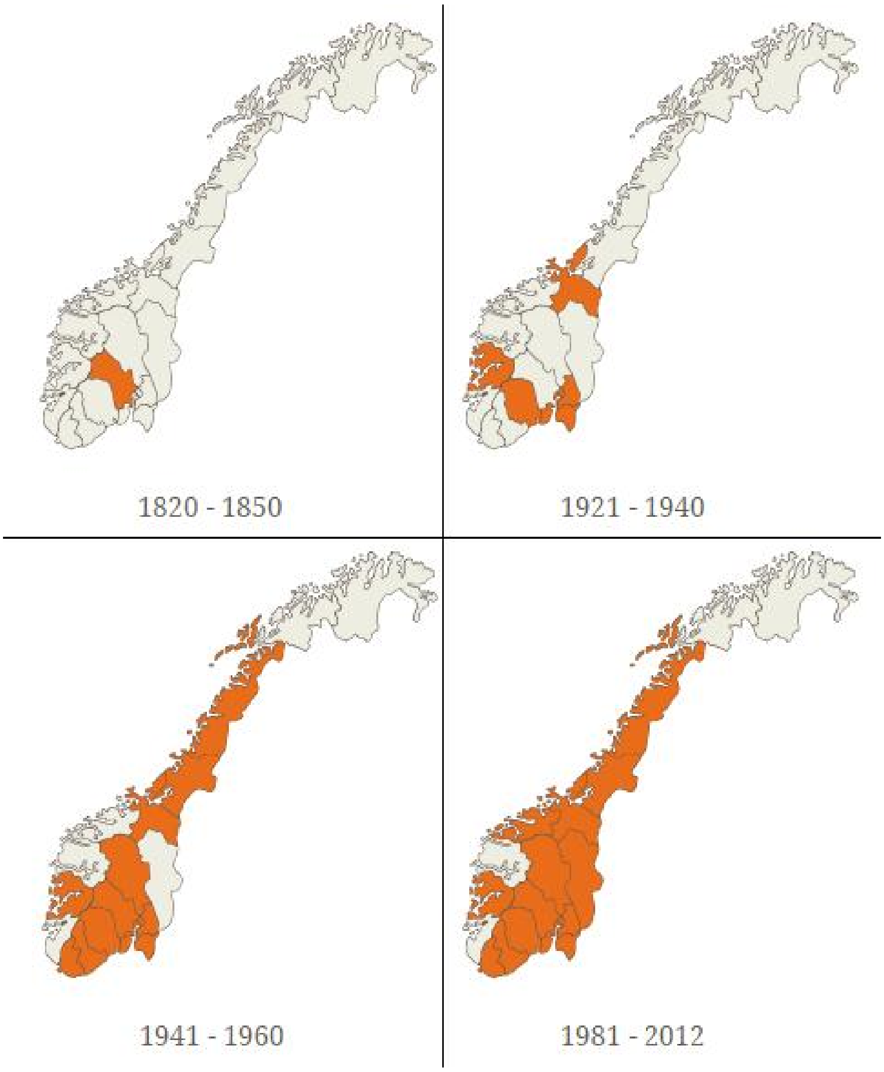

Figure 1: Dispersal history of S. canadensis in Norway (Artsdatabanken 2012).

It is mostly found at sites strongly influenced by human activity. It is often found at disturbed sites, such as industrial areas, junkyards, alongside sidewalks and crop fields as well as transitional areas between forests and cultivated land. It is one of the most common alien species along road verges and on cultivated land in its main range. Cultivated land that is no longer in use is especially vulnerable to *S. canadensis* as it is quick to establish itself, displaces native species and in turn alters the cultural landscape (Artsdatabanken 2012). *Solidago canadensis* alters the conditions of semi-natural grasslands, which is classified as a vulnerable habitat type, by contributing to overgrowing and thereby decreasing biodiversity (Norderhaug & Johansen 2011). Additionally, by invading road verges, it blocks grassland species from a potential substitute habitat and dispersal corridor (Auestad et al. 2011; Tikka et al. 2001).

With *S. canadensis* strong competitive ability, increasing range and invasion of valuable habitat types it is important to gain a deeper understanding of its life form to better manage its spread. The current management practice is mowing to hinder inflorescence, and application of herbicide at its early growth stage (Fløistad 2010).

1.4. Aim

I examined *S. canadensis* ability to survive at different burial depths and if it is possible to propagate it as cuttings.

The aim of this paper:

1) To examine the vitality of the roots at different rhizome lengths
2) To examine the vitality of the rhizomes at different burial depths
3) To examine the possibility of propagating *S. canadensis* as cuttings
4) To determine if there are differences between populations of *S. canadensis*
5) To use the findings above to better weed management

2. Method and materials

2.1. Three sites in Eastern Norway

I collected plant material from three areas in Eastern Norway: Ås, Røyken and Drammen. I recorded the incline, GPS-location, direction of sun exposure, soil type and species composition at each site. The soil type was determined by my own discretion according to 'Skjema for skjønnsmessig bedømmelse av jordarter' (Appendix 1). The species composition was graded from 0 to 3, where 0 is 'not found' and 3 is 'dominating species' (Appendix 2).

Climate

The climate data is based on normal temperature- and precipitation measurements from eKlima (2016) (appendix 3). The data was measured between 1961-1990 from weather stations in Ås, Røyken and Drammen (Figure 2). However, Røyken did not have a weather station, so the annual temperature and precipitation normal has been interpolated (eKlima 2016).

Figure 2: Overview map showing the population locations and weather stations.

Drammen had the warmest annual normal temperature with $5.5C^{O}$, although its proximity to the Drammen River may give the area a colder microclimate and a higher humidity (Table 1). Røyken was the coldest and wettest site, with an annual normal temperature of 5.2Cº and an annual normal precipitation of 880mm. Ås was the driest with 785mm in annual normal precipitation.

Table 1: Temperature- and precipitation normal between 1961-1990 for Ås, Røyken and Drammen.

Normal 1961-1990	**Ås**	**Røyken**	**Drammen**
Annual temperature	5.3Cº	5.2Cº	5.5Cº
Warmest month	July, 16.1Cº	July, 15.9Cº	July, 16.8Cº
Coldest month	January, -4.9Cº	January, -5.6Cº	January, -5.6Cº
Annual precipitation	785mm	880mm	830mm
Wettest month	October, 110mm	October, 113mm	October, 100mm
Driest month	February, 35mm	February, 42mm	April, 43mm

Ås

The *S. canadensis* population was located on a roadside sloping down to the highway, Riksvei 23, near the Vassum tunnel (Figure 3). The construction of the road was finished in June 2000 (Statens Vegvesen 2015). The road is highly trafficked, with a speed limit of 70 km/h.

Figure 3: Panoramic picture of the S. canadensis population in Ås with surrounding vegetation. Riksvei 23 is seen to the right.

The area was heavily vegetated, and had a diverse collection of species with 38 different plant species identified (Appendix 2). In addition to *S. canadensis,* the dominating species were several species of grass and *Tussilago farfara.* On the upper side of the slope the area was densely populated by *Alnus incana,* which provided partial shade.

The *S. canadensis* population was located in an area covering about 5x25 meters, where *S. canadensis* covered roughly 80% of the area (Figure 4). The height of the *S. canadensis*-plants was generally 80-100cm and grew close together in clusters. The area had an average incline of about 25 degrees, with a southeastern sun exposure.

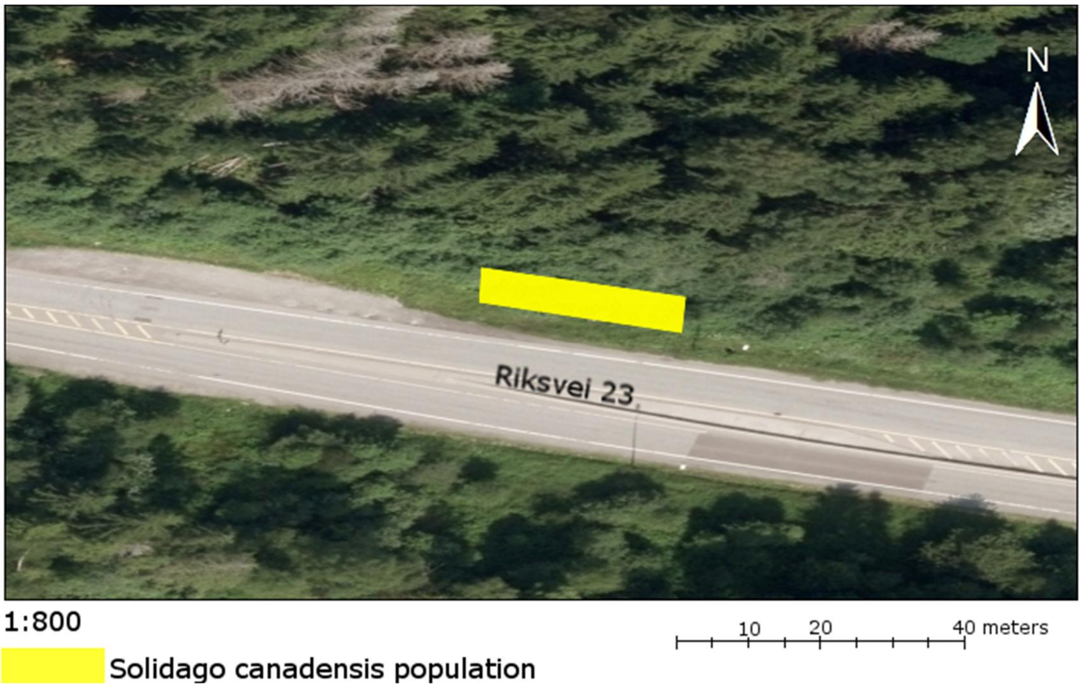

Figure 4: Aerial photo of the S.canadensis population and its surrounding area in Ås.

The soil was generally silty and sandy clay that was compacted. The soil was covered with decaying plant material, primarily from *S. canadensis*, which contributed to keeping the soil moist.

Røyken

The population was located at a disturbed soil site, near a municipal road with little traffic (Figure 5). Riksvei 23 runs about 30 meters south of the population. The site, and the adjoining areas to the west and the east, is a dumping ground for uncontaminated excess soil from construction sites in the Oslo-area (Golder Associates 2015).

Figure 5: Panoramic picture of the S. canadensis population in Røyken with surrounding vegetation. Bråsetveien is seen to the left.

The area was sparsely vegetated, although it had a diverse collection of species with 29 identified plant species (Appendix 2). Other than *S. canadensis*, the dominating species were several species of grass, *T. farfara* and *Lathyrus pratensis.*

The *S. canadensis* covered about 50% of the area and was taller than the other vegetation. Its average length was about 60-80cm. The population covered a 12x6 meter area and had a southeastern sun exposure, with an average incline of about 15 degrees (Figure 6).

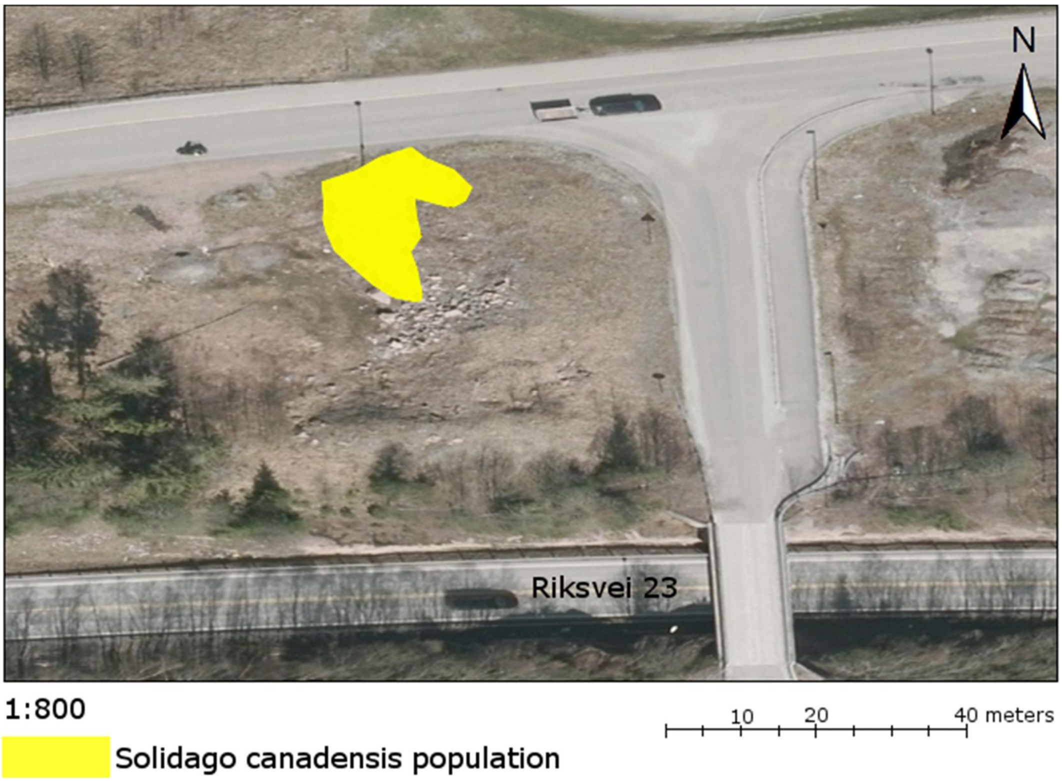

Figure 6: Aerial photo of the S.canadensis population and its surrounding area in Røyken.

The soil had varying texture, ranging from almost pure sand to sandy clay. The soil also contained varying amounts of gravel, with the roots of the *S. canadensis* growing around the stones (Figure 7). The soil was covered with decaying plant material from grasses and *S. canadensis,* which contributed to keeping the soil moist.

Figure 7: The underside of a S. Canadensis-root system from a root clump gathered in Røyken. The soil has been removed.

Drammen

The population was located in a flowerbed along Martin Knutzens gate, a municipal road (Figure 8). The flowerbed is Drammen municipalities' property, but has most likely been used as a flowerbed by one of the nearby properties. It is now untended and largely populated by weeds.

Figure 8: Panoramic picture of the Solidago canadensis population in Drammen with surrounding vegetation. Martin Knutzens gate runs parallel with the plant bed, while the Drammen River can be seen in the background to the left.

The area had the lowest species richness, with *Aegopodium podagraria* and *S. canadensis* being the predominant species and the remaining species were far less numerous (Appendix 2). The *S. canadensis* covered about 40 % of the area, and had an average height of about 60-80cm (Figure 9). The population covered a 10x4 meter area and had a western sun exposure, with an average incline of about 27 degrees.

Figure 9: Aerial photo of the S.canadensis population and its surrounding area in Drammen.

The soil was a sandy clay, and was overall uniform in texture. The entire flowerbed was covered with an estimated three cm layer of bark.

2.3. Inspection of population

To determine the size and depth of the root system, I conducted an inspection of the *S. canadensis* population in Ås at the end of May 2015. I discovered that the root systems were generally very close to the surface, normally around 5cm and no deeper than 15cm. Additionally, the root system was extremely clustered with rhizomes and roots packed closely together (Figure 10). Therefore, I decided to retrieve the soil clumps from a depth of 20cm with a diameter of 50cm to ensure that enough plant material was contained in each soil clump,

Figure 10: Root system of a S. canadensis retrieved from Ås.

The plants grew in clusters of roughly 10 to 20 stems in close proximity, with varying space between the clusters. As *S. canadensis* have ramets that can spread up to 2,5m away from the mother plant (Werner et al. 1980), some patchiness of the populations were expected. Therefore, as long as the plants were in closer proximity to each other than 2,5m they were considered to be part of the same mother plant.

2.4. Retrieval and planting

I retrieved the plant material on the 17th, 18th and 19th of June 2015, one day for each population. Five soil clumps were retrieved at each location, from clusters of plants that looked healthy and had a large amount of stems. The soil clumps were excavated with a shovel and put in plastic bags where they were numbered. To avoid the plant material drying out I planted it on the same day as it was retrieved.

Both the rhizomes and the cuttings were planted in 'pot soil with clay'. The soil came from 80-liter bags, where 20kg was dry matter, containing 85% sphagnum peat, 10% sand and 5% granulated clay. Its pH-value was 5.5-6.5, and had a fertilizer mixture consisting of 1kg PG mix and 4.5kg chalk dolomite.

2.5. Experimental design

Rhizomes

The rhizomes were cut into 5 and 10cm pieces, with their existing roots still attached. The pieces were buried at three depths:

- Surface, but covered with 0.5cm of soil
- 10cm
- 30cm

The experiment was conducted outside to recreate a natural environment. Because desiccation can occur when rhizomes are placed on top of the soil surface (Rask & Andreasen 2007; Weber 2011), this experiment tried to recreate optimal natural conditions for rhizome regeneration by covering the rhizomes at 0cm burial depth with soil. Each rhizome piece was planted in a 25 liter, square pot. To minimize edge effects, I placed pots filled with soil along the border of the pots on the western side, as this is the most sun-exposed side. There were 5 replicates for each combination of soil depth, rhizome size and population; in total 90 replicates.

The pots were placed randomly in a grid of 6x15 pots, were I used a random number generator to assign each pot its position (Figure 11). The pots were watered as needed, usually about 15 minutes every day, with a watering system of nozzles placed over the pots.

Figure 11: The planted and randomly assigned pots with rhizomes at the start and the termination of the experiment.

The height of the tallest shoot was recorded from the first sprouting, afterwards it was recorded on an average of every third day. For the rhizome-experiment, the recordings were taken from June 24th to August 12th, 2015.

The termination of the experiment lasted 3 days, from August 12th to August 14th, 2015. The plants were carefully removed from the pots, to keep the roots as intact as possible. The number of aerial shoots were recorded for all depths. For the rhizomes buried at 10 and 30cm, I also recorded the number of shoots that did not reach the surface and their length, and the number of branching shoots from the underground shoots. Shoots that had inflorescence were also counted. All the root systems were photographed upon termination.

The development of the root system was judged visually on a scale from 0-6, where 0 is dead and 6 is excellent root development (Table 2 and Figure 12).

Table 2: The different root development stages for rootstocks.

Value	**Explanation**
0	Dead
1	Living rhizomes, but no new root development
2	One to two new roots, but no root branching
3	More than two new roots, with root branching
4	Considerable root development with many new roots and root branching
5	Excellent root development with the roots filling most of the pot, and some new rhizomes.
6	Excellent root development with the roots filling most of the pot, and development of thick rhizomes.

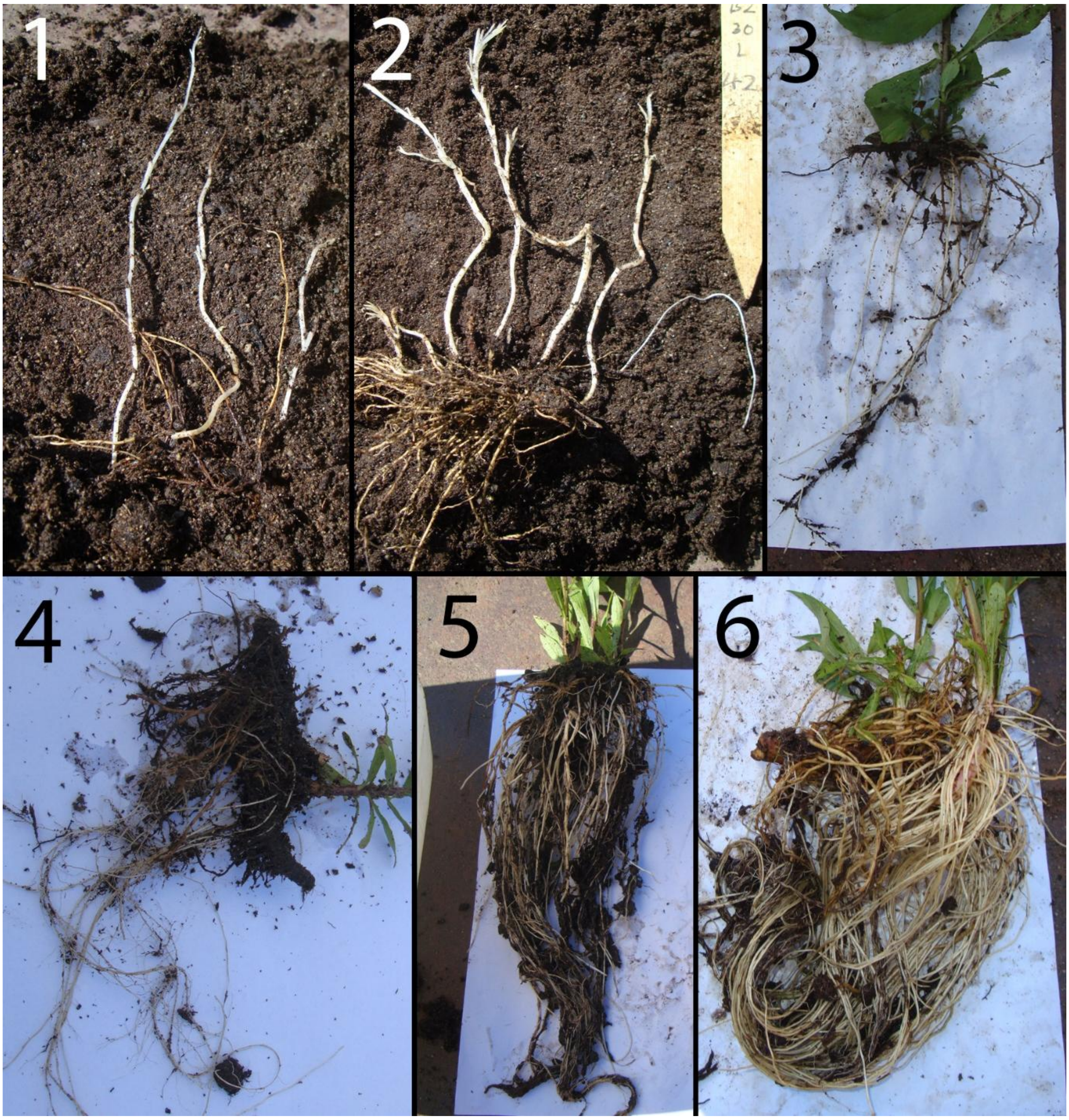

Figure 12: The different root development stages for rhizomes, from top left is root development stage 1 (living rhizome) to 6 (excellent root development).

Cuttings

The cuttings were taken from stems from the same soil clumps as the rhizomes. The stems were cut into 15cm pieces, from above the first pair of leaves on the stem. These 15cm cuttings were potted individually, where the bottom 5cm of the cuttings were pushed into the soil in the middle of each pot. There were 15 replicates for each population: 45 replicates in total. I used a random number-generator to assign each pot its position. In addition, pots were placed around the entire edge to counteract edge effects (Figure 13).

Figure 13: The planted and randomly assigned pots with cuttings.

The height of the tallest shoot was recorded from the first sprouting, subsequent recordings were taken every third day, on average. For the cuttings-experiment, the recordings lasted from July 1st to August 12th, 2015.

The termination of the experiment lasted 3 days, from August 12th to August 14th, 2015. The number of shoots and the development of the root system was recorded after carefully removing the cuttings from the pot. All the cuttings were photographed upon termination.

The development of the root system was judged visually on a scale from 0-6, where 0 is dead and 6 is excellent root development (Table 3 and Figure 14).

Table 3: The different root development stages for cuttings.

Value	Explanation
0	Dead
1	Cutting is alive, but without callus
2	Cutting is alive, with developed callus
3	One to two roots, without branching
4	More than two roots, with branching
5	Considerable root development, with many roots and significant branching
6	Excellent root development. Numerous long roots with significant branching

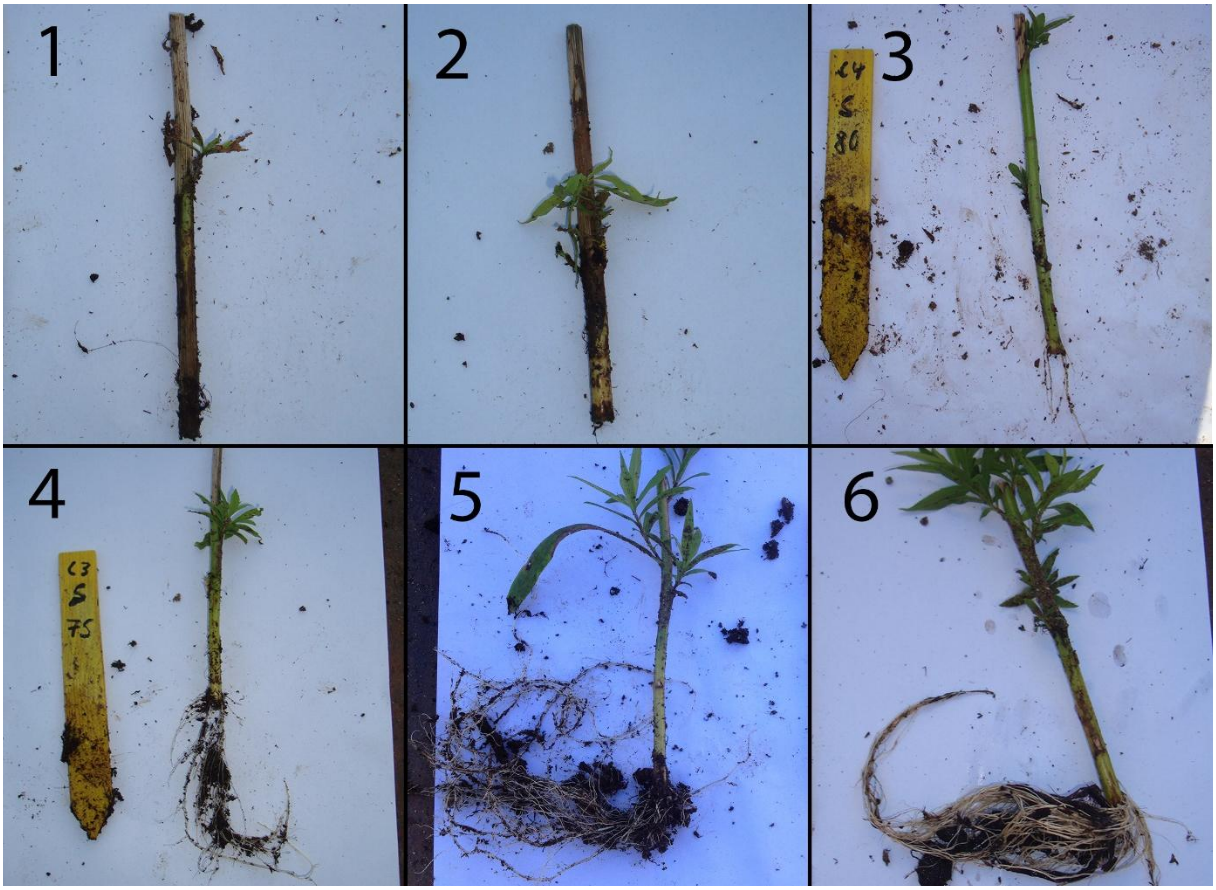

Figure 14: The different root development stages for cuttings, from top left is root development stage 1 (living cutting) to 6 (excellent root development).

2.6. Statistics

To assess the effect from experimental design I used R (version 3.2.3.) as the main statistical tool. For the estimations a Bayesian hierarchic model was used to allow for the experimental design as well as estimating the various treatments effect. In this study I used ‘integrated nested Laplace approximations’ (INLA) (Rue et al. 2009). For all analyses, the mother plant was included as an independent and identically distributed random contribution, whereas the population and treatments were identified as fixed effects central to the investigation. The response variables identified for the individual research question were assumed binomial, meaning presence or absence. For the binomial response variables, we estimate the probability of a positive outcome, i.e. success, conditioned on the treatments.

For root survival we identified root development stage higher than 0 as alive, i.e. success. The probability of survival was estimated for the different populations, with burial depth and rhizome length as treatments.

Subsequent analyses were conditioned on that the roots survived. Firstly, to estimate the probability of a root being well-developed according to:

- Root development stage 1, 2 and 3 = some root development
- Root development stage 4, 5 and 6 = well-developed root system

The presence of a well-developed root system was predicted based on burial depth and the number of aerial shoots.

Lastly, the data used for the analysis was subset to rhizomes that had aerial shoots. The presence of shoots that had developed inflorescence was then predicted based on aerial shoot length.

3. Results

3.1. Root survival

Over half the rhizome pieces from Ås were dead at the end of the experiment, and the rhizomes generally had poorer root development than the rhizomes from the other two populations (Figure 15). The Røyken-population had the highest quantity of rhizomes with well-developed root systems.

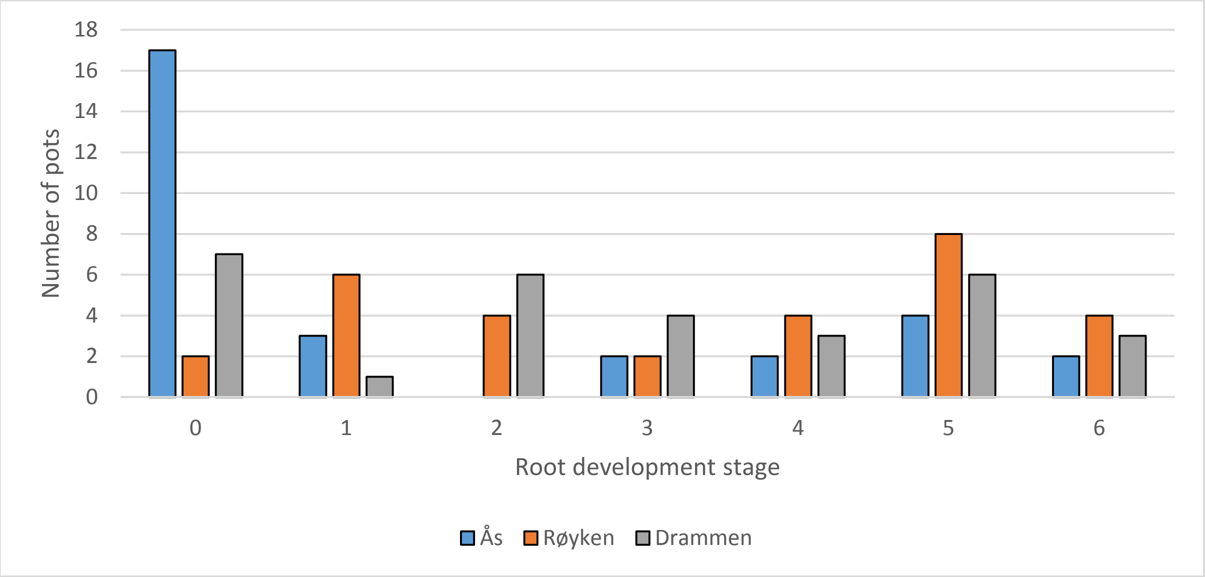

Figure 15: Number of pots at the different root development stages, where 0 is dead and 6 is excellent root development (Table 2). 30 pots each from Ås, Røyken and Drammen.

Rhizome length has no significant effect on the survivability (Table 4). The credibility interval ranges from negative to positive effect, and therefore includes no effect (0). Increasing burial depth has significant negative effect on survivability. Rhizomes from Ås have significantly worse survivability, while Rhizomes from Røyken have significantly better survivability.

Table 4: The intervals with the highest 95% credibility for survival of rhizomes. Intercept is 5cm rhizomes buried at 0cm from the Drammen population. Significant effects are bold.

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

The mean probability of survival is highest for the rhizomes from Røyken and lowest in Ås (Table 5). Survivability is fairly similar for the Drammen and Røyken population at 0cm burial depth, but sinks with increasing burial depth for all populations.

Table 5: Predicted probability of surviving for different burial depths and populations.

Burial depth	**Population**	**0.025 quantile probability**	**Mean probability**	**0.975 quantile probability**
0cm	Drammen	0.831	0.942	0.991
10cm	Drammen	0.502	0.732	0.906
30cm	Drammen	0.357	0.605	0.824
0cm	Røyken	0.949	0.977	0.999
10cm	Røyken	0.771	0.919	0.989
30cm	Røyken	0.660	0.862	0.976
0cm	Ås	0.496	0.744	0.928
10cm	Ås	0.133	0.335	0.578
30cm	Ås	0.069	0.220	0.435

3.2. Root development

There is little difference in root development between the populations at 0cm burial depth (Figure 16). Two rhizomes pieces from Ås and one from Drammen died at 0cm burial depth. All the 5cm rhizome pieces from Ås were dead at 10cm burial depth, while the 10cm rhizome pieces had significantly worse root development than the other populations. Additionally, nearly all the rhizome pieces from Ås were dead when buried at 30cm depths, while several rhizome pieces from Røyken and Drammen were still viable.

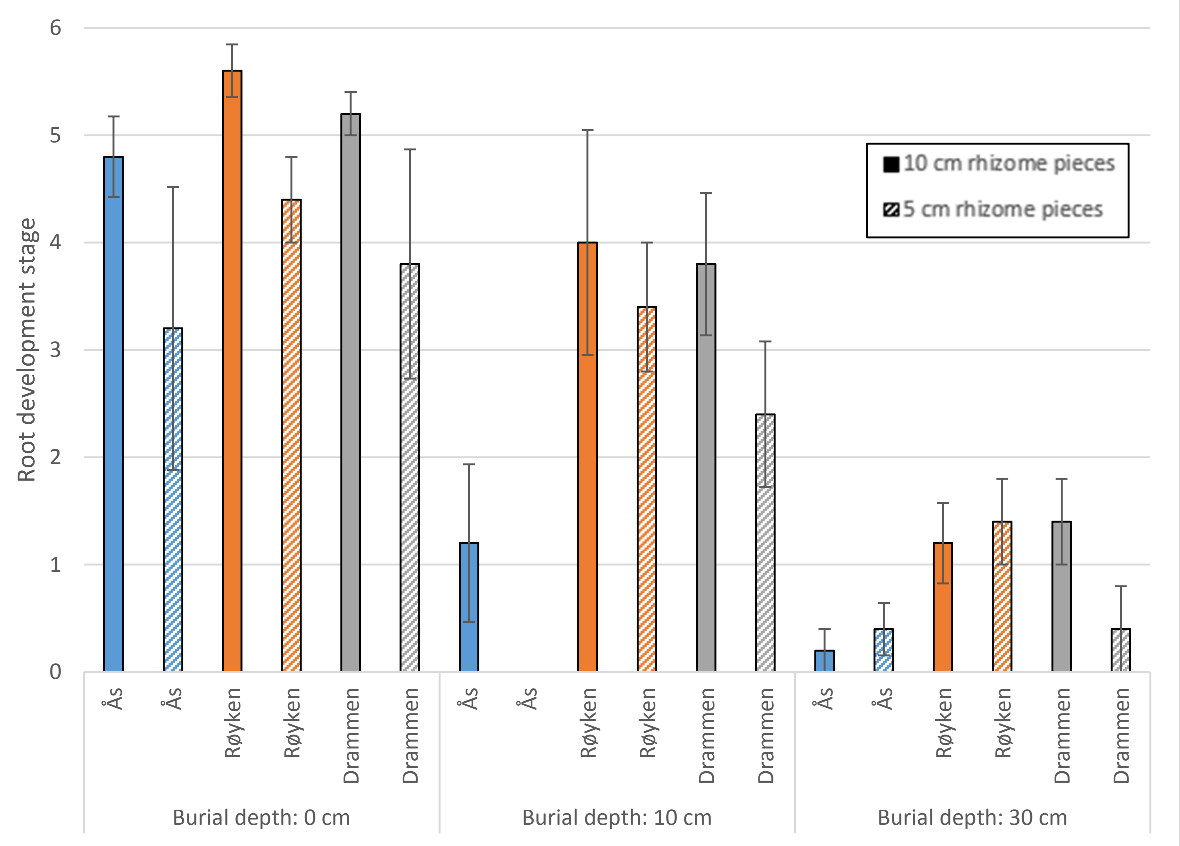

Figure 16: Average root development for different populations, burial depths and rhizome piece lengths, where 0 is dead and 6 is excellent root development (Table 2). Each category is an average from 5 pots. Standard error bars are included.

There were large differences in below-ground shoot growth between populations for rhizomes planted at 30cm (Figure 17). Most of the rhizomes from Ås were dead, and only one 10cm rhizome piece had an aerial shoot. The rhizomes from Røyken had good shoot growth regardless of rhizome size, and none of the rhizome pieces were dead. The 10cm rhizome pieces from Drammen had good shoot growth, while the majority of the 5cm pieces were dead.

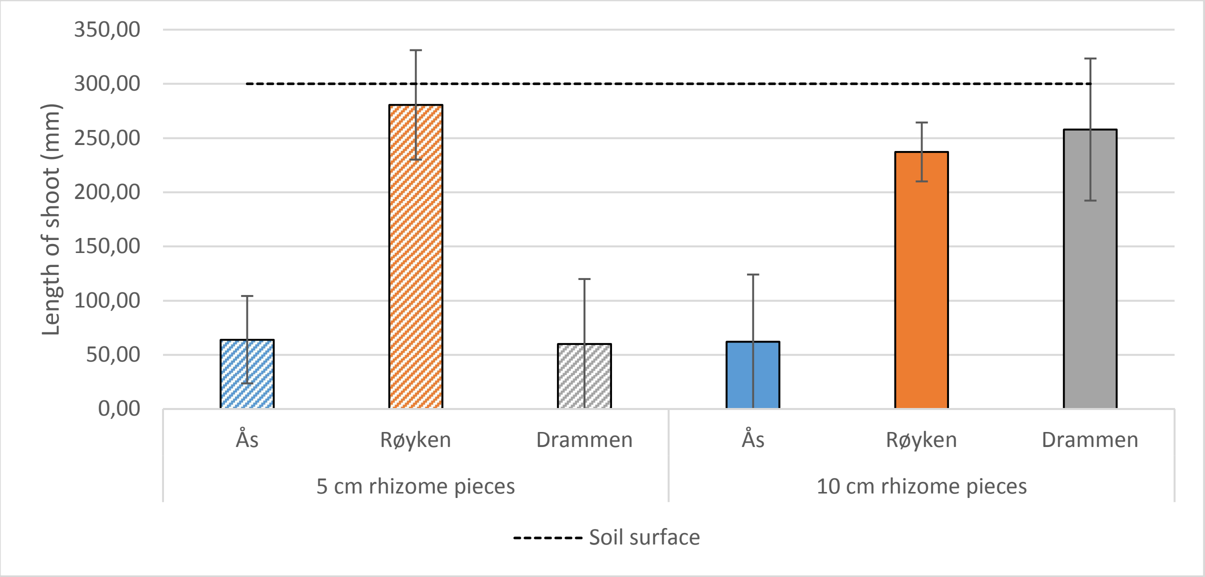

Figure 17: Average length of longest shoot for rhizome pieces at 30 cm burial depth. The average is based on 5 pots for each category, 30 pots total. Standard error bars are included.

Burial depth does not have any obvious effect on achieving a well-developed root system (given that the rhizome has survived), as all the credibility intervals contain no effect (0), although there is a large degree of uncertainty at 30cm burial depth (Table 6). Aerial shoots however have a significant positive effect towards achieving a well-developed root system.

Table 6: 95% credibility interval for achieving a well-developed root system given that the rhizome has survived. Intercept is 0cm burial depth. Significant effect is bold.

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

At 0cm burial depth the Røyken population had more aerial shoots (Figure 18). However, at 10cm burial depth the results were fairly similar for Røyken and Drammen, while the Ås population had far less aerial shoots from the long rhizome pieces and no aerial shoots from the short rhizome pieces. At 30cm burial depth the long rhizome pieces from Drammen had the most aerial shoots.

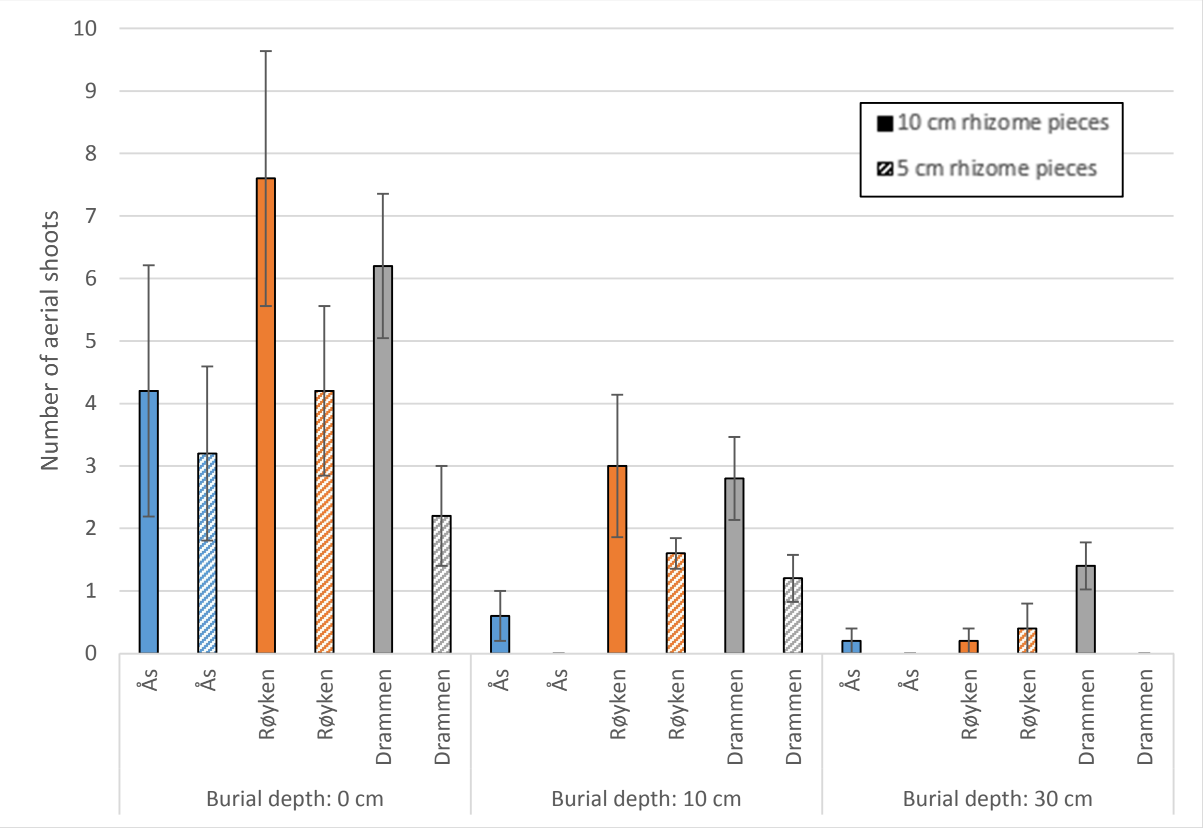

Figure 18: Average number of aerial shoots per pot for different populations, burial depths and rhizome piece lengths. Each category is an average from 5 pots. Standard error bars are included.

The probability of a rhizome achieving a well-developed root system increases with the number of aerial shoots (Figure 19). At 2 aerial shoots, the rhizome has a 50% estimated probability of attaining a well-developed root system. At 4 aerial shoots the estimated probability is over 95%.

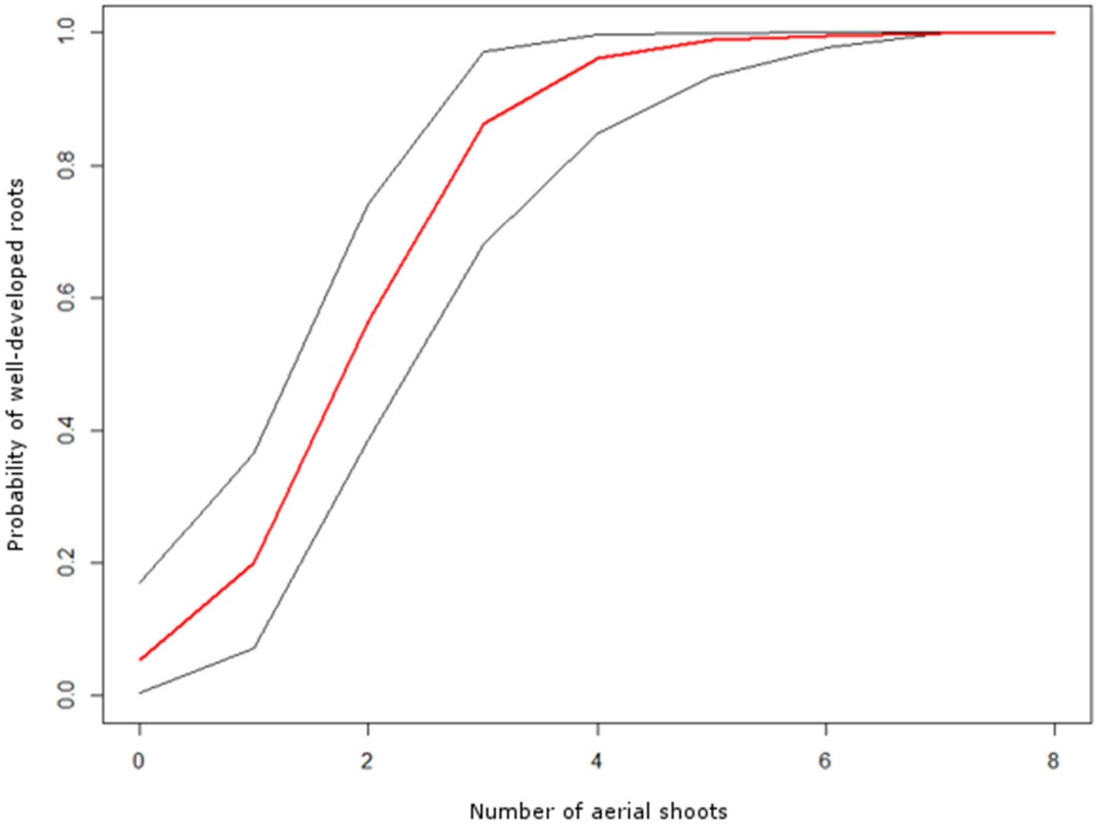

Figure 19: Estimated probability of attaining a well-developed root system with increasing amounts of aerial shoots. 0.025 and 0.975 quantile probability is included, while the red line is mean probability.

Røyken and Drammen had 21 rhizomes with aerial shoots, while Ås had 11. The mean length and number of aerial shoots per rhizome were calculated given that the rhizome had aerial shoots (Figure 20). Mean length of longest aerial shoot and number of aerial shoots per rhizome is similar for the Ås and Røyken populations, with both having close to 500mm mean length and 4 shoots. The Drammen populations had a lower mean length and number of shoots, close to 400mm and 3 shoots. The height of the tallest shoot also increased with increasing root development.

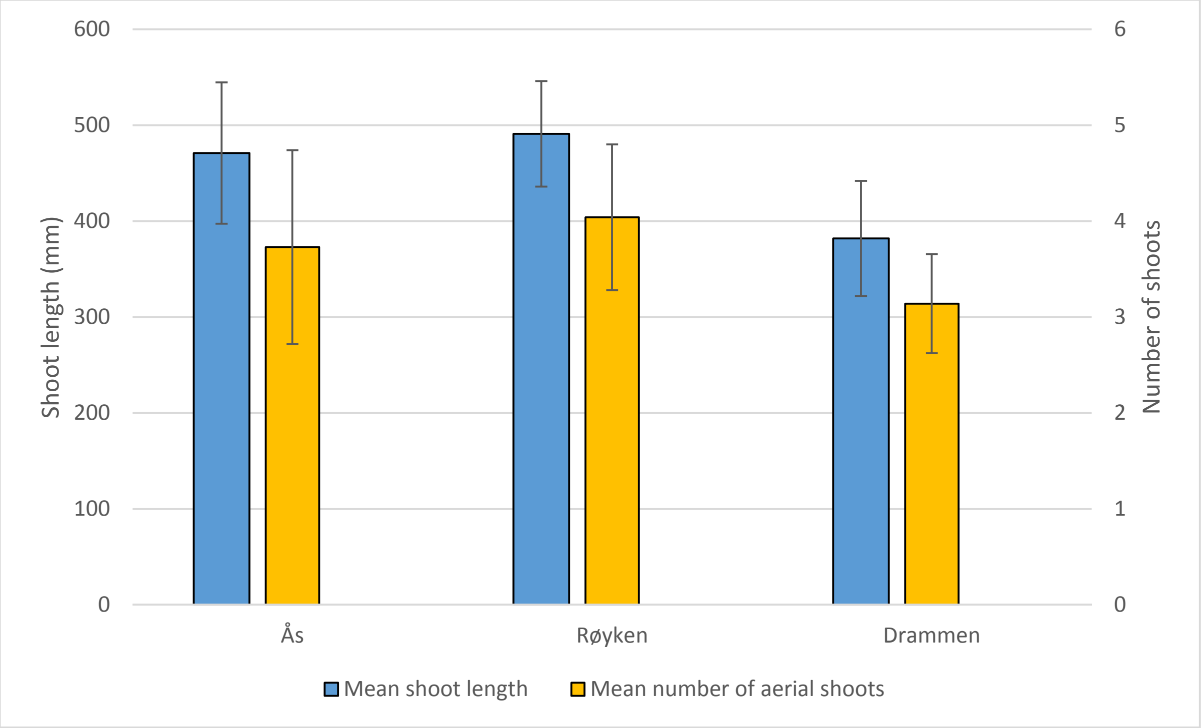

Figure 20: Mean length of the tallest aerial shoot for the different populations, given that they have an aerial shoot, including mean number of aerial shoots per pot. Standard error bars are included.

3.3. Inflorescence

Only rhizomes at root development stage 4, 5 and 6, i.e. well-developed root systems, had inflorescence. At root development stage 5 there was, on average, 1 shoot with inflorescence per pot, while at root development stage 6 there were about 2.5. However, only one plant at root development stage 4 had inflorescence, and it had the tallest shoot of all the plants at that root development stage. The Ås population had 3 rhizomes with inflorescence, the Røyken population had 11 and the Drammen population had 9. The Ås population did not develop inflorescence at 10cm burial depth, while three individuals from the Røyken population and one from the Drammen population did. None of the rhizome pieces buried at 30cm developed inflorescence.

Estimated probability of inflorescence increased gradually with shoot height (Figure 21). The largest increase in mean probability of inflorescence is from 500 to 600mm aerial shoot length, where it increases from about 20% to 90%. At 660mm, the mean probability of inflorescence is 98%.

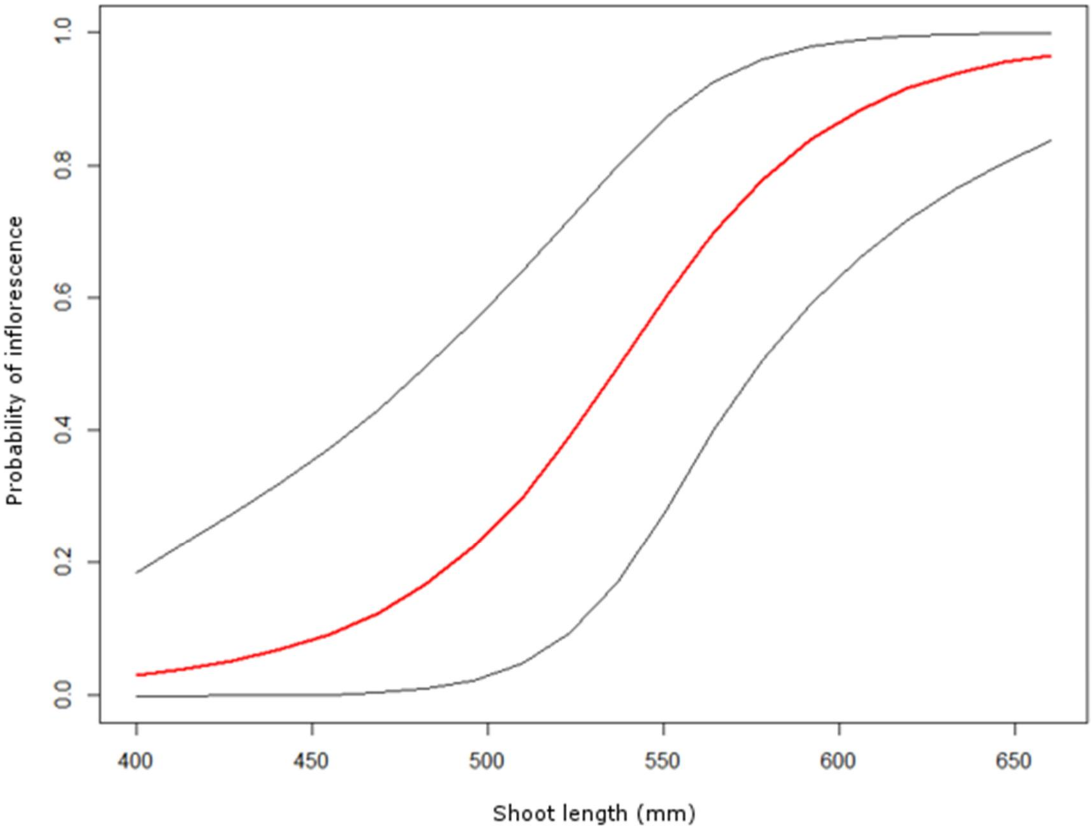

Figure 21: Estimated probability of developing inflorescence with increasing aerial shoot length. 0.025 and 0.975 quantile probability is included, while the red line is mean probability.

3.4. Cuttings

The cuttings generally had better root development than the rhizomes (Figure 22). There was a large difference between the root development of the rhizomes and the cuttings for the Ås population. The Røyken population had little difference in root development between rhizomes and cuttings, while the cuttings were approximately one stage better for the cuttings in Drammen. The cuttings had high survivability, with just 2 dead cuttings from the Røyken population.

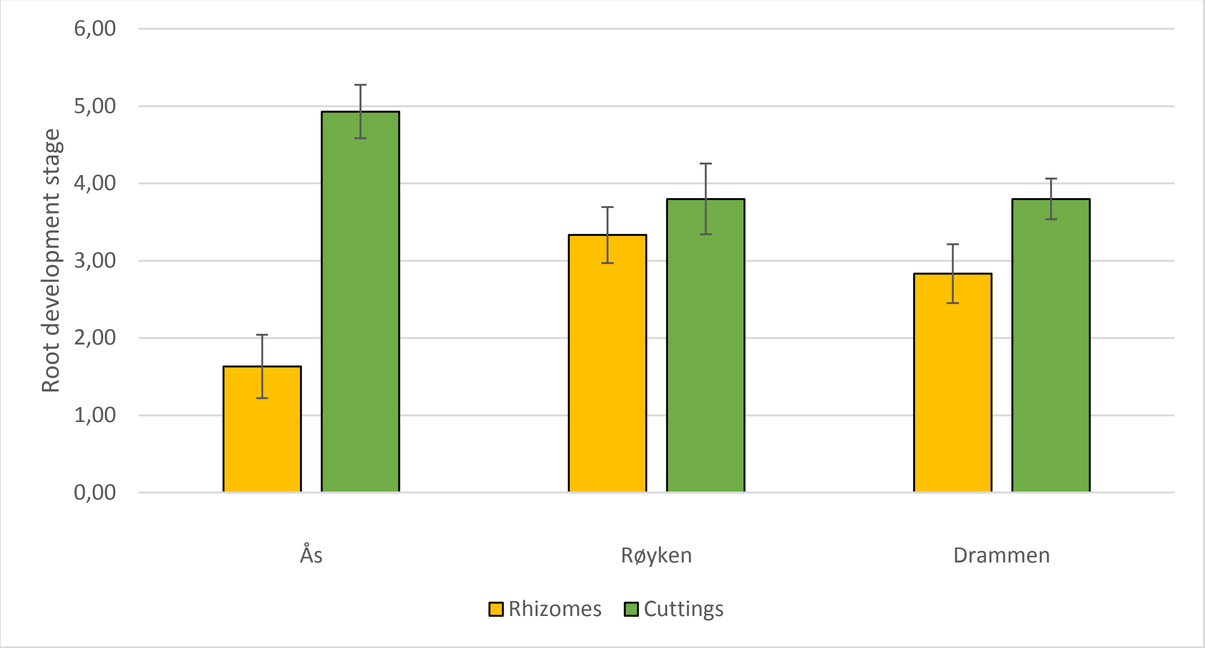

Figure 22: Comparison of average root development for rhizome pieces and cuttings between populations for rhizomes (Table 2) and cuttings (Table 3), where 0 is dead and 6 is excellent root development. For rhizome pieces, each category is based on an average of 30 pots. For cuttings, each category is based on an average of 15 pots.

4. Discussion

The survivability of the rhizomes for the different populations was, from best to worst: Røyken, Drammen and then Ås. The significant difference in survivability and growth between the rhizomes from Røyken, Drammen and Ås may have a number of reasons. *Solidago canadensis* is known to be a species with large genetic variance between populations in Europe (Weber 1997), although it is uncertain how much genetic variance there is between the different populations in this experiment. Herbivory could also be an explanation, as it has shown to negatively affect *S. canadensis* growth and the rhizomes ability to store biomass (Schmid et al. 1990). However, this is unlikely as the herbivore pressure on *S. canadensis* in Europe is low (Kabuce & Priede 2010). According to Werner et al. (1980), *S. canadensis* tends to invest more biomass in sexual reproduction than vegetative reproduction as the plant ages. This could imply that the Ås population is older, in that it uses more energy to produce inflorescence and stores less energy in its rhizomes. Lastly, the Ås population may have a trade-off where the aerial shoots store more energy and have a stronger regenerative ability than the rhizomes. Although the criteria for judging root development is different for cuttings and rhizomes, the Ås population had a larger difference in root development between cuttings and rhizomes compared to the other populations. The root development for the cuttings were also better in Ås compared to Drammen and Røyken. Furthermore, several leaves from the Ås population developed roots (observation, August 14, 2015; Figure 23), which has also been achieved *in vitro* with a growth medium (Li et al. 2012). The heightened activity in root development of the Ås populations cuttings and leaves might indicate an increase in resource allocation which increases adventitiousness. Although there appears to be a linear relationship between allocation of resources to sexual and vegetative growth in *Solidago*-species (Schmid & Weiner 1993; Schmid et al. 1995), there may be a trade-off with vegetative growth between rhizomes and shoots.

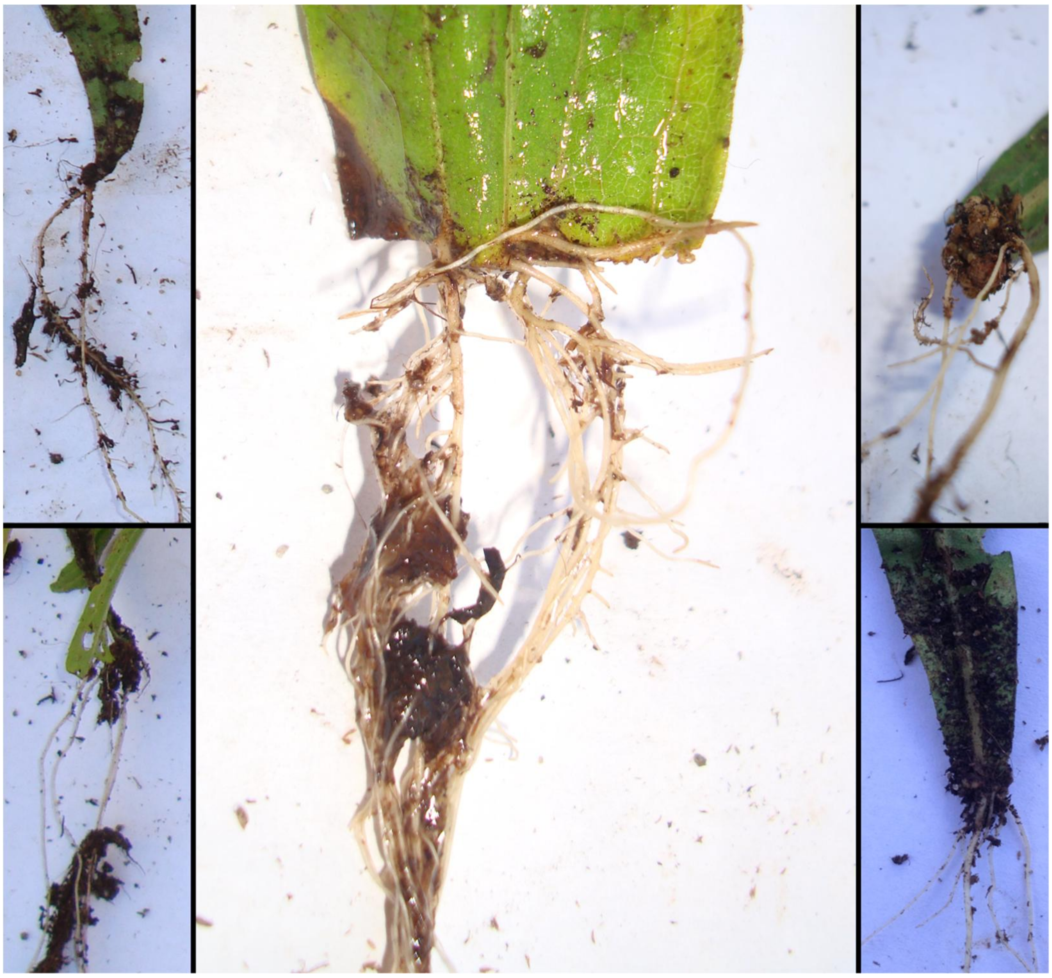

Figure 23: Leaves with root development.

Increasing burial depth has a significant negative effect on rhizome survivability. Decreasing survivability or vigor 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 (Dalbato et al. 2014; Klimes et al. 1993; Rask & Andreasen 2007). There was almost no difference in survivability between the populations at 0cm 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 amount of dead rhizomes and differences in survivability between the populations were exasperated. The rhizomes buried at deeper depths were reliant on using their stored energy to produce aerial shoots, although none of the burial treatments were fully effective at hindering sprouting for any of the populations.

The rhizome length did not have a significant positive effect on survivability. The size of the rhizomes could have an effect nonetheless, as the thickness of the rhizomes was not recorded for this experiment, which may have affected the results. However, by 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. Both the short and long rhizomes pieces from Ås were mostly dead, while only the short rhizomes from Drammen had a high mortality rate. The long rhizome pieces from Drammen had high survivability, as well as both short and long rhizomes from Røyken. In a burial experiment with *S. canadensis* by Weber (2011), the rhizomes were harvested in early April and cut into 3 and 6cm pieces. In Weber's experiment, all the 3cm rhizomes died at 5cm burial depth, while only half of the 6cm rhizomes died at the same burial depth. This may suggest that there are seasonal variations in stored energy of *S. canadensis*, as the rhizomes in Weber's study had a higher mortality rate at shallower burial depths, and were harvested earlier in the season. Early growth in *S. canadensis* is characterized by less carbohydrates in the rhizomes (Bradbury & Hofstra 1977). In conclusion, rhizome length may affect survivability for rhizomes with little stored energy at deep burial depths.

The amount of shoots has a significant positive effect towards attaining a well-developed root system, which is apparent when comparing average root development and number of aerial shoots at different treatments. However, at 30cm 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. However, the rhizomes from Ås and Drammen had underground shoots that were growing towards the surface. If the experiment had been terminated later, the rhizomes may have attained well-developed root systems, considering that burial depth does not have a significant effect towards attaining a well-developed root system. For *Mischantus sacchariflorus,* a rhizomatous grass that has ramet growth like *S. canadensis*, fragmentation and burial at 20cm 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, and store assimilates.

The probability of attaining a well-developed root system is over 95% when the rhizome has four aerial shoots. Given that the rhizome develops aerial shoots, the mean shoot height and number of aerial shoots are similar between the population. Both the Røyken and Ås population's rhizomes had an average of 4 aerial shoots and just under 500mm mean shoot size, while the Drammen population had 3 aerial shoots and around 400mm shoot size. Although the survivability was lower for Ås, the rhizomes that survived performed on average as well as the Røyken population. *S. canadensis* shoots grow fast and produce a great number of leaves early in its life cycle (Schmid et al. 1988). This suggests that once the rhizome has shoot growth that reaches the soil surface it performs well.

The height of the tallest shoot increased with increasing root development. The probability of inflorescence increases gradually between 400 to 650mm, meaning that the height inflorescence occurs at is not absolute. Nonetheless, inflorescence at 400mm is highly unlikely, with under 5% estimated probability. *Solidago canadensis* has shown to flower after reaching a certain size (Schmid & Weiner 1993; Schmid et al. 1995). While Schmid et al. (1995) measured this size relationship in stem volume, the probability of inflorescence has also shown to increase with stem height. Lastly, while *S. canadensis* normally flowers in its second year of growth when propagated from seeds (Bender et al. 2000), many of the clones grown from rhizomes in this experiment flowered in their first growth season.

4.1. Implications for management

There appears to be a significant difference in survivability between populations, yet this difference is not as apparent at 0cm burial depth. Although the mortality was higher with increasing burial depth, none of the burial depths were sufficient to completely stop the rhizomes from sprouting. Granted that they manage to sprout, they have a high likelihood of re-establishing themselves. 30cm burial depth may delay growth and stop development of inflorescence similar to mowing (Fløistad 2010), although this is uncertain given the experiments short timeframe. Preventing *S. canadensis* from spreading by seeds is important to manage its spread, as sexual reproduction may enable it to establish new populations, while rhizomes are more important to maintain existing populations (Dong et al. 2006a). Additionally, as it is a common invasive species in road verges in Norway (Artsdatabanken 2012), the undertow from passing cars might aid the wind dispersal of their seeds. However, the effect of deeper burial depth warrants more research, as the survivability had a marked decrease with increasing burial depth. Moreover, deep burial should be attempted earlier in the season to investigate the seasonal storage effect of the rhizomes. Lastly, considerations should be taken not to transport stems of *S. canadensis* while mowing, as cuttings have shown to re-establish themselves.

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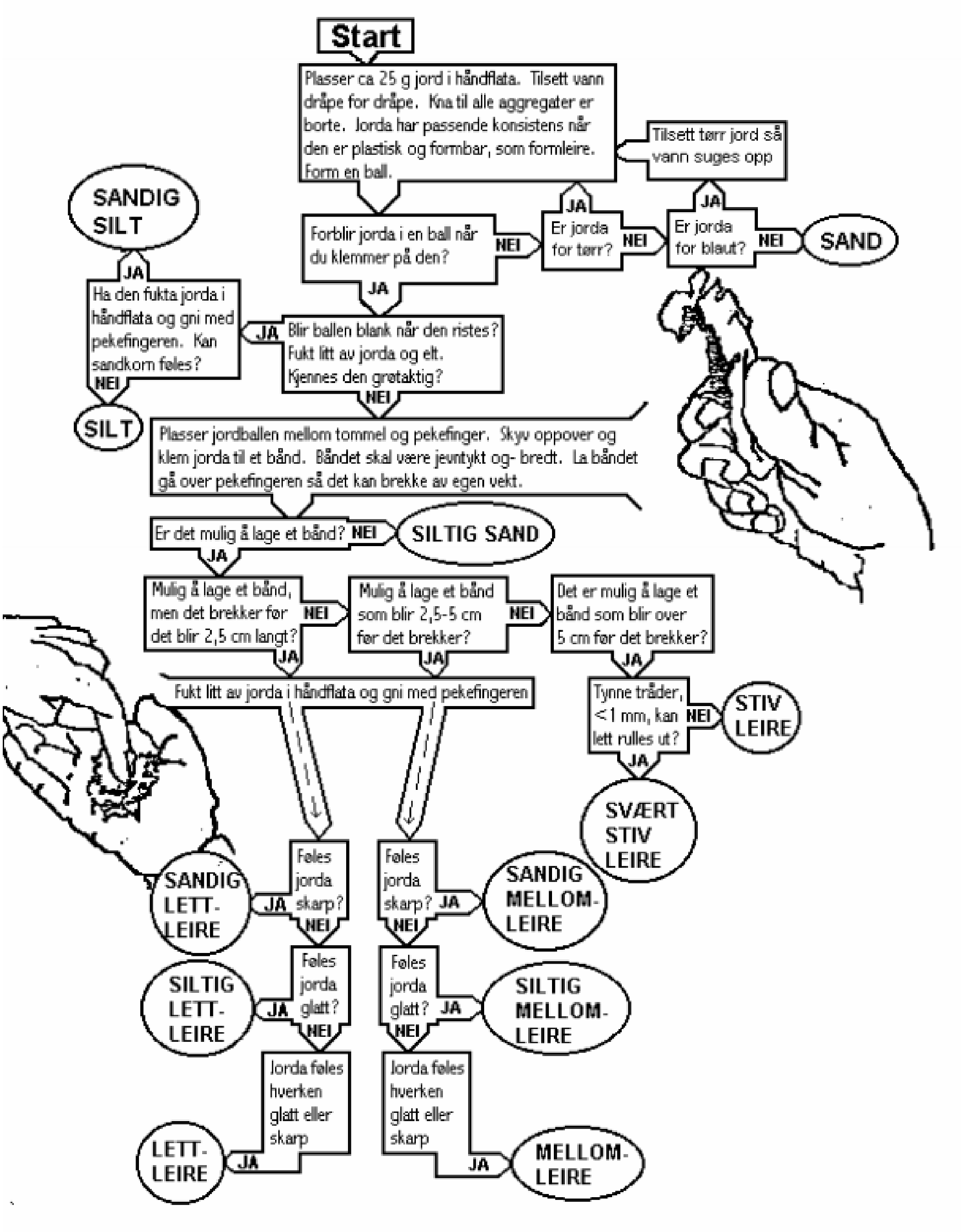
Appendix I - Skjema for skjønnsmessig bedømmelse av jordarter



Appendix II – Species composition at Ås, Røyken and Drammen

Prevalence of species:

- 0 = Not found
- 1 = Few individuals
- 2 = Several individuals
- 3 = Dominating species

SPECIES COMPOSITION				
Common name	**Scientific name**	**Prevalence**		
		Ås	**Røyken**	**Drammen**
Norway maple	*Acer platanoides*	0	0	1
Yarrow	*Achillea millefolium*	1	1	0
Ground elder	*Aegopodium podagraria*	0	2	3
Common lady's mantle	*Alchemilla vulgaris*	0	0	1
Grey alder	*Alnus incana*	3	0	0
Common wormwood	*Artemisia vulgare*	1	2	1
Wavy hair-grass	*Avenella flexuosa*	2	3	0
Downy birch	*Betula pubescens*	1	0	0
Scandinavian small reed	*Calamagrostis phragmitoides*	3	0	0
Bluejoint	*Calamgrostis* sp.	1	0	0
Fireweed	*Chamerion angustifolium*	0	2	0
Creeping thistle	*Cirsium arvense*	3	2	2
Spear thistle	*Cirsium vulgare*	3	0	0
Orchard grass	*Dactylis glomerata*	3	2	0
Tufted hairgrass	*Deschampsia cespitosa*	3	3	0
Couch grass	*Elytrigia repens*	2	0	0
Pale willowherb	*Epilobium roseum*	0	2	0
Field horsetail	*Equisetum arvense*	1	0	0
Wood horsetail	*Equisetum sylvaticum*	1	1	0
Red fescue	*Festuca rubra*	3	3	0
Mead wort	*Filipendula ulmaria*	2	0	0
Wild strawberry	*Fragaria vesca*	2	0	0
Ash	*Fraxinus excelsior*	0	1	0
Yellow bedstraw	*Galium verum*	0	1	0
Wood avens	*Geum urbanum*	1	0	0
Smooth hawkweed	*Hieracium laevigatum*	1	0	0
Hop	*Humulus lupulus*	1	0	0

Spotted St. Johnswort	*Hypericum macilatum*	0	1	0
Heath pea	*Lathyrus linifolius*	1	0	0
Meadow vetchling	*Lathyrus pratensis*	0	3	0
Rough hawkbit	*Leontodon hispidus*	0	0	1
Oxeye daisy	*Leucanthemum vulgare*	1	0	0
Honeyberry	*Lonicera caerulea*	0	0	1
Garden loosestrife	*Lysimachia vulgaris*	1	1	0
Honey clover	*Melilotus albus*	0	2	0
Timothy-grass	*Phleum pratense*	3	2	0
Common reed	*Phragmites australis*	3	0	0
Broadleaf plantain	*Plantago major*	2	0	0
Annual meadow grass	*Poa annua*	0	0	1
Japanese knotweed	*Reynoutria japonica*	0	0	1
Raspberry	*Rubus idaeus*	3	1	0
Dooryard dock	*Rumex longifolus*	0	1	0
Goat willow	*Salix caprea*	1	0	0
Autumn hawkbit	*Scorzoneroides autumnalis*	2	0	0
Bittersweet nightshade	*Solanum dulcamara*	0	0	1
Canadian goldenrod	*Solidago canadensis*	3	3	3
European goldenrod	*Solidago virgaurea*	1	0	0
Perennial sow-thistle	*Sonchus arvensis*	1	0	0
Spiraea	*Spiraea* sp.	0	0	1
Common starwort	*Stellaria graminea*	1	0	0
Lilac	*Syringa vulgaris*	0	0	1
Tansy	*Tanacetum vulgare*	0	1	0
Common dandelion	*Taraxacum officinale*	2	2	1
Red clover	*Trifolium pratense*	2	2	1
White clover	*Trifolium repens*	1	1	0
Zigzag clover	*Trifolum medium*	0	1	0
Coltsfoot	*Tussilago farfara*	3	3	1
Wych elm	*Ulmus glabra*	0	0	1
Common nettle	*Urtica diocia*	0	1	1
Common valerian	*Valeriana sambucifolia*	1	0	0
Bird vetch	*Vicia cracca*	1	1	0
Bush vetch	*Vicia sepium*	0	1	0

Appendix III – Temperature and precipitation normal in Ås, Røyken and Drammen between 1961-1990

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