



Winter Damage to Forage Crops in Sweden in a Changing Climate: A Literature Study

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Degree project/Independent project • 15 credits
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Uppsala 2025



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Vinterskador i vallväxter i Sverige i ett förändrande klimat: en litteraturstudie

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Credits:	15 Credits
Level:	G2E
Course title:	Independent Project in Biology
Course code:	EX0894
Programme/education:	Crop Production (BSc)
Course coordinating dept:	Department of Aquatic Science and Assessment
Place of publication:	Uppsala
Year of publication:	2025
Cover picture:	Mark Mauldin, UF/IFAS
Copyright:	Reference has been indicated for all featured images

Keywords:	Leys, Forage grasses, Forage legumes, Winter Damage, Waterlogging, Ice encasement, Snow Mould, Plant breeding, Renovation, Climate Change.
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Abstract

Leys are the main form of agriculture in Sweden and are especially important in the northern parts of the country. They mostly consist of perennial forage grasses and legumes and are usually grown for two to four years, but sometimes up to eight years in areas where they are the main source of economic supply. In northern climates like Sweden's, some species are selected to reduce winter damage while maintaining good productivity. However, winter kill remains a major problem and can lead to significant yield losses. This literature study reviews scientific articles, mainly from countries with similar climates, aiming to give an overview of the current knowledge and gaps on:

- Abiotic and biotic winter stresses damaging leys
- The resistance of commonly grown species in Sweden to these stresses
- Breeding methods and goals for different species
- Methods to assess winter damage and the potential for renovation through overseeding

Due to climate change, Swedish winters are expected to have higher precipitation, reduced snow cover and warmer autumns and springs. These changes can reduce the plants' ability to harden properly, which affects their tolerance biotic and abiotic stresses. Higher CO₂ levels could also reduce plants cold acclimation level. Some species lose their hardiness after warm spells during winter and are unable to reacclimate. Waterlogging and ice encasement lead to hypoxia (low-oxygen conditions) or even anoxia (complete oxygen deprivation). Timothy is the forage species showing best resistance to these conditions. Snow mould mainly affects grasses, and resistance builds up during cold acclimation. Among legumes, red clover is particularly vulnerable to clover rot during winter and root rot, especially when weakened by other winter stresses. Diploid red clover cultivars tend to be more resistant than tetraploid ones. In order to reduce yield loss, several solutions are possible. It is important to choose species adapted to the specific weather conditions and most common winter damages. Breeding forage for winter tolerance is also possible but challenging since forages have complex genomes. Breeding programs use both field testing and artificial freezing tests. Field tests allow for the evaluation of many genotypes but are less controlled, while artificial tests offer more stable conditions but are costly and limited in scale. There is limited research on how to renovate damaged leys. However, a Swedish project called *Vall-reparera* will explore winter damage assessment using drones and test different seed mixtures for overseeding.

Keywords: Leys, Forage grasses, Forage legumes, Winter Damage, Waterlogging, Ice encasement, Snow Mould, Plant breeding, Renovation, Climate Change.

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Abbreviations

Abbreviation	Description
ATP	Adenosine triphosphate
(ha)	Hectare
LT ₅₀	Median lethal temperature
NADPH	Nicotinamide adenine dinucleotide phosphate
NIR	Near infra-red
NVI	Normalised vegetation index
PSII	Photosystem II
QTL	Quantitative trait locus
RGB	Red, green, blue
ROS	Reactive oxygen species
SLU	Swedish University of Agricultural Sciences
UAV	Unmanned aerial vehicle

List of Plants

Forage legumes:

Common name	Trivialnamn	Scientific name
Alfalfa	Blålusern	<i>Medicago sativa</i> L.
Alsike clover	Alsikeklöver	<i>Trifolium hybridum</i> L.
Birdsfoot trefoil	Käringtand	<i>Lotus corniculatus</i> L.
Red clover	Rödklöver	<i>Trifolium pratense</i> L.
White clover	Vitklöver	<i>Trifolium repens</i> L.
Sainfoin	Esparsett	<i>Onobrychis viciifolia</i> Scop.

Forage grasses:

Common name	Trivialnamn	Scientific name
Bering hairgrass	Tuvtåtel	<i>Deschampsia cespitosa</i> subsp. <i>beringensis</i> (Hultén) W.E.Lawr.
Creeping foxtail	Svartkavle	<i>Alopecurus arundinaceus</i> Poir.
Festulolium	Festulolium	<i>x Festulolium</i> Asch. & Graebn.
Italian ryegrass	Italienskt rajgräs	<i>Lolium multiflorum</i> Lam.
Meadow brome grass	Brinklost	<i>Bromus commutatus</i> Schrad.
Meadow fescue	Ängssvingel	<i>Lolium pratense</i> (Huds.) Darbysh
Meadow foxtail	Ängskavle	<i>Alopecurus pratensis</i> L.
Orchardgrass	Hundäxing	<i>Dactylis glomerata</i> L.
Perennial ryegrass	Engelskt rajgräs	<i>Lolium perenne</i> L.
Reed canary grass	Rörflen	<i>Phalaris arundinacea</i> L.
Red fescue	Rödsvingel	<i>Festuca rubra</i> L.
Smooth meadow-grass	Ängsgröe	<i>Poa pratensis</i> L.
Smooth Brome grass	Foderlost	<i>Bromus inermis</i> Leyss.
Tall fescue	Rörsvingel	<i>Lolium arundinaceum</i> Schreb.
Timothy	Timotej	<i>Phleum pratense</i> L.
Tufted hairgrass	Tuvtåtel	<i>Deschampsia cespitosa</i> subsp. <i>cespitosa</i>

Other plants:

Common name	Trivialnamn	Scientific name
Alpine arctic chuckweed	Fjällarv	<i>Omalotheca supina</i> (L.) CD.
Winter wheat	Höstvete	<i>Triticum aestivum</i> L.

Materials and Methods

A systematic approach was used in order to provide an overview of the existing knowledge and identify gaps. Relevant key words were entered in various platforms to collect articles and data, including Primo, Google Scholar, and Scite. Peer-reviewed scientific papers were primarily used, although this was not a strict requirement. Reputable sources, such as Jordbruksverket and Växtskyddscentralen were also consulted. Only the main results and general explanations from the articles were summarized. Since the purpose of the literature review is to provide the reader with a general understanding of the issue and recent research developments on the topic, in-depth explanations of the methods or the biological and physiological mechanisms behind the study results were excluded. References are provided to allow readers to access more detailed information from the specific papers mentioned. No limit was set on the publication period of the articles, although more recent studies were preferably selected on each topic when possible. The focus was primarily on studies from countries with a climate similar to that of Sweden, including Canada, Russia, and the Nordic countries, as well as relevant studies from Germany, Poland, Japan, and the USA, where cold weather can also occur. Only studies including at least one forage crop grown in Sweden were retained.

1. Introduction

In Sweden, the total area of leys and green fodder crops in 2024 was 1,129,100 ha (*Jordbruksmarkens användning 2024. Preliminär statistik*, Jordbruksverket u.å.). Compared to the total agricultural land area of 2,981,800 hectares, leys and green fodder crops are by far the most common crop, covering nearly three times the area of winter wheat. Leys are divided in pasture leys where the livestock graze and cut leys, harvested several times per season to make silage and hay. Various perennial forage crops are grown in leys. Common perennial forage legumes in Sweden include red clover (*Trifolium pratense* L.), white clover (*Trifolium repens* L.), alsike clover (*Trifolium hybridum* L.), birdsfoot trefoil (*Lotus corniculatus* L.) and alfalfa (*Medicago sativa* L.). Common perennial forage grasses include timothy (*Phleum pratense* L.), meadow fescue (*Lolium pratense* (Huds.) Darbysh), orchardgrass (*Dactylis glomerata* L.), tall fescue (*Lolium arundinaceum* Schreb.), perennial ryegrass (*Lolium perenne* L.), smooth meadowgrass (*Poa pratensis* L.) and creeping red fescue (*Festuca rubra* L.) (Halling et al. 2021). Resistance to winter stresses varies among species and cultivars. For instance, perennial ryegrass is not grown in northern Sweden due to its lower persistence. Winter stresses affecting leys can be either biotic or abiotic. Abiotic winter damages such as frost, ice encasement (when an ice sheet covers the field), waterlogging (flooding of the field), and soil heaving (mechanical expansion of the soil upward due to the formation of ice crystals) regularly occur and can severely affect plant survival. Biotic winter damages are caused by winter pathogens such as snow moulds or clover rot. The weakening of plants due to infections or infestations prior to winter can also contribute to lower persistence. However, little research has been conducted on the combined effects of pre- and post-winter stresses together with other winter stresses. Attempts to reduce winter kill and improve ley productivity have been made through various management strategies and breeding programs. The complexity of forage crop genomes, however, remains an obstacle to identifying genes responsible for resistance to winter stresses. When winter injuries occur in a ley, weeds can take over the dead areas, and nutrients may be lost. Different methods for assessing the damage and reseeding dead areas are currently being investigated in the Swedish project *Vallreparera* (Oliveira u.å.). In the actual literature review two main problematics will be investigated:

- Which forage species are most resistant to current and future winter stresses in Sweden and how can breeding strategies be used to improve their winter hardiness under changing climate conditions?
- How to assess winter damage effectively in order to renovate forages through overseeding and, this way, reduce yield loss?

A selection of studies considered to provide an overall view of research progress on winter damage in forage crops in Sweden, particularly in the context of climate change will be presented. Areas requiring further research will be pointed out.

2. Overview of Winter Injuries and Resistance in the Context of Climate Change

In a report showing future climate models for Scandinavia, Lind et al. (2023) explain that climate change will have greater impacts in northern Europe and arctic regions than they will have on average globally. The main consequence will be reduced snow cover in winter. Precipitation will increase in all seasons in northern Sweden. In southern Sweden, precipitation will increase in autumn, winter and spring but summers will be dryer. Those consequences can have negative impacts on the winter survival of perennial forage crops.

2.1 Hardening

2.1.1 Climate Change Impacts on Cold Acclimation of Different Species

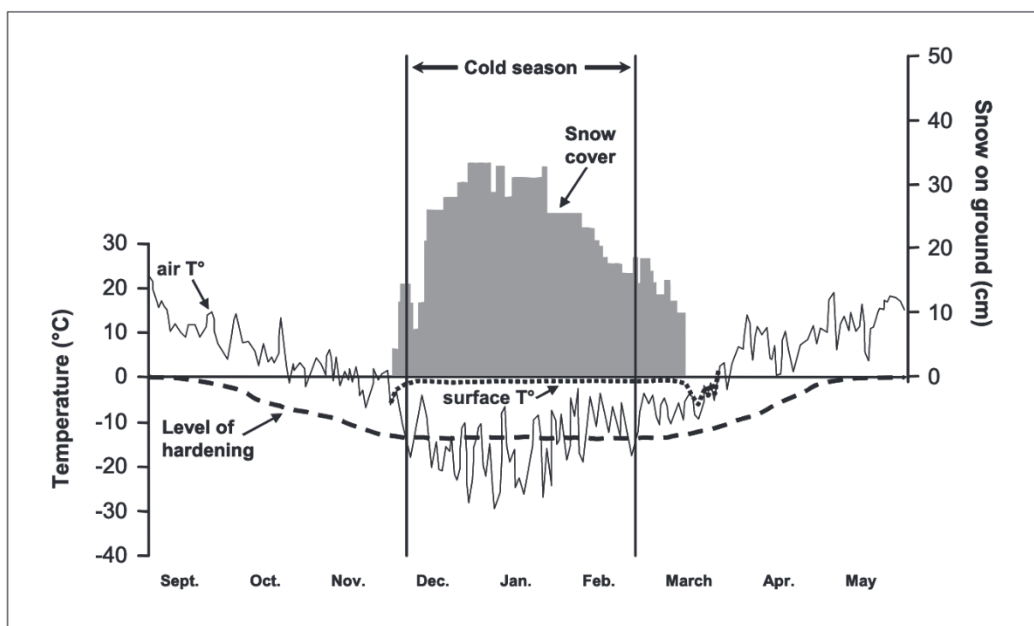
A crucial component guaranteeing higher winter survival of plants in northern areas is a good hardening / cold acclimation of the plants in autumn. The cold acclimation process starts at around 10°C but is mostly active at temperatures between 5°C and 0°C. Maximum freezing tolerance is generally reached mid-winter (Vyse et al. 2019). Upon warmer temperatures and longer photoperiod in spring, plants progressively deacclimate and restart growth. Not only the temperature plays a role in cold acclimation but also photoperiod, irradiance, Photosystem II redox state, soil water potential and nutrient status (Rapacz et al. 2014). Photosystem II or PSII is a protein complex involved in the light reactions of photosynthesis. It is particularly important in the photolysis process that splits water molecules, releasing oxygen and providing electrons to the electron transport chain along which reducing power such as ATP and NADPH molecules are produced. (*PSII - (General Biology I) - Vocab, Definition, Explanations | Fiveable* u.ä.)

It is also important that plants remain hardened throughout the entire cold period. Dehardening before the end of the cold season significantly increases the risk of frost kill. For example, well acclimated alfalfa could survive subfreezing temperatures as low as -15 to -20°C in winter but not less than -5°C would be fatal to unacclimated plants (Bélanger et al. 2006). Optimal winter conditions to minimize injuries include a gradual decrease in temperature during autumn and the establishment of a stable snow cover as soon as average temperatures fall below 0°C, as shown in figure 1 (Bélanger et al. 2006). It is important that temperatures remain consistently cold throughout the winter season to preserve the protective snow layer. In spring, temperatures should not fall below the freezing point once plants have fulfilled their dehardening process and cold events can be damageable depending on the degree of frost resistance of the plant.

In Sweden, the number of days with snow cover is projected to decrease in the future (SMHI, 2024). In the southern parts of the country, a decrease in the duration of the snow cover has already been noticed. Even if the cold period is also predicted to be shorter, temperatures potentially damageable to plants will still occur. Reduced snow cover combined with dehardening processes will therefore lead to a higher risk of direct exposure to subfreezing temperatures which can harm plants (Rapacz et al. 2014).

Figure 1. Graphical representation of the ideal scenario for the winter survival of perennial forage crops under the conditions of eastern Canada. This scenario mainly takes into account air temperature and snow insulation throughout the overwintering period in relation to cold hardening and dehardening (Bélanger et al. 2006).

<https://doi.org/10.4141/P04-171> [2025/04/22]



Increased precipitation as projected by the climate models for Sweden could affect acclimation of perennial forage crops negatively (Bélanger et al. 2006). In early autumn, some precipitation is still needed to allow plants to build up the organic reserves required to survive in winter. The negative effect of high precipitation and high soil moisture on hardening is principally observed in late autumn. During acclimation in late autumn, plants protect themselves from extracellular ice by increasing the concentration of intercellular solutes. Higher tissue water content reduces intercellular solutes concentration and thus lessens their protective effect (ibid.).

As a consequence of those observations, Bélanger et al. (2002) implemented two parameters to measure autumn hardening. FH-RAIN is the mean daily rainfall during the autumn hardening period. A higher value, i.e. higher precipitation, implies a worse acclimation and vice versa. Not only the amount of precipitation affects acclimation. The second parameter FH-COLD was based on Alfalfa and represents the “net accumulation of cold degree-days below 5 °C (CDD5) during the autumn hardening period from the start date of autumn hardening (FH-SD) to

the date of first occurrence of daily minimum temperature $T_{\min} \leq -10^{\circ}\text{C}$ (FD-10)” (Bélanger et al. 2002; Qian et al. 2024).

Qian et al. (2024) estimated that climate change would over the long-term lead to an enhanced autumn hardening in Canada due to a later snow cover and a greater number of days with temperatures between 0°C and 5°C . However, precipitation is modelled to decrease in most parts of Canada during winter, which is not the case in Scandinavia.

Some studies indicate that warmer temperatures in autumn and a later winter start would have a negative effect on cold acclimation (Rapacz et al. 2014). Cold acclimation is strongly dependent on light and is possible only when the intercepted light intensity doesn't fall under a critical level. A delay in the onset of cold acclimation to a time in the season when the photoperiod is shorter, due to the late arrival of cold temperatures, may therefore have a negative impact, especially in high-latitude regions like Sweden. Low temperatures combined with high irradiance lead to an overreduction of PSII, acting as a trigger for the cold acclimation mechanisms. In the future, if low temperatures occur at lower irradiance, PSII reduction will decrease significantly, negatively affecting cold acclimation (Rapacz et al. 2014).

A study investigated the effect of higher pre-acclimation temperatures (due to warmer autumns) on freezing tolerance and photoacclimation in timothy, perennial ryegrass and red clover (Dalmannsdottir et al. 2016). It showed that the more cultivars were adapted to northern climate conditions, the more freezing tolerance was affected negatively. However, timothy and perennial ryegrass were more sensitive to warmer pre-acclimation temperatures than red clover. In general, forage grasses seem to be more sensitive than forage legumes.

Climate change is caused by increasing CO_2 levels in the atmosphere, with consequences for the cold acclimation and frost tolerance of plants (Rapacz et al. 2014). Jurczyk et al. (2013) showed that increased levels of CO_2 to 800 ppm during cold acclimation was related to a lower freezing tolerance of meadow fescue. However, PSII redox state and photosynthetic acclimation were more effective under higher CO_2 concentrations. The study highlights that changes in the expression of the *CBF6* and *LOS2* genes, which disrupt the chloroplast redox signalling pathway that triggers cold acclimation, may be responsible for the decreased freezing tolerance. Further research is needed since significant differences can exist between species and results can differ depending on the chosen method.

2.1.2 Consequences of More Frequent Deacclimation-reacclimation Periods

As a result of warmer temperatures during the cold season, deacclimation and reacclimation processes may occur more regularly. Autumns and springs are getting warmer, and thaw events are becoming more frequent during winter (Vyse et al. 2019). Deacclimation is a much faster process than acclimation (Bélanger et al. 2006; Rapacz et al. 2014). It may occur upon warmer temperatures or

regardless of temperatures as a result of organic reserves depletion. The process can be either reversible or irreversible depending on species specific physiological characteristics but also on the length and the intensity of the exposure to warmer temperatures (ibid.) as well as the photoperiod (Bélanger et al. 2006; Bertrand et al. 2017). Plants acclimate or deacclimate at different degrees. Warm spells during winter can initiate deacclimation processes, leading to a loss of hardening, which could be detrimental for plants that may subsequently be unable to withstand new cold waves later in the season (Bélanger et al. 2006). Some species can reacclimate to some degree if temperatures drop again after warm spells in mid-winter or early-spring.

It has been shown in some species and cultivars that warm spells do not have the same impact depending on whether the photoperiod is shorter or longer. Bélanger et al. (2006) relay a study on a winter-hardy cultivar of timothy, which showed that this specific cultivar remained well-hardened despite a temperature of 10°C when the photoperiod was short (8 hours). However, it deacclimated at a lower temperature of 4°C when the photoperiod was long (16 hours). The velocity at which plants de-harden varies between species and cultivars. A study demonstrated that perennial ryegrass deacclimated more quickly than timothy at similar temperatures. It also showed that the winter-hardy timothy cultivar Engmo de-hardened faster than the less-hardy cultivar Grindstad, but Engmo developed a higher initial frost tolerance in autumn (Jørgensen et al. 2010). Cultivar Engmo maintained a higher level of frost tolerance in early spring at 3°C compared to Grindstad, which had already fully de-hardened.

Deacclimation may also depend on the vernalization requirements of some species. Vernalization is the process through which some plants become capable of flowering and producing seeds after a period of cold (*vernaliserings* - *Uppslagsverk - NE.se* u.å.). A Norwegian study compared cultivars of meadow fescue having high vernalization requirements with vernalization-insensitive and photoperiod-insensitive cultivars (Kovi et al. 2016). It was shown that vernalization-insensitive and photoperiod-insensitive cultivars hardly developed freezing tolerance. Deacclimation and the capacity to reacclimate in cultivars with high vernalization requirements are influenced by the photoperiod during vernalization, which affects freezing tolerance. When vernalization occurs under long days, freezing tolerance is negatively impacted, and the plant's ability to reacclimate is reduced. In contrast, vernalization during short days has a lesser effect on freezing tolerance and reacclimation capacity (ibid.).

2.2 Ice Encasement and waterlogging

Ice encasement occurs when water, accumulated from snowmelt during a thaw period or from rain, freezes and forms an ice sheet that inhibits most gas exchange with the surface, see figure 2 (Gudleifsson 2013). A smaller number of studies has been done on injuries caused by ice encasement compared to frost kill. A major part of them have been undertaken by Canadian teams led by Gudleifsson, the most recent being from 2013.



Figure 2 Ice sheet damage to a field of alfalfa (Sheaffer et al. 2023)

Ice encasement is more common in northern maritime areas such as Iceland, Northern Norway or the coast of Canada but is even an increasing problem in the northern and central parts of Sweden with climate change. Thaw periods are getting more frequent during winter (Vyse et al. 2019). Lindfors (2024) explains that precipitation will increasingly take the form of rain instead of snow. The risk for ice encasement will therefore increase (Rapacz et al. 2014).

Waterlogging is when water is flooding lower areas of the field. Both water logging and ice encasement are principally harming plants due to anoxic or hypoxic conditions under the ice sheet. While hypoxia refers to low O_2 availability, anoxia is the complete deprivation of oxygen, often resulting from ice encasement or complete flooding of land (Vartapetian et al. 2014). Mechanical or freezing death due to ice encasement may also happen since ice doesn't have the same insulating properties as snow, but to a smaller extent than anoxic death. In addition, anaerobic respiration accelerates the use of plant carbon reserves and affects substrate availability for respiration and regrowth (Bélanger et al. 2006). In such conditions, plants accumulate metabolites, mostly CO_2 , ethanol, lactate and malate. Acetate, propionate, citrate, private, shikimate and butyrate were also detected (Gudleifsson 2013). The accumulation of metabolites damages cell membranes. Gudleifsson (2009) has also confirmed the formation of ROS (Reactive Oxygen Species) potentially lethal to the plants after ice has melted when contact with O_2 is reestablished. It indicates that plants could still be alive underneath the ice sheet and be killed by ROS when again in contact with O_2 . As a rule of thumb, after three months of ice cover, most grass plants regardless of the specie are killed. In Iceland, ice encasement is the most widespread kind of winter damage (Gudleifsson 2013).

As mentioned, both waterlogging and ice encasement result in hypoxic or anoxic conditions for the root zones. In an English study, Striker & Colmer (2017)

compared resistance to water logging between common forage legumes. Species often grown in Sweden present in the study are alfalfa, red clover, white clover and birdsfoot trefoil. Compared to the controls, alfalfa is the most sensitive species, followed by red clover, with both >50% growth reduction in anoxic conditions. On the other hand, white clover and birdsfoot trefoil showed resistance to waterlogging. Root porosity of resistant plants increases under hypoxic conditions by the formation of aerenchyma in the root cortex. Aerenchyma is “a tissue composed of a network of interconnected gas conducting intercellular spaces which provide plant roots with oxygen under hypoxic conditions.” (Kacprzyk et al. 2011:208). The formation of adventitious roots and aerenchyma was also contrasted in orchardgrass and tall fescue after waterlogging, with a greater proportion of adventitious roots in orchardgrass while a greater proportion of aerenchyma in tall fescue (Mui et al. 2021). Further research is needed to identify the effects of hypoxia on other forage grass species. A more detailed and extensive screening program could also provide valuable information on variations within species and help identify genetic markers responsible for resistance, which could be used in breeding programs (ibid.).

Bertrand et al. (2001) compared the sensitivity of four forage species (alfalfa, red clover, timothy and orchardgrass) to anoxia. Sensitivity to anoxia is quite similar to that of hypoxia. Among the species included in the study, red clover was most sensitive to anoxia, followed by alfalfa. Orchardgrass performed better than the legumes, but timothy had best resistance. Timothy’s ability to resist anoxia is due to its slow metabolism during winter (Bélanger et al. 2006). This allows timothy to delay the onset of anoxia and prevent the accumulation of CO₂ and ethanol in plant tissues, while simultaneously maintaining high carbohydrates reserves.

Gudleifsson (2013) summarises the results of two studies conducted in 2009 and 2010, which compare the frost and ice tolerance of four species representing four different plant groups. Alpine arctic chuckweed (*Omalothea supina* (L.) DC.), winter wheat (*Triticum aestivum* L.), red clover and timothy are used to respectively represent the four plant groups alpine snow bed plants, winter cereals, forage legumes and forage grasses. Alpine snow bed plants such as alpine arctic chuckweed are plants accustomed to a stable snow cover throughout the season. It has been observed that alpine arctic chuckweed had higher resistance to frost than all plants from the other groups but that it didn’t have a good tolerance to ice. In conclusion, plants used to long snow cover as it is the case in alpine conditions are well adapted to cold temperatures but not necessarily to other stresses such as ice encasement (ibid.).

Gudleifsson (2013) showed that most grasses, for instance timothy or tufted hairgrass, are more tolerant to ice encasement than forage legumes and winter cereals. They can tolerate 11-12 weeks of ice. Gudleifsson et al. (1986) compared frost and ice resistance of 10 pasture grasses in controlled environments. From the most frost tolerant LT₅₀ = -15.7°C to the least frost tolerant LT₅₀ = -4.7°C, grass species were ranked as follows: timothy, smooth meadow-grass, meadow foxtail (*Alopecurus pratensis* L.), red fescue, meadow fescue, tufted hairgrass (*Deschampsia cespitosa* subsp. *cespitosa*), creeping foxtail (*Alopecurus arundinaceus* Poir.), bering hairgrass (*Deschampsia cespitosa* subsp. *beringensis*

(Hultén) W.E.Lawr.), orchardgrass and reed canarygrass (*Phalaris arundinacea* L.). Timothy was also among the most ice tolerant species, together with tufted hairgrass and bering hairgrass. Despite good resistance to ice encasement and an acceptable resistance to frost, tufted hairgrass can be challenging to use in forages due to its low preference among grazing animals. It is even considered as a weed in Sweden, since it has a tendency to take over in the field when animals avoid it (*Ogräsrådgivaren* u.å.). Legumes are less resistant to ice than grasses. For instance, white and red clover can withstand encasement 3-4 weeks, less than half the time of grasses (Gudleifsson 2013). Winter cereals are least tolerant and support only 1-2 weeks of ice cover.

2.3 Biotic Winter Damage

2.3.1 Snow Moulds

Snow mould is a disease caused by multiple fungi; it is therefore common to talk about snow moulds in plural. They primarily affect grasses but can also attack alfalfa and clover to a smaller extent. They are psychrophilic opportunistic parasites, highly stress-tolerant and benefiting from the low concurrence with other pathogens prevailing under snow. There are two categories of snow moulds as shown in Table 1: obligate snow moulds thriving only in winter with or without snow cover and facultative snow moulds thriving even during the growing season of plants (Matsumoto 2009b). Some fungi have an individualistic strategy, especially obligate snow moulds: they do not coexist with genetically distinct strains. In contrast, facultative snow moulds tend to adopt a collectivist strategy since they also are present during summer together with other pathogens. Snow moulds have developed specific mechanisms to resist to freezing temperatures. They are usually endemic, but outbreaks may be caused by unusual winter climates (ibid.).

Table 1. Obligate and facultative snow moulds. (Matsumoto 2009b) with addition of the authors names to the scientific names (*Mycobank* u.å.). Species found in Sweden are in **bold characters**.

Obligate Snow Moulds	Facultative Snow Moulds
low-temperatures basidiomycetes (= <i>Coprinosia psychromorbida</i> (Redhead & Traquair))	<i>Ceratobasidium gramineum</i> (Ikata & T. Matsuura)
<i>Phacidium abietis</i> (Dearn.)	<i>Microdochium nivale</i> ((Fr.) Samuels & I.C. Hallett))
<i>Pythium iwayamai</i> (S.Ito)	<i>Pythium graminicola</i> (Subraman.)
<i>Racodium therryanum</i> (Thüm.)	<i>Pythium paddicum</i> (Hirane)
<i>Sclerotinia borealis</i> (Bubák & Vleugel)	<i>Rhynchosporium secalis</i> ((Oudem.) Davis)
<i>Sclerotinia nivalis</i> (I. Saito)	<i>Sclerotinia trifoliorum</i> (Erikss.)
Sopponuke fungus (= <i>Athelia</i> sp. (Pers.))	
<i>Typhula incarnata</i> (Lasch)	
<i>Typhula ishkariensis</i> (S. Imai)	
<i>Typhula trifolii</i> (Rostr.)	

The presence of snow moulds and the severity of their outbreaks may decrease with climate change since the duration and regularity of the snow cover is planned to decrease in general (Rapacz et al. 2014). However, winter precipitation is also planned to increase in Scandinavia, and this could sometimes lead to heavier snowfalls and thick durable snow cover in some years. Snow mould fungi capable of living saprophytically (feeding on dead or decaying organic matter (*saprofyt* - *Uppslagsverk* - *NE.se* u.å.)) and sclerotia-forming species could remain several years in the soil and lead to strong outbreaks when favourable conditions are present (high soil moisture and snow cover). Such unstable climate could favour facultative snow moulds while it would have a negative impact on obligate snow moulds.

Resistance to snow mould generally develops during cold acclimation and reaches its maximum afterward (ibid.). A loss of cold acclimation in late winter or early spring may favour infection. For this reason, if climate change affects cold acclimation negatively, grasses might be more susceptible to infections (Abdelhalim et al. 2016). Meadow fescue is particularly prone to fungal attack during the regrowth phase in spring (Rapacz et al. 2014). An insufficient hardening in autumn can lead to a decreased resistance to both cold and snow mould infection in timothy, alfalfa, meadow fescue and winter cereals (Hwang et al. 2002).

Resistance to the LTP (low temperature basidiomycete) *Coprinus psychromorbidus*, responsible for cottony snow mould, between two cultivars of seven grass species were compared: smooth brome grass (*Bromus inermis* Leyss.), meadow brome grass (*Bromus commutatus* Schrad.), creeping red fescue, timothy, tall fescue, orchardgrass, and crested wheatgrass (Hwang et al. 2002). The most resistant species were smooth brome grass and meadow brome grass, followed by timothy and creeping red fescue. Finally, tall fescue and orchardgrass were most prone to infections. The developmental stage of plants (i.e., plant age) is decisive in their resistance to snow moulds. Older plants showed greater resistance to snow mould than younger ones. Even species usually susceptible can develop tolerance when older. In perennial forage species such as alfalfa and sainfoin (*Onobrychis viciifolia* Scop.), early establishment has been identified as a way to enhance resistance. It is believed that this allows plants to accumulate more non-structural carbohydrates, which are depleted more slowly over the winter, thereby improving the plants' ability to resist infections.

In Sweden and Norway (Abdelhalim et al. 2016), the most common fungus responsible for snow mould is *Microdochium nivale* (Fr.) Samuels & I.C.Hallett (Olvång 2000) (*snö mögel Microdochium nivale* - *taxonomi* - *Artfakta från SLU Artdatabanken* u.å.), a facultative snow mould also called "pink snow mould" (Pociecha & Płazek 2010). It attacks forages and winter cereals principally in autumn and winter under snow. There might be so-called "cross tolerance" in some species between frost tolerance and resistance to this snow mould (ibid.). The resistance to pink snow mould of meadow fescue, Italian ryegrass (*Lolium multiflorum* Lam.), festulolium (*Festulolium braunii*) and tall fescue was compared. *Festulolium braunii* is a hybrid grass species between meadow fescue and Italian ryegrass. The most resistant grass species were meadow fescue and tall

fescue, followed by festulolium. Italian ryegrass was the least resistant. Except Italian Ryegrass, the three other species showed similar responses to cold and biotic stress. For instance, an augmentation of the phenolic compounds level was noticed in them, contributing to the lignification of cell walls conveying higher resistance to snow mould.

2.3.2 Clover Rot

Clover rot is a disease caused by the fungus *Sclerotinia trifoliorum* (Erikss.), which affects all perennial forage legumes without host specialization, see figure 3 (Öhberg 2005). It can also be caused by *Sclerotinia sclerotiorum* ((Lib.) de Bary), a pathogen not only affecting forage legumes but also other plants such as oilseed and various vegetables (Vleugels et al. 2013).



Figure 3 Red clover leaf showing spots where ascospores of *S. trifoliorum* have penetrated). Apothecia of *S. trifoliorum* are present on the soil surface below the leaf. Picture taken in October in a red clover field. (Vleugels 2013).

Depending on the fungal species responsible for the disease, it can infect plants in autumn and develop during the cold season (*S. trifoliorum*) or in spring and develop in early summer (*S. sclerotium*). Red clover is particularly susceptible, but other species such as white clover, alfalfa, and birdsfoot trefoil can also be affected. Tetraploid cultivars of red clover tend to be more resistant than diploid ones (ibid.). Dense crop stands and a high proportion of legumes in the field are favourable conditions for the development of clover rot. Clover rot often causes more serious problems during the first year of forage establishment (*Grovfoderverktyget* u.å.). Clover rot can build sclerotia in the soil and survive over 5 years, in waiting for favourable growth conditions. Sclerotia break down easier during wet and warm summers. They are therefore favoured by dry summers (Öhberg 2005).

Very little studies have been done on the cumulative effect of several stresses on winter survival of forages. However, a recent study investigated the combined effect of frost stress and clover rot on winter survival (Ergon & Amdahl 2024). Resistance to clover rot is favoured by cold acclimation. The length of the cold

acclimation did not have much influence excepted when the plants were incubated at 16°C in the darkness due to higher consumption of stored carbohydrates by respiration in such conditions. This situation is though unlikely to happen in real conditions in Sweden. Plants with stronger resistance tend to have lower shoot growth potential due to greater allocation of resources toward stress management rather than growth. When frost stress and clover rot occur simultaneously, the damage is significantly greater than under either stress alone.

2.3.3 Root rot

Root rot is an infection caused by several fungi, mostly of the genus *Fusarium* spp., especially *Fusarium avenaceum* and *Fusarium solani* in Sweden. Another pathogen causing root rot identified in Sweden is *Phoma medicaginis* var. *pinodella* (Rufelt, 1994). In a more recent paper from Canada, the species *Fusarium culmorum* and *Fusarium graminearum* were also identified as common causes of root rot.

Root rot can develop in all forage legumes, but it has the most severe consequences in red clover. Plants usually develop the disease in combination with other stresses when they already have been weakened. Plants get more sensitive to root rot with age. Winter stress can significantly weaken plants and make them prone to root rot during spring. It is right after winter, during the regrowth season that damage is the greatest. For this reason, root rot is also considered to be a winter disease in Sweden and Northern/Western Europe more generally (Vleugels et al. 2013).

3. Plant Breeding and Restoration Strategies

3.1 Improving Winter Survival through Plant Breeding

3.1.1 Breeding Challenges

As presented earlier, winter survival is determined by the interaction of various abiotic factors (e.g., frost, ice encasement, soil heaving, excessive rainfall) and biotic factors (e.g., fungal pathogens such as snow mould, clover rot and root rot), as well as a multitude of genes. Many plant breeding programs have been carried out to improve the winter survival of forage crops, but it remains a long and costly process. Traditional in-field breeding techniques are slow and subject to inconsistent environmental conditions, while breeding in controlled environments can fail to capture the complexity of real-world conditions. It is not always evident which genes contribute to specific resistance traits. Moreover, the uncertainty surrounding climate change makes it difficult to predict the ideal winter-hardy plant ideotype (Rapacz et al. 2014). An ideotype refers to the “combination of morphological and/or physiological traits, or their genetic bases, optimizing crop performance to a particular biophysical environment, crop management, and end-use” (Martre et al. 2015). Therefore, there is a need to develop accurate climate models and improve genetic diversity among species to enable rapid and optimal responses to increasingly unstable environmental conditions in the long term (Rapacz et al. 2014). Among all the components playing a role, freezing tolerance is the single component most strongly correlated with winter survival (Rognli 2013; Rapacz et al. 2014). Consequently, many breeding programs aim to improve plants freezing tolerance (Parsons et al. 2024). Improving crops’ winter survival capacity while maintaining high yield is one of the main challenges since those two parameters are sometimes negatively correlated (Bertrand 2019).

3.1.2 Common Breeding Methods: Pros and Cons

In general, breeding programs follow specific steps, regardless of the method used. The first step is to screen different genotypes and identify characteristics of interest (elite genotypes). Then, parents are crossed, and the progeny is tested and developed through recurrent mass selection. New cultivars must follow specific rules before commercialisation. They must be distinct from already existing cultivars, uniform (separate specimen must perform equally) and stable (the new characteristics must be stable over breeding series). New cultivars must also have a name and are tested in field during at least two years to assess their “value for cultivation and use” (Jäck 2023). The following methods can be used in all stages of the breeding schedule.

Field testing has been the principal breeding method for winter survival improvements for a long time and is still largely used today. The principal advantages of field testing are that it has a relatively low cost at the same time as

it enables testing of many different genotypes (Rognli 2013). The median lethal temperature, also called LT_{50} , is a common parameter used to measure freezing tolerance. It is defined as the temperature at which 50% of the test population is killed (Humphreys & Eagles 1988). When testing plants in field, the value of LT_{50} is usually higher than when testing the same plants in controlled environments (e.g. freezing tests). This is probably due to the natural hardening conditions in the field, which include many more parameters than when plants are artificially hardened (Rognli 2013). Natural hardening can be more or less optimal from one year to another. Consequently, on average, LT_{50} is higher in field than in artificial conditions where the hardening conditions remain stable. The length of the hardening period, as well as other variables such as the photoperiod, irradiance, fluctuations between day and night, or the weather, can explain the higher LT_{50} values when plants are hardened naturally as opposed to artificially (ibid.). To obtain more stable and reliable results, it is important to conduct tests at many different locations and over many years when testing in the field, as it is rare to get perfect breeding conditions in a natural environment.

Artificial freezing can be performed either on whole plants or on specific plant parts, such as the crown (ibid.). Since environmental conditions can be more easily controlled, artificial freezing offers greater stability than field testing. It also allows plants to be tested in a more uniform manner. However, it is more expensive and doesn't allow for the screening of a large number of genotypes, which can be particularly challenging when screening winter tolerant genotypes with low variation in frost tolerance since low experimental errors are necessary to make conclusions. Natural conditions may be more advantageous in this context as it allows to test a larger number of genotypes, lowering the experimental errors. It is however a slower process: plants need to be tested over several locations and during several years to limit the impact of environmental variations. The main advantage of artificial freezing, but also one of its most challenging aspects, is the process of cold acclimation. The goal is to replicate natural hardening conditions, which are not always ideal in field testing. However, under ideal circumstances, field testing may give more complete results, as it involves a longer period of cold acclimation and includes additional realistic environmental factors that may be absent in artificial conditions. Cold acclimation under artificial freezing conditions typically consists of a pre-acclimation period of 2-4 weeks at temperatures around 8-10 °C, followed by 2-3 weeks at lower temperatures of 1-2 °C. During this process, light intensity is relatively high, usually ranging from 100 to 150 $\mu\text{mol}/\text{m}^2/\text{s}$. In natural cold acclimation conditions, light intensity can vary depending on the location and time of year which may contribute to differences in the quality of acclimation between natural and artificial environments. Other environmental factors, such as the soil water content and amount of precipitation, are not always realistic in artificial conditions, further contributing to these differences. After the cold-acclimation part, freezing temperatures are applied on plants for a period of usually 24h (which is also not always realistic) with a lowering of temperature of 1°C/h. Plants are then put into normal growing conditions to observe their regrowth capacity.

Biotechnologies, including gene and cell engineering, have relatively recently opened for new possibilities when breeding crops. A Russian study aimed to develop biotechnological methods to create new hypoxia and anoxia resistant plants (Vartapetian et al. 2014). Two main plant adaptation strategies in hypoxic and anoxic conditions already described in previous studies were confirmed and used as a basis to improve resistance. True tolerance (controlled by resistant genes) is reached by molecular acclimation. The cell metabolism goes through an important reorganisation to withstand anaerobic conditions. The second strategy confirmed by the study is so-called apparent tolerance and is obtained through avoidance mechanisms. The whole plant metabolism changes to facilitate oxygen transport from the aerial parts of the plant to the waterlogged or ice-encased parts of the plant and formation of aerenchyma. The experiments presented in the study weren't conducted on forage species but on wheat and oat (*Avena sativa* L.). Tolerance to anaerobic stress was successfully implemented in the plants. Biotechnologies could therefore be a lead in the breeding of forage crops, especially species susceptible to ice-encasement and waterlogging. However, genetically modified organisms are currently not allowed to be grown outside of scientific trials in closed environments in Sweden.

3.1.3 Breeding Goals in Various Forage Crops

In order to be able to breed forage crops, it is important to understand the mechanisms leading to tolerance to different stresses at a molecular level. Compared to other crops, forages have complex genomes, which is restricting the research for cold tolerance improvement (Adhikari et al. 2022). Often, tolerance to various winter stresses is a consequence of many genes. Quantitative Trait Locus (QTL) analysis, is used to identify genes resulting in specific phenotypical characteristics (Yamada et al. 2004; *Quantitative Trait Locus (QTL) Analysis | Learn Science at Scitable* u.å.). Even if QTL analysis could give valuable information about genetic markers coding for winter-resistance associated traits, the scanning of complex genomes as those of many forage crops in a large scale is still a challenge and a very costly process (Bélanger et al. 2006). For instance, identification of winter-hardiness associated traits through QTL analysis in perennial ryegrass was unsuccessful (Yamada et al. 2004).

Alfalfa's winter survival is made possible thanks to a dormancy state, sacrificing plant growth in fall and spring. In order to improve alfalfa yield, the dormancy period must be shortened, making it less resistant to winter conditions. Dissociate cold tolerance from dormancy in alfalfa is still a breeding challenge (Bélanger et al. 2006). By using a recurrent selection method in a controlled environment, followed by field testing of the new cultivars, positive results have been obtained with cultivars exhibiting lower dormancy without compromising their persistence. (ibid.).

White clover is one of the most common forage legume species in Sweden, alongside red clover and alfalfa. In the northern parts of the country, red clover tends to be grown more frequently than white clover. White clover is quite winter hardy; however, it has been observed that there is a negative correlation between persistency and leaf size (Helgadóttir et al., 2008). Specifically, white clover leaf

size decreases with increasing latitude. This is because white clover allocates more energy to the development of a dense stolon network instead of leaves to increase its persistence. Consequently, yield amounts are smaller in northern Sweden than in the south. Therefore, the main goal has been to breed cultivars that combine winter resistance with high productivity.

In an Icelandic study, Helgadóttir et al. (2008) managed to successfully break the negative relationship between persistency and productivity. This study is now relatively old but no recent papers treating of the same problematics were found. In currently commercialized seed mixes adapted to the climate conditions of Norrland, white clover is either not included or constitutes only a small percentage (*Scandinavian Seed Utsäde vår 2025 web u.å.*).

Snow mould is a recurring problem mostly in grasses. Therefore, resistance to the fungi causing this disease has become a common breeding goal. A Norwegian paper screened resistance to the snow mould *M. nivale* of three cultivars of meadow fescue, six cultivars and two breeding populations of perennial ryegrass as well as nine breeding populations and two cultivars of festulolium (Abdelhalim et al. 2016). The study aimed to find adapted plant material to the new parameters brought about by climate change such as warmer autumns with a decrease in plant hardening and a longer growth season. A distinct feature of this study is that non-acclimated plants were used. Since resistance to snow mould is typically enhanced by cold acclimation, using non-acclimated plants ensured that this environmental factor didn't influence the results. This way, the observed differences could be attributed to genetic variation. Plants were tested in controlled conditions in spring and in autumn. A field experiment was also conducted. Results showed no significant correlation between resistance in controlled conditions and resistance in the field. In the field, all cultivars of meadow fescue survived well since this species is more adapted to Nordic conditions. Festulolium and perennial ryegrass had a lower survival rate than meadow fescue and within species, more winter tolerant cultivars resisted better. In artificial conditions, resistance depended highly on the growth conditions before inoculation. Meadow fescue was least resistant to snow mould. Tetraploid entries of festulolium were significantly more resistant than diploid ones. Entries (i.e. cultivars and breeding populations) of festulolium and perennial ryegrass adapted to northern climates survived better than the ones adapted to continental European conditions. However, even entries adapted to continental European conditions exhibited some resistance to snow mould. Southern adapted breeding sources could therefore be considered in breeding programs for snow mould resistance, especially since the prerequisite of cold acclimation for winter-hardy cultivars may not always be met in the future due to climate change. It is worth noticing that some problems have been encountered when breeding festulolium such as low seed production and genetic instability. Meadow fescue's lower persistence in artificial conditions could be a result of method imprecisions. However, it could also confirm the fact that meadow fescue is susceptible to fungal attack in the regrowth phase in spring, as mentioned in 2.3.1 (Rapacz et al. 2014).

Red clover is particularly prone to clover rot and root rot. Breeding for resistance to these diseases has also gained interest. Detailed work on the topic has been carried out by Tim Vleugels (Vleugels 2013). In another research paper, Vleugels et al. (2013) screened 117 different accessions of red clover, searching for the most appropriate methods when breeding for clover rot. An accession is “A distinct, uniquely identifiable sample of seeds representing a cultivar, breeding line or a population, which is maintained in storage for conservation and use.” (Glossary | Food and Agriculture Organization of the United Nations u.å.).

Breeding possibilities are, however, still limited due to a lack of resistant material to breed from and little knowledge about the mechanisms leading to clover rot resistance. The disease depends heavily on weather conditions. For this reason, it is very difficult to breed under natural conditions, as infection occurs in different places and at different times from year to year (Vleugels et al. 2013). It is recommended to use bio-tests, i.e., artificial inoculation of the plant material with the pathogen to test for resistance. In addition, breeding programs should prioritise the use of local landraces and recently developed cultivars as sources of genetic variation. Wild populations, while rich in genetic diversity, are often more challenging to breed from due to the presence of many associated undesired traits that are difficult to eliminate. Moreover, existing cultivars are already more resistant than wild populations (Vleugels et al. 2013).

Although little material is available, Vleugels et al. (2013) have identified different characteristics of resistance to clover rot in red clover. Tetraploid sorts as well as creeping, intensively branching varieties seem to be more resistant. Contradicting results have however been found in a Swedish study where polyploidy didn't play a role in resistance (Öhberg et al. 2005). It was also found that late flowering cultivars were more resistant in comparison to medium-lates ones. Since red clover is an outbreeding, species, i.e. reproducing through cross-pollination, variability is found both in-between and within populations. The most appropriate way for further breeding is therefore to recurrently select the most resistant cultivars within population with low susceptibility (Vleugels et al. 2013).

When it comes to timothy, it is predicted to remain the principal forage grass crop in Swedish climate conditions and other high-latitude countries. This is due to its already good persistency. Existing timothy cultivars show particularly good tolerance to ice-encasement. Rapacz et al. (2014) suggest that breeding in timothy could aim to take advantage of the longer growing season resulting of climate change. By adapted timothy cultivars to these new growing conditions, an additional cut could potentially be harvested in autumn.

3.2 Forage Restoration to Minimise Winter Damages Impacts on the Yield.

3.2.1 Restoration Challenges

Winter damage is not uniform across the field; some areas are more severely affected than others, resulting in “patches” of dead plants due to winterkill. In

these affected zones, weeds often establish themselves and proliferate, forming seed banks in the soil that can have a long-lasting negative impact on yield. Additionally, when the soil is left bare, nutrient losses may occur (Oliveira u.å.). The development of restoration methods, such as overseeding, aimed at mitigating yield loss and suppressing weed growth, has therefore garnered increasing interest. However, before such renovation strategies can be effectively implemented, several challenges must be met. The Swedish project *Vall-reparera*, conducted in the Västerbotten region, will investigate several aspects of the restoration of winter-damaged leys (Oliveira u.å.).

The first challenge lies in the inability to plough or harrow the dead patches without causing collateral damage to the surviving crops. One alternative for overseeding is the use of direct drilling (Brandsæter et al. 2005; Oliveira u.å.). The development of multifunctional robots in agriculture could maybe participate to reduce the current mechanical challenges. The usefulness of such robots will be studied in the *Vall-reparera* project (Oliveira u.å.). A second challenge involves the release of phytotoxins from dead plants, which can inhibit the growth of newly sown seeds. The single kind of winter stress after which phytotoxins were found is ice-encasement (Brandsæter et al. 2005). It wasn't possible to tell if those phytotoxins were released by the plant or were of microbiological origin. The main biochemical compound causing phytotoxicity that was found is butyrate. If severe winterkill due to ice encasement is observed in the field, a delay of sowing between 1-2 weeks could limit the influence on the growth of overseeded plants (ibid.).

3.2.2 Short Review of Assessment Technologies

In order to provide an appropriate response to different types of winter damage, it is necessary to assess the damage with precision. Traditional methods of visual (ocular) assessment are not accurate enough and are time-consuming. Remote sensing technologies, deployed via satellites, aircraft, or unmanned aerial vehicles (UAVs), can now provide detailed quantitative data on various crop conditions. (Ioja et al. 2023). Various vegetation indexes can provide useful information to adapt for instance watering, fertilization or harvest time.

The Normalized Vegetation Index (NVI) is one of the most commonly used indices in remote sensing (*Vegetation indices and their interpretation: NDVI, GNDVI, MSAVI2, NDRE, and NDWI* u.å.). It provides indications of vegetation greenness, density, and health. NVI uses reflected light from vegetation in the visible and near-infrared (NIR) bands. When photosynthesis is functioning well, plants appear greener due to the absorption of red light and the reflection of near-infrared radiation.

In the context of assessing winter damage in leys, high-resolution RGB (red, green, blue) drone imagery, as will be used in the *Vall-reparera* project, may provide sufficient information at a low cost (Oliveira u.å.). In the project, images will be captured from both 20 meters and 80 meters above ground level.

Orthomosaic images will be generated from the photos taken by the drone. An orthomosaic is a “detailed, georeferenced image of a place, created by piecing

together high-resolution photos taken from drones or other aerial platforms.”
(*Orthomosaic Mapping: What’s Orthomosaic & How to Make it?* 2023)

3.2.3 Potential Species for Forage Restoration

So far, no study has investigated which forage species would suit best for overseeding in the specific context of winter-damaged leys. It is one of the interrogations the project *Vall-reparera* will also try to answer (Oliveira u.å.). Seven treatments will be tested in this project, five ley mixes and two controls. The original ley mix in the context of the study is timothy, red clover and meadow fescue and will be tested to be overseeded (mix 1). Other mixes will include only annual forage species (mix 2), annual forage species combined with the original ley mix (mix 3 and 4) as well as annual cereal species combined with the original mix (mix 5). The project document contains a list of possible annual species that could be used. Forage grasses include Italian ryegrass and annual ryegrass. Forage legumes include crimson clover, berseem clover, Persian clover, subterranean clover, common vetch, hairy vetch and black medic. Cereal species include winter wheat, winter barley, winter rye and oat. The project will be carried out until 2027 and provide new insights in the renovation possibilities of winter-damaged leys.

4. Discussion

This literature study identified various current and future challenges related to the overwintering of forage grasses and legumes in the context of climate change. It first examined the effects of climate evolution on cold acclimation, as well as the hardening and dehardening processes, and highlighted both biotic and abiotic factors leading to winter damage. An overview of strategies to reduce yield loss was then provided. The resistance levels of different species and cultivars were compared. Breeding methods and goals in order to increase winter resistance were explored. Finally, ley renovation was mentioned as a potential approach to mitigate yield loss, although limited research is currently available on this specific topic. Another topic that could have been included in this study is the impact on winter damage of crop management methods such as drainage, fertilization, number of harvests or timing of the last harvest before winter. This part was voluntarily excluded since this literature study didn't aim to present an exhaustive list of all factors influencing winter damage.

4.1 Areas requiring further research

Further research is required in several areas discussed in this paper. First, results regarding the impact of climate change on cold acclimation are mixed. Qian et al. (2024) estimated that cold acclimation in Canada could be enhanced by climate change due to a potentially greater net accumulation of cold degree-days below 5 °C. However, this conclusion may not apply to Swedish conditions. While some regions of Canada are expected to experience drier autumns, autumns in Sweden are projected to become wetter. Even if Sweden also sees a greater net accumulation of cold degree-days below 5 °C, questions remain about the extent to which the negative impact of increased precipitation might counterbalance this potential benefit. Additionally, it is still unclear whether the projected temperature trends in autumn will lead to an improved hardening. Therefore, more research is needed to determine how climate change will affect cold acclimation in the Swedish context.

Regarding white clover, a key challenge identified is the decrease in leaf size (and consequently in yield) at higher latitudes. Positive results have been achieved in attempts to break the correlation between winter hardiness and leaf size (Helgadóttir et al. 2008). However, since white clover is still infrequently used in northern Sweden, additional research is necessary to further improve the existing cultivars.

As mentioned in the results, resistance to frost varies among species. Plants accustomed to long snow cover such as alpine plants are well adapted to cold temperatures but not necessarily to other stresses such as ice encasement. This is an important aspect to keep in mind when trying new forage species.

Some research has been conducted to assess the impact of temperature and photoperiod length on the cold acclimation of forage species. The effects of

higher pre-acclimation temperatures on freezing tolerance and photoacclimation have been studied in timothy, perennial ryegrass, and red clover. However, further research is needed to determine the specific temperature and light requirements of other forage species.

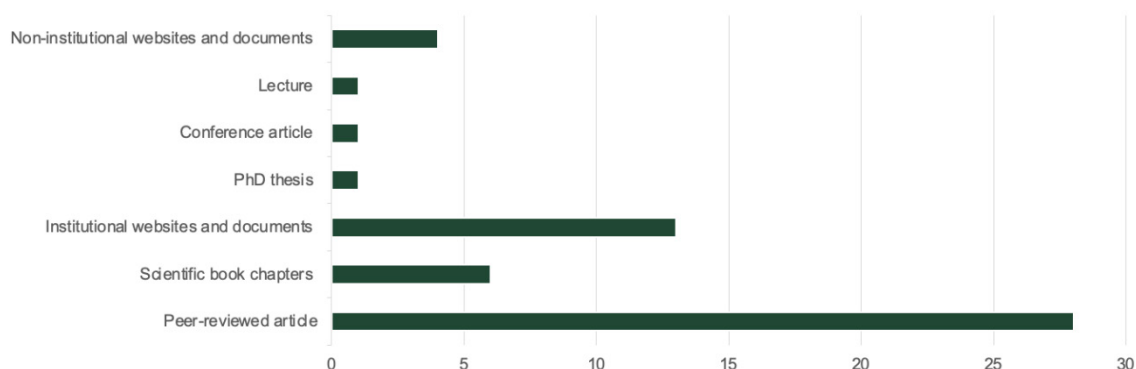
In timothy, it has been shown that deacclimation is regulated by photoperiod. This suggests that freezing temperatures following warm spells in early spring could be particularly harmful, whereas warm spells during winter may have little impact on hardiness. Further research is needed to identify which other species or cultivars exhibit this type of photoperiod-regulated deacclimation.

Attempts were made to find literature on the topic of forage renovation; however, no relevant studies were identified. The Vall-reparera project is currently the only initiative investigating the renovation of winter-damaged leys in the specific context of Sweden. Since no other studies are available for comparison, the methodology of this project could not be evaluated or discussed. Therefore, any conclusions should be withheld until the results of the project are available.

4.2 Relevance of the method

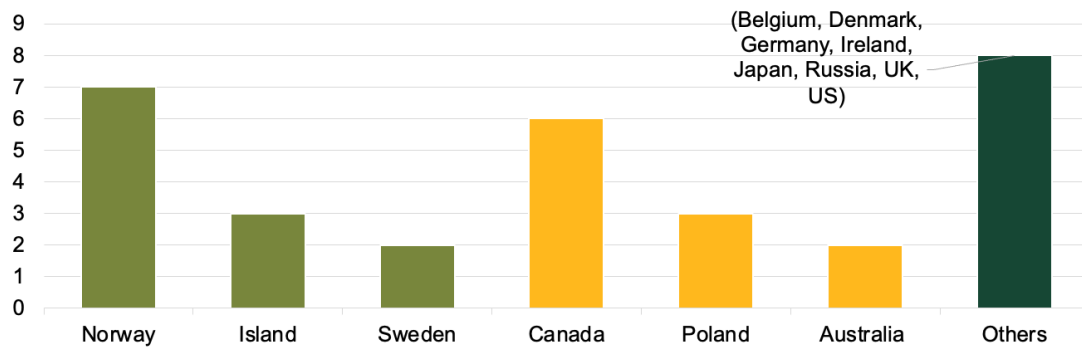
The method used in this paper enabled the identification of numerous relevant and trustworthy sources on the topic of interest. The vast majority of the sources were peer-reviewed articles (28), as shown in figure 4. Many sources which are not peer-reviewed come from institutional websites and documents which are generally considered as reliable. Less reliable sources, such as non-institutional websites and documents, were used to a much smaller extent (4), and only to define a few specific terms. Lectures and conference articles are not peer-reviewed and are therefore generally considered less reliable. However, only written content from the lecture's PowerPoint slides was used, in order to minimize the risk of misinterpretation. The conference articles included in this literature study were authored by researchers whose work is also represented by several cited peer-reviewed articles. As a result, the information from these sources was deemed reliable.

Figure 4 Type of source. Non-institutional websites and documents include blogs, educational websites or catalogues. Institutional websites and documents include universities, government agencies, recognized scientific journals or national encyclopaedia.



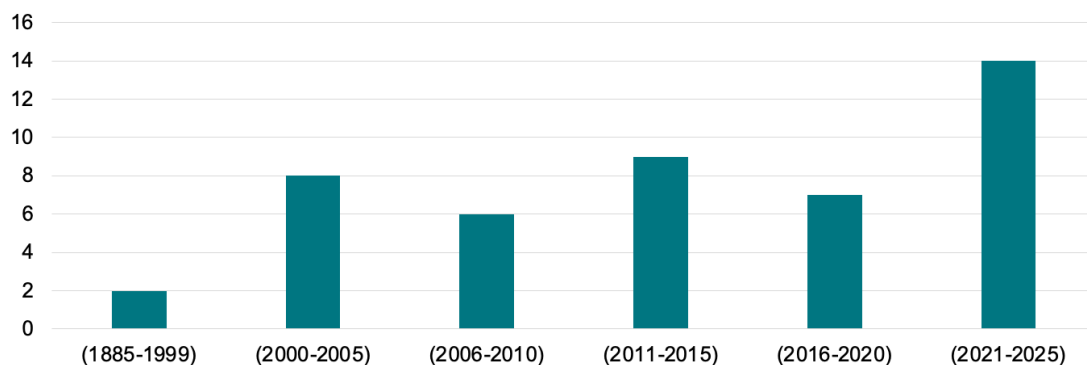
As mentioned in the Materials and Methods section, papers from countries with climates similar to that of Sweden were preferred. Approximately two-thirds of the sources used in this literature study originate from such countries, including Norway, Iceland, Canada, Denmark, and Russia; see figure 5. A major part of studies was carried out fully or partly in the Nordics (12). Canada is the only country outside the Nordics that brought a significant number of studies (6). The remaining third comes from countries with generally warmer climates, such as Poland, Australia, Belgium, Germany, Ireland, Japan, the United Kingdom, and the U.S. These papers were still considered relevant, as cold events can occur and cause damage in specific regions of these countries, for example in parts of the U.S., Poland, or Japan. Additionally, for articles focused on waterlogging, two of which are from Australia, the overall climate of the country was considered less relevant to the specific topic.

Figure 5 Number of peer-reviewed studies per country.



Of the 46 sources used in this study, 21 (just under half) were published between 2016 and 2025; see figure 6. Approximately 30% of the sources are less than five years old, indicating that the majority of the information remains current and relevant. Additionally, 10 sources were published before 2005, suggesting that either these older studies are still considered foundational and continue to be cited in more recent research, or that certain areas have seen limited updates in the literature.

Figure 6 Year of publication of the sources. Sources were excluded from the diagram when the year of publication wasn't specified. All types of sources are included (peer-reviewed studies, websites, books etc.).



5. Conclusion

Winter damage of abiotic or biotic origin is favoured or disfavoured depending on various factors (e.g. environmental conditions, plant resistance level, crop management, field characteristics). Moreover, in order to give an appropriate response to climate change, breeding for more resistant species and increased genetic variability is a foremost goal. Finally, new technologies could allow ley renovation and be used as a complement, contributing to reduced yield losses.

First of all, it was shown that biotic and abiotic stresses as well as the extent of the damage will evolve as a consequence of climate change:

- Wetter conditions in autumn could impact hardening positively in early autumn but negatively in late autumn.
- Delayed acclimation under shorter photoperiod could impact hardening negatively, especially in timothy and perennial ryegrass.
- The dehardening and rehardening capacity of Species and cultivars during warm-spells in the cold season varies and can depend on various factors such as photoperiod length (e.g. timothy) or vernalization requirements (e.g. meadow fescue).
- Ice encasements could become an increasing problem due to shorter snow cover. Plants are killed mostly due to anoxic/hypoxic conditions under the ice sheet leading to the formation of metabolites and reactive oxygen species. Waterlogging brings similar conditions. Grasses tend to be more tolerant than legumes, with timothy being the most tolerant species.
- Shorter snow cover will generally be unfavourable for snow moulds. However, opportunistic snow moulds could still give significant outbreaks.
- Resistance to snow moulds, root rot and clover rot is highly dependent on cold acclimation. Damage could therefore increase due to less optimal hardening conditions in autumn and earlier deacclimation in spring with climate change.

Also, breeding objectives for various species were identified:

- Alafala: break the correlation between dormancy and winter resistance.
- Clover: increase resistance to pathogens, especially clover rot and root rot.
- White clover: break the correlation between persistency and leaf size.
- Timothy: Take advantage of longer growing season resulting of climate change.
- Grasses in general: increase snow moulds resistance.

Finally new technologies could allow for more accurate assessment of winter damage. Using maps, patches of winter-killed plants in leys could be renovate through overseeding. Various challenges still need to be addressed, such as the inability to plough or harrow, as well as the presence of phytotoxins, especially after ice-encasement.

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