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Review

Cold hardiness research on agricultural and horticultural crops in Finland

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This paper represents an overview of cold hardiness research conducted on agricultural and horticultural crops, as well as on amenity plants in Finland. Inadequate freezing tolerance and/or winter hardiness often prevents introduction of new species and cultivars to Finland. Field observations on winter hardiness and more recently the results from laboratory freezing tests, have assisted breeders to select hardy genotypes. Research approaches for agricultural crops have evolved from observations on winter and frost damage to studies on molecular mechanisms of cold acclimation and freezing injury. The results of experiments on survival of winter cereals, grasses and clovers and frost tolerance of potato and turnip rape are discussed. The studies conducted on horticultural crops, including apple, strawberry, raspberry, currants, blueberry, sea buckthorn, perennial herbs as well as on ornamental trees and shrubs have included field evaluations of cultivars, or selections for winter hardiness, and studies on the effects of cultural management practices on winter survival. During the last decade detailed studies including controlled freezing tests have provided tools to assist in explanation of the underlying mechanisms of cold hardiness also in horticultural plants.

Key words: cold acclimation, cold resistance, controlled freezing test, field evaluation, frost tolerance, winter survival

Introduction

Cold hardiness is a critical factor in distribution, survival and productivity of cultivated plants in Finland and other northern regions. The principal factors for winter survival in the semi-maritime climate of Finland are length of the growing season, minimum temperatures and depth and duration of snow cover (Fig. 1). For annual plants, freezing tolerance is important for surviving summer night frosts. Cold hardiness implies resistance to low temperatures, whereas winter hardiness comprises also other biotic (low-temperature fungi etc.) and abiotic (fluctuating temperatures, wind etc.) stresses associ-

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ated with the winter environment. In addition to ultimate mid-winter hardiness, timing and level of cold acclimation largely determine the northern limits and economic productivity of cultivated plants. Knowledge on hardiness of different species and cultivars in Finland is based on long-term observations and field experimentation. Trials of over-wintering plants, mainly conducted by the Agricultural Research Centre of Finland (MTT) in various regions of the country, even as far north as the Polar Circle, always include evaluation of winter injury under field conditions.

A new era of cold hardiness research began in Finland in the 1980's. The cumulating information on the mechanisms of cold hardiness and the development of artificial freezing tests have enabled researchers to study closer the phenomena underlying winter injury and survival. This paper aims to provide an overview of cold hardiness research conducted on agricultural and horticultural crops, as well as on amenity plants in Finland. Cold hardiness of forest trees is extensively studied in various institutions in Finland. However, those studies and studies on chilling sensitive species and chilling injury are not reviewed here.

Agricultural crops

Over-wintering crop species

Winter-hardy plant species can develop tolerance mechanisms against abiotic and biotic stresses by cold acclimation. Since the minimum temperature and the duration and depth of snow cover vary greatly between years and locations, it is not clear whether abiotic or biotic factors cause the major winter damage to over-wintering crop plants in Finland. Freezing tolerance may become a limiting factor for winter survival where the snow cover is thin. This is often the case in the coastal regions of Finland. In the eastern and northern areas of the country snow cover is more often thick and lasts for a long period (Jamalainen 1958). Survival under snow for prolonged period requires adequate carbohydrate reserves for metabolic activities as well as resistance to low-temperature fungi (Nissinen 1996). In conclusion, the over-wintering crops may therefore require different strategies for winter survival in different parts of Finland. New introductions for cultivation in Finland are consequently carefully tested for winter survival in different locations around the country.

Jamalainen (1958) studied winter hardiness of over-wintering cereals, grasses and clover, and characterized their tolerance to abiotic (freezing, flooding) and biotic stresses (winter pathogens). Winter rye (*Secale cereale* L.), timothy (*Phleum pratense* L.) and meadow fescue (*Festuca pratensis* Huds.) were classified as freezing tolerant species, whereas English ryegrass (*Lolium perenne* L.), red clover (*Trifolium pratense* L.), cocksfoot (*Dactylis glomerata* L.) and winter wheat (*Triticum aestivum* L.) were listed as freezing sensitive species. Species classified as freezing tolerant, seldom suffered from freezing injury and winter damage to them was almost entirely caused by winter pathogens.

Winter cereals

In Finland, winter damage accounts for 60% of the annual variation in winter wheat yields (Mukula and Rantanen 1989b). In rye, crop failure caused by heavy precipitation or winter conditions can vary annually from 0 to 37% of the cultivated area (Mukula and Rantanen 1989a). For the less hardy winter wheat the estimate is from 0 to 53%. Although breeding for winter hardiness in wheat was initiated in 1918 (Pesola 1932), it is still one of the most important traits requiring improvement. Varis (1965) found a positive correlation between the vernalization requirement and winter hardiness of Finnish winter wheat cultivars. Long vernalization requirement in 'Linna' and 'Elo' was favorable especially under mild winter conditions when the risk of fungal injury was high. The duration of the snow-free period in autumn and hence the duration of cold acclimation, was the most im-

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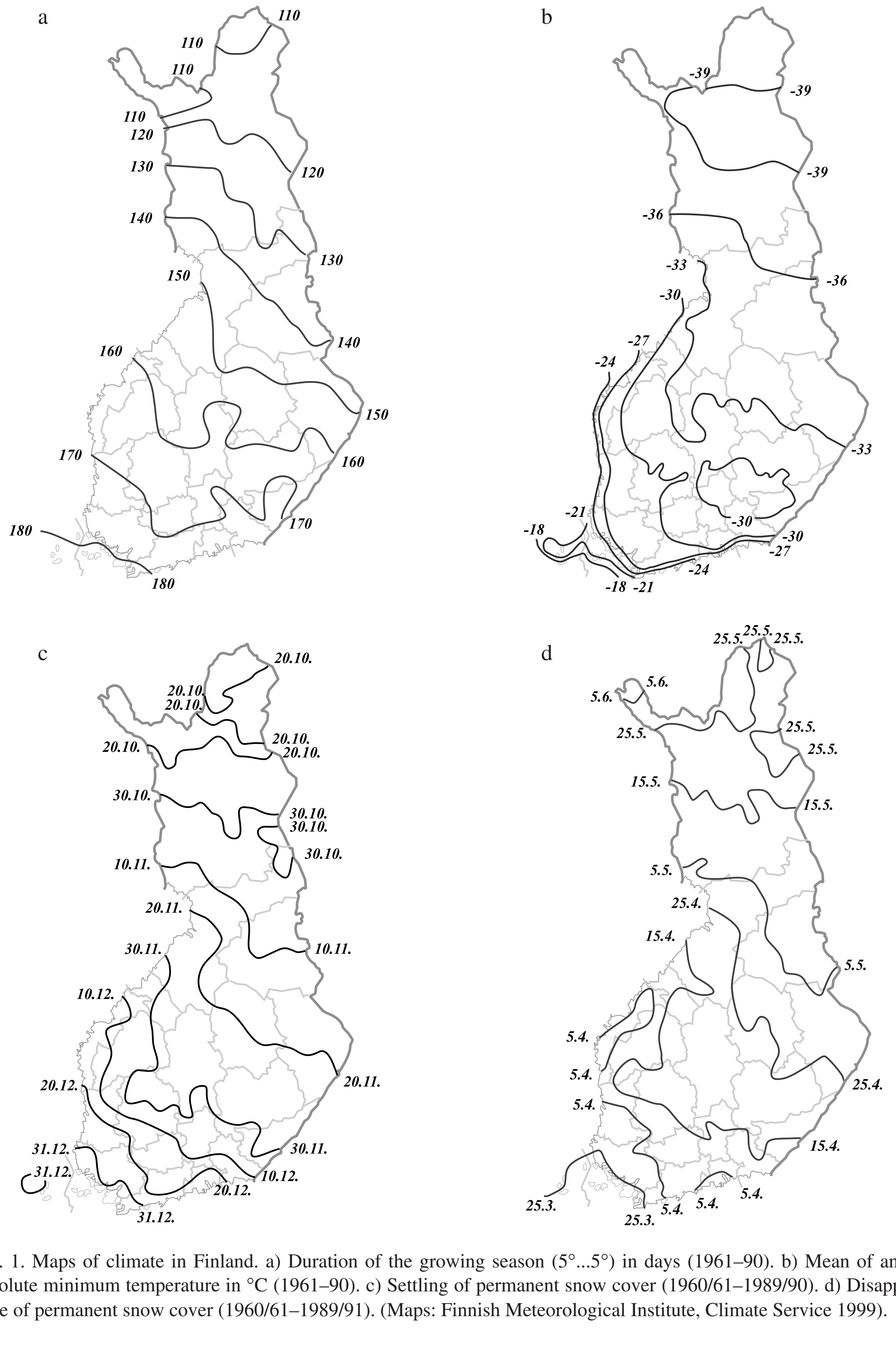

Fig. 1. Maps of climate in Finland. a) Duration of the growing season (5°...5°) in days (1961–90). b) Mean of annual absolute minimum temperature in °C (1961–90). c) Settling of permanent snow cover (1960/61–1989/90). d) Disappearance of permanent snow cover (1960/61–1989/91). (Maps: Finnish Meteorological Institute, Climate Service 1999).

portant climatic factor influencing winter survival and yield performance of winter wheat and rye cultivars in Finland (Pulli 1986). Breeding for winter hardiness is important in winter wheat and rye since foreign breeding materials are generally less winter hardy (Varis 1965, Mukula and Rantanen 1989a).

Pohjanheimo (1959) tested the freezing tolerance of winter wheat ('Varma') and rye ('Toivo') in the laboratory and observed that more freezing tolerant ryes were also tolerant to flooding and ice-encasement. Since then, the winter survival of over-wintering cereals has been examined both in the laboratory and in field trials (e.g. Manner 1967, Kukkonen and Pihakaski 1988, Hömmö and Pulli 1993, Pulli et al. 1996). A joint Nordic research project was established to compare the results of standard laboratory tests with field observations (Pulli et al. 1996). A good correlation between most laboratory tests and winter survival was obtained for winter wheat. The accuracy of laboratory tests to predict the winter survival of rye cultivars was lower. The cold acclimation conditions that were used may have been optimal for winter wheat but not for rye. Thus, the genetic potential of rye to cold acclimate was not fully exhibited in the laboratory tests (Pulli et al. 1996).

Hömmö and Pulli (1993) studied the hardiness of winter cereals in Finland. The hardiest species was rye followed by winter wheat, triticale (x *Triticosecale* Wittmack) and winter barley (*Hordeum vulgare* L.). Although the ranking of the most winter hardy cultivars varied among trials, significant differences were observed between cultivars within the same species. In cold winters, with a relatively long period of snow cover, winter wheat cultivars 'Vakka' and 'Linna' and rye cultivars 'Jussi' and 'Voima' were most winter hardy. In general, the winter-hardiness of triticale cultivars was similar or slightly poorer than the average for winter wheat cultivars (Hömmö and Pulli 1993). Hardening ability was reliably measured as release of potassium and calcium ions from frost treated plants (Hömmö 1992). Electrolyte leakage also correlated well with the hardening ability evaluated in field trials (Hömmö 1994a). In accordance with the earlier observations by Jamalainen (1958), Hömmö and Pulli (1993) concluded that breeding for snow conditions e.g. resistance to low temperature fungi rather than freezing stress, is more important. When tested in Canada, where the winter is colder than in Finland, Finnish cultivars were only moderately hardy (for review see Hömmö 1994b). This implies that the freezing tolerance of Finnish cultivars was the limiting factor for Canadian conditions. Screening for genotypes with good winter hardiness in Finland might have favored good resistance to low-temperature fungi rather than freezing tolerance. It can also be speculated that a shorter cold acclimation period and day length in Canada may have reduced the acclimation ability of Finnish cultivars since they are adapted to a long acclimation period during autumn (Hömmö 1994b).

Attempts have been made to characterize the metabolic processes associated with cold acclimation and to reveal components that are characteristic for winter-hardy genotypes. Metabolic processes during cold acclimation have been studied most intensively in winter wheat and rye. Changes in sugar and protein metabolism during cold acclimation have been monitored in several studies (Hömmö 1994b, Antikainen and Pihakaski 1993, 1994). More intensive accumulation of soluble sugars including raffinose, sucrose, fructose and glucose, was recorded for a hardy ('Linna') than in a sensitive ('Apollo') winter wheat cultivar (Hömmö 1994b). The sensitive cultivar accumulated more proline. Similarly, cold acclimation in rye ('Voima') was accompanied by increasing amounts of the soluble carbohydrates; glucose, fructose and sucrose (Antikainen and Pihakaski 1994).

In rye ('Voima'), the early response of protein metabolism to cold acclimation was investigated by Antikainen and Pihakaski (1993, 1994). Plants accumulated soluble proteins and RNA and, in addition, a transient increase in polysome content was detected after three days of cold acclimation. More detailed investigation of the changes in protein metabolism revealed two new polypeptides induced on the first day

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of cold stress (Antikainen and Pihakaski 1993). The accumulation of apoplastic antifreeze proteins (AFPs) was investigated by Antikainen et al. (1996) in collaboration with Prof. Marilyn Griffith's group at the University of Waterloo, Canada. AFP activity was detected in cold acclimated rye leaves, crowns and roots (Antikainen et al. 1996). When antibodies were raised against these AFPs and localized by immunolocalization studies, the distribution in cold acclimated rye tissue correlated with the location of extracellular ice (Antikainen et al. 1996). Further investigations supported this observation and showed that AFPs may function in the crystallization of water during freezing (Pihakaski-Maunsbach et al. 1996).

Harvey and Pihakaski (1989) studied freezing injury in non-acclimated and cold acclimated winter rye cells by transmission electron microscopy. Mitochondria in frozen leaf cells were more sensitive to freezing than were chloroplasts. Plasma membrane stability was also changed during cold acclimation. Pihakaski-Maunsbach and Puhakainen (1995) found that the stability of microtubules during freezing was increased in cold acclimated plants. The microtubule arrays were unpolymerized in cold acclimated rye cells, whereas shorter and less polymerized microtubules were found in non-acclimated cells.

Grasses

The most widely cultivated grass species in Finland is timothy. It was introduced for cultivation in 1801 by the Finnish Agricultural Society (for review see Nissinen 1996). Timothy is more freezing tolerant than meadow fescue, the other widely cultivated grass species and is therefore suitable for cultivation in areas where the snow cover is thin (Nissinen and Hakkola 1995). Meadow fescue, in contrast, is more resistant to snow scald (*Sclerotinia borealis*) which ensures over-wintering in conditions where resistance to low-temperature fungi is the limiting factor. Field experiments on the effect of grass species and harvesting system on grassland production showed that the better freezing tolerance of timothy might explain its good winter survival in Finnish coastal areas (Jamalainen 1958, Nissinen and Hakkola 1995). Harvesting system e.g. whether the yield was harvested for silage, hay or pasture, had only little effect on the amount of winter damage in the following year. However, the early timing of the last cut in silage swards may have increased the incidence of the low-temperature fungus, pink snow mould (*Fusarium nivale*) (Nissinen and Hakkola 1995). In addition, the weather in mid- and late summer had a marked effect on the occurrence of the low-temperature fungus, *S. borealis*, infection. The depth of soil frost in November and the depth of snow cover correlate well with the severity of *S. borealis* infection (Nissinen 1996).

Hahtonen et al. (1994) monitored ion leakage in a study of the early steps of cold acclimation, the speed of acclimation and deacclimation in timothy. Two timothy cultivars 'Bilbo' and 'Iki', differing significantly in their winter hardiness, were studied. Improved freezing tolerance was detected in both genotypes shortly after transfer to cold acclimating conditions. The differences between the cultivars became significant only after ten days of cold acclimation. In cold acclimated timothy plants the amount of raffinose, sucrose and total soluble sugars correlated with the freezing tolerance in both cultivars.

Repo and Pulli (1996) applied impedance spectroscopy to identify freezing tolerant genotypes among 12 English ryegrass cultivars. Two model parameters of impedance spectrum increased during cold acclimation. However, the authors concluded that changes in the conductivity parameters in meristematic tissue rather than in entire stems, should be monitored to detect differences between cultivars in the further studies.

Niemeläinen (1990) examined the effect of freezing on panicle production and dry matter accumulation in cocksfoot. In autumn, cold acclimated cocksfoot plants were collected from the field and exposed to –20°C in the laboratory. Freezing reduced panicle production, number of large tillers and lowered the dry matter yield.

In another experiment, carbohydrate reserves were depleted by keeping cocksfoot plants for 0 to 42 days in darkness (Niemeläinen 1990). In samples harvested in spring, carbohydrate content decreased rapidly and panicle production was reduced. This was not noted in cocksfoot plants collected in the fall.

Clovers

The first red clover (*Trifolium pratense* L.) cultivars were imported into Finland from southern latidudes and were sensitive to freezing and winter pathogens. From those cultivars, natural selection under field conditions occurred, producing local varieties that were more adapted to northern conditions (Pohjakallio et al. 1960). Although red clover is relatively freezing sensitive, most of the winter damage is caused by winter pathogens such as clover rot (*Sclerotinia trifoliorum*) (Jamalainen 1958). Clovers are regularly cultivated in mixtures with grasses. The proportion of clover often rapidly decreases due to a more aggressive growth habit and better winter survival of grass species (Nissinen and Hakkola 1995). Also, the persistence of red clover in grass mixtures is greatly influenced by management techniques, soil structure and drainage (Jamalainen 1958, Pulli et al. 1996). Of the abiotic stresses, freezing tolerance may become a limiting factor for winter survival in regions where the snow cover is thin (Nissinen and Hakkola 1995).

As a part of a larger European research project, Nykänen-Kurki and Rönkä (1998) evaluated the winter survival of white clover (*Trifolium repens* L.) cultivars in the MTT, Mikkeli (61°40'). Carbohydrate and starch contents were analyzed in late autumn and early spring, and compared with the winter survival of the cultivars. During this experiment the permanent snow cover lasted for ca. 5 months. The results indicated that the winter hardy cultivar 'AberHerald' accumulated starch more rapidly and produced slightly larger dry matter yields in the following year. In addition to the limited amount of reserve carbohydrates for winter, the winter survival of clovers may be limited by the daylength during autumn in the north. The overwintering of red clover in Lapland was improved if the daylength was artificially shortened in autumn (Pohjakallio et al. 1960).

Oilseed crops

Jamalainen (1958) characterized critical winter conditions for the over-wintering of winter turnip rape (*Brassica rapa* L.) seedlings. The seedlings seldom suffered from freezing injuries, but were more often damaged by flooding and winter pathogens (*Typhula* sp., *Sclerotiana sclerotiorum*). In the 1970's, the interest in winter turnip rape cultivation and breeding decreased dramatically. This was partly due to serious winter damages, but also because new spring turnip rape cultivars with favorable fatty acid composition were released for cultivation (K. Pahkala, personal communication).

Annual plants

Potato

Annual crop species, including cultivated potato (*Solanum tuberosum* L.), may be damaged by frosts. Valmari (1959) studied the effect of potassium fertilization on the freezing injury of potato in field experiments at the Frost Research Station, Pelsonsuo (64°31') (Valmari 1959). In those studies, adequate nitrogen fertilization rather than potassium lead to decreased frost damage. The minimum temperature in the potato canopy was higher during frost episodes in nitrogen fertilized plots than in the unfertilized ones. This may have been due to greater capacity of the plants to capture heat radiating from the soil during frost. Also, since the leaf area was only partially damaged by frosts in the nitrogen fertilized plants, the plants easily recovered from frost damage (Valmari 1959).

The lethal temperature for cultivated potato is ca. –3°C (Seppänen et al. 1998), although the photosynthetic capacity is reduced already at higher temperatures. Since potato cultivars do not exhibit genetic variation in freezing tolerance, nor a capacity to cold acclimate, the traits

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need to be transformed in existing germplasm. Freezing tolerant wild potato species such as *S. commersonii* Dun. can be used as donors. Somatic hybrids between S. *commersonii* and *S. tuberosum* have been shown to exhibit intermediate freezing tolerance compared to parents (Cardi et al. 1993). To study the mechanisms of freezing tolerance and acclimation capacity in *S. commersonii,* a selfed progeny of a somatic hybrid (*S. commersonii* + *S. tuberosum*) was produced (Seppänen et al. 1998). The population segregated in freezing tolerance and genotypes expressing freezing tolerance similar to *S. commersonii* were identified.

Under field conditions, light stress is an important component in the frost episode since the plants may be exposed to high light intensities even when frozen. The combination of high light intensity and low temperature increases the risk of formation of active oxygen species (AOS) and oxidative stress (Krause 1994). The capacity of a plant to remove harmful AOS was evaluated by screening for AOS resistance (Seppänen et al. 1998) and by analyzing the content of the antioxidant enzyme, superoxide dismutase (SOD) in non-acclimated and cold acclimated potato plants (Seppänen and Fagerstedt, unpublished results). When potato plants were exposed to low temperature, the resistance to AOS in addition to activity of SOD, was increased simultaneously with improved freezing tolerance. This was observed both in freezing sensitive as well as in freezing tolerant genotypes. The induction of SOD isoenzyme transcription was, however, differentially regulated in freezing sensitive *S. tuberosum* and in *S. commersonii* (Seppänen and Fagerstedt, unpublished results). The results indicate that freezing sensitive and tolerant genotypes may recognize the low temperature signal differently.

The molecular basis of freezing tolerance was further investigated by isolating cold regulated genes from *S. commersonii* and by studying their expression in freezing tolerant and sensitive genotypes (Seppänen et al. 1999). Experimental conditions that simulated night frost indicated a significant difference between freezing tolerant *S. commersonii* and sensitive *S. tuberosum* in their response to low temperature stress.

Spring cereals

Occasionally night frosts can damage the flower initials and developing kernels of spring cereals in northern Finland. Mukula and Rantanen (1989c, 1989d, 1989e) summarized the climatic risks for spring wheat, barley and oats production in 1969–1986. Low temperature and night frosts resulted in yield loss of spring wheat in two years. In barley and oats, which are cultivated further north, the variation in annual yield was more often explained by the occurrence of night frosts. The inflorescence of oats is more freezing tolerant than that of barley (for review see Mukula and Rantanen 1989e). However, when the frost tolerance of cereals was compared, oats seedlings were the most freezing sensitive followed by barley and spring wheat (Manner 1967). Carbohydrate concentration was higher in spring wheat seedlings than in barley or oats, indicating a correlation with frost tolerance.

Oilseed crops

Pahkala et al. (1991) studied the freezing tolerance of spring turnip rape (*Brassica rapa* L.) seedlings. Non acclimated seedlings survived at –3°C but were seriously damaged or killed at –5°C. Improved freezing tolerance was detected after cold acclimation, especially in one of the genotypes studied. In the same study, the effect of freezing on the fatty acid composition of seeds was analyzed. Frost treatment at pod filling stage did not change α-linolenic acid (18:3) content but slightly increased the amount of hexadecatrienoic acid (16:3).

Horticultural crops

Apple

In Finland, apple trees (*Malus* x *domestica* Borkh.) are grown on the fringe of their northern growing limits. Commercial production is restricted to the south-west of the country. Severe frosts in November and December may destroy floral and vegetative buds, and prolonged periods of very low temperatures injure vascular tissues leading to death of annual shoots or general dieback of branches (Kaukovirta and Syri 1985). Since the 15th century, when the first fruit trees were imported, growers gathered experience on the factors that affect survival, growth and yield of the trees. Thus, guided by a cumulating practical know-how, fruit tree growing slowly became more common and expanded northwards, despite frequently recurring winter injuries (Collan 1934).

In 1929, after an exceptionally severe winter, the Ministry of Agriculture commissioned a thorough survey on winter injuries in Finnish fruit orchards (Collan 1934). The aim was to establish the degree, nature and potential causes of injuries to different cultivars. The results highlighted the overriding importance of cultivar and rootstock selection in northern conditions, but even factors such as tree age, soil texture, fertilizing and pruning practices were shown to affect the cold resistance of fruit trees (Collan 1934). Collan's work was the first systematic approach to studying winter hardiness of fruit trees in Finland. Since then similar surveys have been made after severe winters. Kaukovirta and Syri (1985) attempted to re-analyse the results of the surveys made in 1929–1966, seeking to identify the underlying causes of winter injury. They concluded that most apple cultivars grown in Finland are lacking ability to maintain their cold hardiness during mild spells during early winter. Thus, the stability of cold hardiness, and the rate of rehardening, should be considered as prime factors in breeding and selection of new cultivars (Kaukovirta and Syri 1985).

Injury surveys made after the two most recent severe winters, 1984–85 and 1986–87, further demonstrated the close relationship between weather conditions and the final degree of winter injury in apple. In 1984–85, an extremely cold period in mid-winter caused less injury than the hard frosts of December 1986 and January 1987 (Säkö and Yli-Pietilä 1987, Säkö and Lundén 1988). Moreover, in spring 1985, the weather favored recovery (Säkö and Yli-Pietilä 1987), while the cool and rainy autumn preceding the cold winter of 1986–87 probably caused a reduction in the rate and degree of cold acclimation and, therefore, added to the severity of injuries in apple trees later in the season (Säkö and Lundén 1988). A new analysis of winter injury data from Finnish apple orchards is underway; therein, the historical records and meteorological data are combined in a statistical analysis using multivariate techniques (Lindén, unpublished). The aim is to determine the critical weather variables leading to winter injury in apple and thus provide a sound basis for breeding and selection of hardy cultivars in Finland.

Säkö (1985a) studied the winter hardiness of several apple rootstock clones in field trials as well as in laboratory experiments using an electrolyte leakage test after freezing treatment. The Finnish YP rootstock (*Malus baccata* [L.] Moench seedling), 'Antonovka' seedling rootstock and the Swedish A2 rootstock were the hardiest. The apple breeding program at MTT aimed at developing winter hardy cultivars, and five cultivars were released (Säkö 1985a). Lindén et al. (1996) applied controlled freezing tests to compare the cold hardiness characteristics of 'Samo' to those of 'Antonovka', an old cultivar of Russian origin. Sampled in mid-March at Helsinki (60°10'N), both cultivars displayed a high and stable level of cold resistance. However, 'Samo' was proven slightly less hardy than 'Antonovka'.

The influence of soil properties on overwintering of apple trees was studied by Vuorinen (1958). He concluded that the effect of rootstock was negligible compared with that of site and soil conditions, which had a greater influence on susceptible than on hardy cultivars. The most important factor affecting winter survival of the trees was their location on the slope, a higher location being beneficial. Soil moisture, nitrogen and calcium increased winter damage, whereas potassium enhanced winter survival.

Säkö (1958) studied the influence of the rootstock on overwintering of apple cultivars. Trees

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grafted on to M2, M12 or seedling rootstocks, exhibited least winter damage. The overwintering of several susceptible apple cultivars could be improved also by top-working on hardy framebuilders (intermediates) (Säkö and Meurman 1960). Apple cultivars 'Lobo' and 'Raike' were least damaged when grafted on to YP rootstock, compared with rootstocks A2 and M26 (Säkö 1985b). Similarly, three of the five new apple cultivars released from MTT (Säkö 1985a) overwintered better when grafted on to YP than on to A2 (Valo 1996). 'Make' suffered more injury on YP, while 'Maikki' was equally hardy on both. However, Aaltonen (1995) found no difference in overwintering of apple cultivars or selections whether grafted on to YP or A2.

Application of growth regulator B-995 in summer or autumn had a deleterious effect on winter survival of apple trees, presumably because it decreased the carbohydrate content of the shoots (Säkö 1970). Growing 'Lobo' and 'Transparante Blanche' on 30-cm-high raised beds covered with black plastic mulch improved winter survival, possibly because of the improved moisture conditions and soil temperature compared with flat beds (Säkö and Laurinen 1986).

Strawberry

Strawberry (*Fragaria* x *ananassa* Duch.) is a relatively cold susceptible crop. At a crown temperature of –8°C flower initials are damaged, while at –12 to –15°C most of the plants die. Thus, snow cover is a prerequisite for the successful overwintering of strawberry in Finland. Because snow cover has often been thin or absent in recent years, even older cultivars successfully grown in Finland for decades have encountered winter injury problems.

Dalman and Matala (1997) compared different strawberry cultivars in a field trial and found 'Jonsok' more winter hardy than 'Senga Sengana', the principal cultivar in Finland, or a Finnish cultivar 'Mari'. In 1995–98 several imported cultivars were tested in field trials carried out on strawberry farms (V. Matala, personal communication). 'Bounty', 'Dania', 'Jonsok', 'Korona', 'Polka', 'Senga Sengana' and 'Venta' suffered least winter injury.

Winter survival of strawberry may be enhanced by management practices. The effect of different row covers applied in November and the height of raised beds was studied by Dalman and Matala (1997). All cultivars suffered more winter injury and produced lower yields under straw cover compared with polypropylene (Agryl P17) cover. Plants on 10-cm-high beds were less damaged during winter than those on 25-cm-high beds. The use of polypropylene covers applied in September increased the yield of all seven cultivars studied by Pietilä et al. (1999). 'Honeoye' exhibited the most dramatic response; its yield was almost double under the cover compared with the uncovered control. The beneficial effect of polypropylene cover is due to its protecting effect in winter, as well as the more stable temperature under the cover in autumn and spring, which enhances the development of flower initials (Pietilä et al. 1999). Micropropagated 'Senga Sengana' overwintered better and produced higher yields than did the plants produced from runners (Dalman and Matala 1997).

Rubus

Frequent winter injuries are a primary limiting factor for expanding raspberry (*R. idaeus* L.) production in Finland. Winter injury in raspberry appears as tip dieback or bud injury, and usually occurs in late winter or early spring, most often when a warm spell is followed by frost. Some damage to the canes above the snow level, causing 10 to 15% yield loss, is observed almost every year. Total death of the canes above the snow level due to winter injury can occur every five to ten years even on favourable growing sites. (I. Ruutiainen, personal communication).

Earlier breeding of *Rubus* at MTT, aimed at developing nectar raspberry, a hybrid between *R. idaeus* L. and *R. arcticus* L. Of the two cultivars obtained, 'Heisa' is superior in winter hardiness to 'Heija' (Hiirsalmi and Säkö 1976, 1981). Arctic bramble species *R. stellatus* Sm. and *R. arcticus* L., as well as selections from their interspecific progenies, were also evaluated for winter hardiness in field trials (Hiirsalmi and Säkö 1980).

Säkö and Hiirsalmi (1980) tested several foreign raspberry cultivars along with some Finnish native selections for winter hardiness in a field trial. Native selections were found to be the hardiest. The gene pool of wild raspberry has been exploited in breeding to obtain winter hardy cultivars (Hiirsalmi 1989b). When 11 red raspberry cultivars were tested in a four year trial, 'Ville', a hybrid of 'Ottawa' and a Finnish wild raspberry, proved the hardiest, followed by the Canadian cultivars 'Ottawa', 'Muskoka' and 'Boyne' (Hiirsalmi 1989b, Dalman et al. 1991). Two new raspberry cultivars 'Jenkka' and 'Jatsi' were released in 1997 (Dalman et al. 1997). 'Jenkka' proved superior in hardiness as compared with 'Jatsi', 'Muskoka' and 'Ville' (Linna et al. 1993). In a breeding program at the University of Helsinki, aiming at developing winter hardy raspberry-blackberry hybrids, crosses between red raspberry and a hybrid cultivar 'Tayberry' (*Rubus* sp.) produced several relatively hardy hybrids (Antonius-Klemola et al. 1998). Winter injury was restricted only to the upper half or the tips of the floricanes. The possibility of screening for cold hardiness of raspberry cultivars *in vitro* was studied by Palonen and Buszard (1998). The relative cold hardiness of the cultivars *in vitro* corresponded to their known hardiness level in field conditions, when growth regulators were omitted from the culture medium and plants were cold acclimated before determination of hardiness with controlled freezing.

A positive correlation between the early growth cessation and winter hardiness of raspberry cultivars was found by Säkö and Hiirsalmi (1980). The effect of dormancy on cold hardiness, dehardening and a capacity to reharden was studied in three raspberry cultivars by Palonen and Lindén (1999). Plants were subjected to dehardening and rehardening treatments before cold hardiness was determined with controlled freezing. Maximum midwinter hardiness was observed in January, after breaking of endodormancy. Endodormancy had a greater influence on dehardening and rehardening in buds than in canes, and cultivars differed in their response. Dehardening of 'Maurin Makea' canes and buds, and 'Muskoka' buds was slightly enhanced by breaking of dormancy, whereas dehardening in 'Ottawa' was not affected. Raspberry canes and buds were able to reharden even after dormancy release; rehardening capacity was affected by the state of dormancy only in 'Maurin Makea' buds. Thus, changes in dormancy status failed to explain why cultivars differed in characteristics associated with cold hardiness, dehardening and a capacity to reharden (Palonen and Lindén 1999). Some explanation was offered by a study on seasonal changes in carbohydrates and their relationship to cold hardiness in the same cultivars (Palonen 1999). High levels of sucrose, total soluble carbohydrates, and a high ratio of sucrose to glucose plus fructose in canes and buds were found to be characteristic of a hardy cultivar. Changes in carbohydrate concentrations were related to the changes in cold hardiness and the mean air temperature during a 5-day period preceding sampling. Starch decreased during the autumn, whereas soluble carbohydrates accumulated reaching a maximum in midwinter. The most striking increase occurred in the concentration of sucrose, but glucose, fructose, raffinose and stachyose also accumulated. These results indicate the importance of carbohydrates, especially sucrose reserves on winter survival of raspberry.

The influence of exogenously applied sucrose on cold hardening of raspberry 'Preussen' *in vitro* was examined by Palonen and Junttila (1999). Sucrose applied in the culture medium was taken up by plants. Cold hardiness was primarily affected by acclimation treatment, but sucrose increased cold hardiness of nonacclimated plants and significantly enhanced the effect of acclimation treatment. Plant sugar content was increased by increasing the sucrose level in the medium, and to a greater extent by cold acclimation. Sucrose was the predominant sugar, and the rate of sucrose accumulation during cold acclimation was independent of the sucrose lev-

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el of the medium or the initial plant sucrose content. Palonen and Junttila (1999) concluded that sugars have more than a purely osmotic effect in protecting acclimated raspberry plants from cold.

Currants

Black currant (*Ribes nigrum* L.), as well as red and white currant (*Ribes rubrum* L. group) are generally very hardy and their winter survival is usually not a problem in Finland. Spring frosts during bloom may sometimes cause problems. There was no difference in winter survival among the new Finnish blackcurrant cultivars 'Mortti' ('Öjebyn' x 'Wellington XXX') and green-fruited 'Vertti' ('Öjebyn' x self), both released from MTT, and the commonly grown 'Öjebyn' (Hietaranta and Hiirsalmi 1989). In a field trial comparing eight red currant cultivars, 'Red Dutch' and 'Rotes Wunder' were the most winter hardy, whereas 'Jonkheer van Tets' and 'Rondom' exhibited least hardiness (Dalman 1999).

Blueberry

Blueberry (*Vaccinium* spp.) is a relatively new cultivated crop in Finland. Adequate snow cover is essential for successful overwintering of cultivated blueberry. North American and central European highbush cultivars have not proven winter hardy in Finland. So called half-high blueberries suffer less winter damage since they are more often covered by snow. To obtain winter hardy selections, highbush blueberry was crossed with bog blueberry (*V. uliginosum* L.) (Hiirsalmi 1985). Hybrid selections were generally superior in hardiness to highbush cultivars. Cultivar 'Aron' was chosen from this material and released in 1982 (Hiirsalmi 1985). Among several imported highbush blueberry cultivars evaluated for freezing injury after a severe winter 1986–87, 'June' and 'Rancocas' were the hardiest, but only 30 to 50% of their shoots survived (Hiirsalmi 1989a, Hiirsalmi and Hietaranta 1989). 'Aron' was least injured. Its shoots exhibited only slight injury, but most of its flower buds were destroyed.

Sea buckthorn

Native Finnish selections of sea buckthorn (*Hippophae rhamnoides* L.) incur no winter injury problems (Pietilä and Karvonen 1999). However, imported Russian cultivars are adapted to a more continental climate and suffer winter injury in Finland because their dormancy is broken in winter during warm periods. During dormancy, critical temperatures for sea buckthorn are –30 to –35°C and –40 to –45°C, for male and female plants respectively (Pietilä and Karvonen 1999). As a part of a breeding project, Yao and Tigerstedt (1995) evaluated winter damage in 24 sea buckthorn populations belonging to three different subspecies. Early growth cessation, leading to more compact growth habit, was positively correlated with winter survival.

Herbs

Cultivation of aromatic and medicinal herbs is considered an interesting alternative to traditional agriculture on small-scale Finnish farms. Most herb species are perennials and thus, winter hardiness is one of the key factors setting the limits for commercial production. Galambosi et al. (1991) investigated the biological and economic potential of 54 herb taxa under Finnish growing conditions. Cultivation of 22 species was proved feasible. However, most of the perennial herbs grown for phytomass yield, should be grown as annuals due to their poor winter survival (Galambosi et al. 1991, Galambosi and Svoboda 1994, Putievsky et al. 1998).

There are, however, perennial herbs sufficiently winterhardy to be grown even in northern Finland. Aflatuni (1998) studied the yield and winter hardiness of 20 mint (*Mentha* sp.) taxa at Ruukki (64°41'N) and Sotkamo (64°06'N). The survival of mint species varied between 0 and 100% in 1995–1998. A Chinese clone of peppermint (*Mentha* x *piperita* L.) was the most hardy. Plant age tends to affect the winterhardiness of mint: young plants are generally hardier than older ones. Kemppainen et al. (1997) proved the winter hardiness of spearmint (*Mentha spicata* L.) sufficient for commercial cultivation in northern Finland. Sorvari (1998) compared the winter survival of three tarragon (*Artemisia dracunculus* L.) clones at Ruukki and Sotkamo. Two of them seemed fairly well adapted; their winter hardiness will be studied closer with the aim of releasing a hardy cultivar.

Amenity plants

The majority of amenity plants grown in Finland are of foreign origin. Winter damage in woody plants is seen as dead flower buds or more severely as dieback of twigs and branches or of the whole plant. Information about their hardiness and potential growing area has been gradually gathered through practical experience and the work done in botanical gardens and arboreta. Exceptionally cold winters have served as hardiness tests: recorded winter injury evaluations (e.g. Vaarama 1941, Yli-Pietilä et al. 1987, Lundén and Säkö 1988) have yielded valuable data on the potential of different species. Several surveys were made nationally and locally around the country; those made before 1987 were summarised by Lundén and Säkö (1988). Only recently have hardiness studies of amenity plants been developed from evaluations of field performance to controlled freezing tests. These have also been incorporated into systematic breeding programs.

The first attempt to compare the performance of landscape plants of equal size and origin in different parts of Finland was a field experiment comprising 37 deciduous and 12 coniferous commonly grown tree and shrub species (Kaukovirta 1967). The plants were evaluated in the field for four years after planting in 1961–65. Only *Ribes alpinum* L. survived without any injury in all four test locations. Even the species considered very hardy were susceptible during the first years after planting. On the other hand, a protected northern site proved better than a windy, open location further south. It also seemed that it was not the very low temperatures (< –30°C), but longer spells of fairly cold weather (< –20°C) that damaged woody ornamentals, especially when the snow cover was thin.

A comprehensive evaluation of the distribution and hardiness of ornamental trees and shrubs in the whole country was first done in 1963–64 (Kallio 1966). Information on 937 taxa was recorded. In addition to native plants, 24 taxa were hardy throughout the country. Data on several taxa were not sufficient to provide information on their northern limit, since the plants were grown only in southern parts of the country where they were sufficiently hardy.

The performance of 384 species planted since 1927 at Piikkiö in south-western Finland, was followed during decades (Meurman 1963, Kallio 1977). The main reasons for poor adaptation of 136 species were poor cold hardiness or unsuitable location in the park. Numerous tree and shrub species were also planted in trials at 15 experimental stations or agricultural schools throughout the country from 60 to 69°N in 1970–1990. Their performance was recorded annually and tables of each species in each location and year were presented by Juhanoja and Hiirsalmi (1991).

Improving hardiness by selection and breeding

A project called KESKAS (kestävät kasvit; hardy plants) for collecting and selecting old, hardy and attractive specimens of woody ornamentals grown in parks, nurseries, botanical gardens etc. was carried out at the University of Helsinki in 1984–88 (Alanko and Tegel 1989). More than 700 strains of woody ornamentals were registered, representing about 20 arborescent and 60 bushy genera. In 1988 the project was moved to MTT and the field trials for comparing promising clones of *Forsythia* Vahl*, Hydrangea* L.*, Lonicera* L.*, Philadelphus* L., *Rosa pimpinellifolia* L., *Spiraea* L., *Syringa* L. and *Viburnum* L. at 4–5 locations around Finland were established in 1988–94 (Juhanoja and Heikkilä 1995). Winter hardiness was an important characteristic

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among the 30 attributes evaluated annually during the five-year test period. It was visually assessed in field performance of the bushes. A FinE-trademark was created for the superior, recommended clones. It has been given to twelve selected clones and four more will be included in 2000 (Juhanoja et al. 1998, S. Juhanoja, M. Aaltonen, A. Aflatuni, M. Heikkilä, A. Heinonen, R. Kemppainen, P. Paasikivi and K. Sorvari, unpublished).

The cold hardiness characteristics of the *Hydrangea paniculata* Sieb. 'Grandiflora' and *Philadelphus lewisii* Pursh. var. *lewisii* 'Waterton' clones registered in KESKAS were studied with controlled freezing tests (Suojala and Lindén 1997). The selected clones of both species displayed a high level of mid-winter cold hardiness, but *Hydrangea* deacclimated less than *Philadelphus*. No interclonal differences in the actual, potential or minimum hardiness level were found in either species.

Since the 1930's different *Rhododendron* L. species and hybrids have been collected at the Arboretum Mustila in south-eastern Finland. Many have been lost due to cold winters and poor adaptation during subsequent years. Two breeding programs were started at the University of Helsinki based largely on the genetic resources of Mustila. Breeding of broad-leaved evergreen rhododendrons aiming at cultivars able to tolerate temperatures below –35°C was started in 1973 (Uosukainen and Tigerstedt 1988) and that for deciduous azaleas in 1988 (Väinölä 1992). Two very cold winters occurred during the evaluation period of the evergreen progenies. Many hybrid families proved susceptible and 60% of the total of 14000 plants planted for trial were removed being dead or badly damaged (Uosukainen and Tigerstedt 1988). It was shown that *R. brachycarpum* ssp. *tigerstedtii* Nitz. transmitted frost hardiness to its hybrid progenies far better than any other hardy species (Uosukainen 1992). The most hardy combinations resulted from crossing *R. brachycarpum* ssp. *tigerstedtii* with *R. smirnowii* Trautv., *R. metternichii* Siebold & Zucc., *R. catawbiense* Michaux. or the so-called Seidel hybrids. Nine cultivars have been released from this breeding program. Azaleas have mostly been under snow cover during the coldest periods. About half of the planted 21000 hybrids have been removed for various reasons, only some cross combinations because of poor hardiness, those usually including non-adapted American germplasm (Väinölä 1999).

Efforts towards breeding shrub roses began at the University of Helsinki in 1992. The main aim was to combine remontancy (repeat flowering) with winter hardiness (Joy 1995). Remontancy in roses is recessively inherited and therefore seldom expressed in hardy genotypes, thus the desired genotypes can only be recovered from an F_2 generation (Joy and Kangaspunta 1999). Remontancy is sought from *Rosa rugosa* Thunb. ex Murray and Canadian *R.* Kordesii hybrids, hardiness from *R. gallica* x *majalis* hybrids.

Väinölä et al. (1997) compared stem and flower bud hardiness of five deciduous Lights azalea clones at Minnesota Landscape Arboretum, USA. Freezing tests of stem sections and floral buds collected outdoors six times during the dormant period were conducted. In mid November the five clones possessed identical flower bud hardiness (–22°C), but varying stem hardiness. Stems of all cultivars were at least 2°C hardier than the corresponding flower buds throughout the winter, and both organs achieved their maximum hardiness in January. Midwinter stem hardiness was at greatest at –40°C. Stems deacclimated substantially less, if at all, than flower buds between January and March. The hardiness of stems varied less than that of the flower buds during the winter.

Rhododendrons were grown at 15 or 24°C combined with a photoperiod of 14 h (SD, short day) or 20 h (LD, long day), and acclimated in a decreasing temperature regime. The hardiness was determined by controlled freezing tests of the leaves. Photoperiod and temperature during the growing season affected not only the growth (Väinölä and Junttila 1998), but also the cold hardiness of rhododendrons (Väinölä et al. 1999). Cultivars differed in their responses. 'Pohjola´s Daughter' benefited from SD as well as from high temperature, while 'Helsinki University' attained better hardiness at a cool growing season temperature, and was less sensitive to photoperiod. The timing of cessation of growth correlated with the hardiness of 'Helsinki University', but no such correlation was seen with 'Pohjola´s Daughter'.

Induced polyploidy can improve the ornamental value of flowering plants. Freezing tolerance of diploid and corresponding tetraploid rhododendron genotypes was compared by Väinölä and Repo (1999). The hardiness was studied with controlled freezing tests during a hardening regime. The leaves of both diploid clones attained at ca. 13°C better cold hardiness than those of the corresponding tetraploid clones, ranging from –47.1°C for the hardier diploid to –22.7°C for the more sensitive tetraploid. There was no difference in the stem hardiness associated with ploidy, which occured between –33°C and –40°C depending on test and date. Diploid florets were, however, significantly hardier than the tetraploid ones.

Repo et al. (1998) studied timing of growth cessation, leaf senescence, initiation of frost hardening and maximum hardiness of one- to two-year-old seedlings of oak (*Quercus robur* L.), maple (*Acer platanoides* L.), elm (*Ulmus glabra* Hudson) and silver birch (*Betula pendula* Roth). Oak, maple and elm, which have their natural northern distribution limit in southern Finland, exhibited low temperature exotherms (LTE) between –33 and –37°C. LTE reveals the temperature at which the remaining supercooled intercellular water freezes, and heat is released from a sample, in differential thermal analysis. Normally freezing of supercooled water is lethal to the tissues, but the phenomenon does not apply to all species. No LTEs were found in birch, the most frost tolerant species in the experiment.

Cultural practices for improving winter survival

Winter injury in tender crop and amenity plants can be diminished by cultural practices. Timing of growth cessation is critical for the winter survival of woody plants: autumn frosts may frequently destroy the non-acclimated, vegetative shoots of exotic species. In nurseries the problem is pronounced, as shoot growth often lasts longer in young than in adult plants. Konttinen (1997) studied the potential of short-day treatments for improving the rate of cold acclimation in one- to four-year-old coniferous seedlings. In most spruce (*Picea* A. Dietr.) and fir (*Abies* Miller) species a 2–4 weeks exposure to shortened days in August improved both the rate of acclimation and the winter survival of seedlings. Nevertheless, susceptible species and provenances were not able to attain the same level of cold resistance as the hardier taxa.

In nurseries plants are increasingly produced in containers. Over-wintering of container-grown plants is problematic since roots are far less cold resistant than aerial parts of plants. Kallio (1980) studied root cold hardiness of ca. 20 commonly grown species. Ten hours at –10 to –15°C destroyed most roots. *Caragana arborescens* Lam., *Spiraea* 'Grefsheim' and *Syringa josikaea* Jacq. fil ex Reichenb. were the hardiest among the species studied. Different over-wintering methods for maintaining container-grown landscape plants were compared by Lehmushovi (1985, 1986, 1987). The most successful practice was to keep the plants horizontal and covered with plastic mulch. However, in a cold winter with little snow, even the best practice resulted in a 60% loss of container-grown plants (Lehmushovi 1987).

Fertilizer practices may also contribute to cold acclimation of woody plants. Rikala and Repo (1997) studied frost hardening of second-year pine (*Pinus sylvestris* L.) seedlings under different fertilization regimes. Late summer application prolonged the growth period of needles, increased root collar diameter and slightly increased the level of hardiness in the needles. Rikala and Repo (1997) concluded that a wider spectrum of fertilization applications should be assessed to obtain a comprehensive picture of the effects of fertilization on frost hardiness.

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Future prospects

Most of the cultivated winter cereals and grass species are relatively freezing tolerant and in most cases winter damage is caused by ice-encasement and winter pathogens. Thus, current breeding programs focus on screening for pathogen resistance and on improving yield potential and growth after cutting. These characters may be transferred to existing germplasm through crosses with more productive European genotypes. At the same time, less winter-hardy germplasm is obtained and the risk of freezing damage increases. Regarding horticultural crops, different types of protected culture and winter protection systems (row covers and mulches) are becoming more common. Future work on amenity plants is aimed at adding to the choice and improving the genetic quality of plant material. Improved cold hardiness remains one of the major objectives in both crop and ornamental plant breeding.

To date, the recommended growing zones for new cultivars have been determined by field tests in different areas. The field experiments will maintain their significance, but they will be supported and accelerated by the results from laboratory tests. Modern methods of cold hardiness measurement, such as *in vitro* screening, differential thermal analysis, impedance spectroscopy and use of biochemical indicators, will assist to eliminate the most susceptible genotypes. Recent advances in reducing heterozygosity of crop plants through anther culture will enable an efficient use of molecular markers in plant breeding. In addition, using effective statistical techniques for analysis of cold hardiness data will aid in distinguishing the most desirable traits and genotypes.

Molecular techniques develop rapidly and permit increased accumulation of information on the mechanisms of cold hardiness. However, the regulation of freezing tolerance and cold acclimation is complex and controlled by numerous unknown genes. At the moment, hundreds of cold-regulated genes have been identified from a wide range of plant species. To date, an overexpression of these genes has failed to improve freezing tolerance significantly. Therefore, gene cloning is focused on the identification of regulatory elements that control a large number of genes responsible for governing response to stress. Overexpression of these regulatory elements under the action of stress-inducible promotors may force the plants to acclimate rapidly under unfavorable conditions. Whether these modifications improve crop productivity and whether they operate without any negative effect on yield potential remains to be seen.

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References

Aaltonen, M. 1995. The effect of apple rootstocks YP and A2 on yield and winter hardiness of apple in Finland. *Acta Agriculturae Scandinavica, Section B, Soil and Plant Science* 45: 202–205.

Aflatuni, A. 1998. Minttuöljyä jokaiseen makuun! *POHERIKA (Pohjoisen Erikoiskasvit 1996–1999) -seminaari*, Sotkamo 23.11.1998. p. 14–19.

Alanko, P. & Tegel, S. 1989. KESKAS-tutkimus. Kestäviä koristekasveja viherrakentamisen tarpeisiin (with English summary). *Sitra sarja B* 98: 1–111.

Antikainen, M., Griffith, M., Zhang, J., Hon, W.-G., Yang, D.S.C. & Pihakaski-Maunsbach, K. 1996. Immunolocalization of antifreeze proteins in winter rye leaves, crowns, and roots by tissue printing. *Plant Physiology* 110: 845–857.

– & Pihakaski, S. 1993. Cold-induced changes in the polysome pattern and protein synthesis in winter rye (*Secale cereale*) leaves. *Physiologia Plantarum* 89: 111–116.

– & Pihakaski, S. 1994. Early development in RNA, protein, and sugar levels during cold stress in winter rye (*Secale cereale*) leaves. *Annals of Botany* 74: 335–341.

Antonius-Klemola, K., Selonen, K. & Tigerstedt, P. 1998. Breeding of winter hardy raspberry-blackberry hybrids in Finland. In: Niskanen, A.-M. (ed.). *Plant breeding* *and forest tree breeding today*. Department of Plant Biology, University of Helsinki. p. 15.

Cardi, T., Puite, K.J., Ramula, K.S., Ambrosio, F.D. & Frusciante, L. 1993. Production of somatic hybrids between frost tolerant *Solanum commersonii* and *S. tuberosum*: Protoplast fusion, regeneration and isoenzyme analysis. *American Potato Journal* 70: 753–764.

Collan, O. 1934. Suomen hedelmänviljelys hedelmätarhojamme v. 1929 kohdanneen tuhon valossa. *Valtion Maatalouskoetoiminnan Julkaisuja* 60: 1–59.

Dalman, P. 1999. Evaluation of red currant cultivars in Finland. *Acta Horticulturae* (In press).

– , Hiirsalmi, H., Hietaranta, T. & Linna, M.-M. 1997. Jenkka and Jatsi, two new red raspberry cultivars. *Agricultural and Food Science in Finland* 6: 19–24.

– , Laurinen, E., Aaltonen, M. & Hiirsalmi, H. 1991. 'Ottawa' ja 'Muskoka' varmimmat vadelmalajikkeet. *Koetoiminta ja Käytäntö* 48: 62.

– & Matala, V. 1997. The effect of cultivation practices on the overwintering and yield of strawberry. *Acta Horticulturae* 439: 881–886.

Galambosi, B., Kaukovirta, E. & Sz-Galambosi, Z. 1991. Mauste- ja rohdosyrttien viljely (Summary: Cultivation of spices and medicinal herbs). *Helsingin Yliopiston Puutarhatieteen Laitoksen Julkaisuja* (*Department of Horticulture, University of Helsinki, Publication*) 18: 1–114.

– & Svoboda, P.K. 1994. Overwintering, growth and essential oil content of 12 *Origanum vulgare* species of different geographical origin grown at 62°N latitude in Finland. In: Ahonen, S. (ed.). *Production of Herbs, Spices and Medicinal Plants in the Nordic Countries*. Proceedings of NJF seminar 240, Mikkeli, Finland, 2–3 August 1994. p. 84–85.

Hahtonen, M., Borg, M. & Pehu, E. 1994. Acclimation and deacclimation of timothy (*Phleum pratense* L.). *Workshop on Plant Adaptation to Cool Climates*, 12–14 October, Hamburg, Germany. p. 91–96.

Harvey, D.M.R. & Pihakaski, K. 1989. Ultrastructural changes arising from freezing of leaf blade cells of rye (*Secale cereale*): an investigation using freeze-substitution. *Physiologia Plantarum* 76: 262–270.

Hietaranta, T.P. & Hiirsalmi, H.M. 1989. Blackcurrant breeding in Finland. *Acta Horticulturae* 262: 157–160.

Hiirsalmi, H.M. 1985. Breeding highbush blueberry in Finland. *Acta Horticulturae* 165: 71–76.

– 1989a. Research into *Vaccinium* cultivation in Finland. *Acta Horticulturae* 241: 175–184.

– 1989b. Breeding *Rubus* species in Finland. *Acta Horticulturae* 262: 75–81.

– & Hietaranta, T.P. 1989. Winter injuries to highbush and lowbush blueberries in Finland. *Acta Horticulturae* 241: 221–226.

– & Säkö, J. 1976. The nectar raspberry, *Rubus idaeus* x *Rubus arcticus* – a new cultivated plant. *Annales Agriculturae Fenniae* 15: 168–174.

– & Säkö, J. 1980. Hybrids of the arctic bramble species (*Rubus stellatus* x *R. arcticus*). *Acta Horticulturae* 112: 103–108.

– & Säkö, J. 1981. 'Heisa' – a new nectar raspberry variety. *Annales Agriculturae Fenniae* 20: 268–272.

Hömmö, L.M. 1992. Hardening ability of some winter wheat, winter rye and winter barley varieties. Use of conductivity method in evaluating the hardening ability of overwintering crop species. *Norwegian Journal of Agricultural Science* 7 (suppl.): 39–50.

– 1994a. Hardening of some winter wheat (*Triticum aestivum* L.), rye (*Secale cereale* L.), triticale (x *Triticosecale* Wittmack), and winter barley (*Hordeum vulgare* L.) cultivars during autumn and the final winter survival in Finland. *Plant Breeding* 112: 285–293.

– 1994b. Resistance of winter cereals to various winter stress factors – inter- and intraspecific variation and the role of cold acclimation. *Agricultural Science in Finland* 3: 1–32. (Academic dissertation).

– & Pulli, S. 1993. Winterhardiness of some winter wheat (*Triticum aestivum*), rye (*Secale cereale*), triticale (x *Triticosecale*) and winter barley (*Hordeum vulgare*) cultivars tested at six locations in Finland. *Agricultural Science in Finland* 2: 311–327.

Jamalainen, E.A. 1958. Kasvien talvehtimisesta ja sen parantamismahdollisuuksita. *Kasvinsuojeluseuran julkaisuja* 13: 1–39.

Joy, P. 1995. Breeding roses adapted to a high-latitude, semi-maritime climate. In: Raatikainen, M. (ed.). *Adaptation in Plant Breeding.* Proceedings of the XIV EUCARPIA Congress, Jyväskylä, Finland, 31 July – 4 August, 1995. p. 61–62.

– & Kangaspunta, M. 1999. Miten yhdistää pitkä kukinta ja talvenkestävyys. *Puutarha&kauppa* 3, 5: 18–19.

Juhanoja, S. & Heikkilä, M. 1995. Selection of hardy and true-to-type woody ornamental clones in Finland. In: Raatikainen, M. (ed.). *Adaptation in Plant Breeding.* Proceedings of the XIV EUCARPIA Congress, Jyväskylä, Finland, 31 July – 4 August, 1995. p. 100–101.

– , Heikkilä, M. & Virtanen, A. 1998. Clone selection of woody ornamentals in Finland. *Acta Agriculturae Scandinavica, Section B, Soil and Plant Science* 48: 113–127.

– & Hiirsalmi, A. 1991. Tuloksia puiden ja koristepensaiden menestymisen seurannasta vuosina 1970–90. *Maatalouden tutkimuskeskus, Tiedote* 24/91: 1–116.

Kallio, T.K. 1966. Koristepuiden ja -pensaiden levinneisyydestä ja menestymisestä Suomessa (Zusammenfassung: Über Verbreitung und Gedeihen von Zierbäumen und – sträuchern in Finnland). *Annales Agriculturae Fenniae* 5, Suppl. 1: 1–107.

– 1977. The ornamental trees and shrubs grown at the Institute of Horticulture in the years 1927–1976. *Annales Agriculturae Fenniae* 16: 27–36.

– 1980. Eräiden taimitarhakasvien juuriston pakkasenkestävyydestä. *Maatalouden tutkimuskeskus, Puutarhantutkimuslaitoksen tiedote* 24: 36–43.

Kaukovirta, E. 1967. Eräiden puuvartisten koristekasvien talvehtimisesta Viikissä, Jyväskylässä, Kauhajoella ja Rovaniemellä. *Maataloustieteellinen Aikakauskirja* 39: 216–228.

– & Syri, P. 1985. An attempt to reanalyze winter injury of apple trees in Finland during this century. *Acta Horticulturae* 168: 73–83.

Kemppainen, R., Galambosi, B. & Niskanen, M. 1997. Vihermintun menestyminen luonnonmukaisessa

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viljelyssä Kainuussa. *Mauste- ja Rohdosyrttien Tutkimusseminaari,* Jokioinen, 4.12.1997. p. 47–49.

Konttinen, K. 1997. Ulkomaisten havupuiden ja kuusen karaiseminen lyhytpäiväkäsittelyllä. *Metsäntutkimuslaitoksen Tiedonantoja* 650: 57–75.

Krause, G.H. 1994. The role of oxygen in photoinhibition of photosynthesis. In: Foyer, C.H. & Mullineaux, P.M. (eds.). *Causes of Photooxidative Stress and Amelioration of Defense Systems in Plants*. CRC Press, Boca Raton. p. 43–76.

Kukkonen, M. & Pihakaski, K. 1988. Eräiden ruislajikkeiden kylmänkestävyydestä. *Luonnon tutkija* 92: 114–116.

Lehmushovi, A. 1985. Astiataimien talvettamiskoe. *Puutarha* 88: 556–560.

– 1986. Astiataimien talvettaminen. *Puutarha* 89: 592–593.

– 1987. Astiataimien talvettaminen ulkona. *Puutarha* 90: 666–668.

Lindén, L., Rita, H. & Suojala, T. 1996. Logit models for estimating lethal temperatures in apple. *HortScience* 31: 91–93.

Linna, M.-M., Dalman, P. & Hiirsalmi, H. 1993. Recent progress in the Finnish raspberry breeding program. *Acta Horticulturae* 352: 373–376.

Lundén, K. & Säkö, J. 1988. Koristepuiden ja -pensaiden talvehtiminen: Talvi 1986/87. *Maatalouden tutkimuskeskus, Tiedote* 13/88: 1–86.

Manner, R. 1967. Viljalajien oraiden hallankestävyydestä. Kokemuksia pakkashuonekokeista (Summary: Frost resistance of young cereal plants). *Maatalous ja Koetoiminta* 21: 57–62.

Meurman, O. 1963. Puutarhantutkimuslaitoksella Piikkiössä kokeilluista koristepuista ja -pensaista. (Summary: Notes on ornamental trees and shrubs at the Department of Horticulture (Piikkiö, Finland)). *Acta Forestalia Fennica* 76, 3: 1–44.

Mukula, J. & Rantanen, O. 1989a. Climatic risks to the yield and quality of field crops in Finland. III. Winter rye 1969–1986. *Annales Agriculturae Fenniae* 28: 3–11.

– & Rantanen, O. 1989b. Climatic risks to the yield and quality of field crops in Finland. IV. Winter wheat 1969–1986. *Annales Agriculturae Fenniae* 28: 13–19.

– & Rantanen, O. 1989c. Climatic risks to the yield and quality of field crops in Finland. V. Spring wheat 1969–1986. *Annales Agriculturae Fenniae* 28: 21–28.

– & Rantanen, O. 1989d. Climatic risks to the yield and quality of field crops in Finland. VI. Barley 1969–1986. *Annales Agriculturae Fenniae* 28: 29–36.

– & Rantanen, O. 1989e. Climatic risks to the yield and quality of field crops in Finland. VII. Oats 1969–1986. *Annales Agriculturae Fenniae* 28: 37–43.

Niemeläinen, O. 1990. Factors affecting panicle production of cocksfoot (*Dagtylis glomerata* L.) in Finland. III. Response to exhaustion of reserve carbohydrates and to freezing stress. *Annales Agriculturae Fenniae* 29: 241–250.

Nissinen, O. 1996. Analysis of climatic factors affecting snow mould injury in first-year timothy (*Phleum pratence* L.) with special reference to *Sclerotinia borealis. Acta Universitatis Ouluensis, series A* 289: 1–115. (Academic Dissertation.)

– & Hakkola, H. 1995. Effects of plant species and harvesting system on grassland production in northern Finland. *Agricultural Science in Finland* 4: 479–494.

Nykänen-Kurki, P. & Rönkä, T. 1998. White clover cv. AberHerald in Mikkeli over the period 1993–1997. *Crop Development for the Cool and Wet Regions,* Proceedings of the Annual Workshop of the Working Group on Overwintering and Spring Growth of White Clover, COST 814. DvO Melle, Belgium, 20–22 August, p. 13–19.

Pahkala, K., Laakso, I. & Hovinen, S. 1991. The effect of frost treatment on turnip rape seedlings, ripening seeds and their fatty acid composition. *Proceedings on GCIRC Eight International Rapeseed Congress*, Saskatoon, Saskatchewan, Canada, 9–11 July. p. 1749–1753.

Palonen, P. 1999. The relationship of seasonal changes in carbohydrates and cold hardiness in canes and buds of three red raspberry cultivars. *Journal of the American Society for Horticultural Science* 124: 507–513.

– & Buszard, D. 1998. *In vitro* screening for cold hardiness of raspberry cultivars. *Plant Cell, Tissue and Organ Culture* 53: 213–216.

– & Junttila, O. 1999. Cold hardening of raspberry plants *in vitro* is enhanced by increasing sucrose in the culture medium. *Physiologia Plantarum* 106: 386–392.

– & Lindén, L. 1999. Dormancy, cold hardiness, dehardening, and rehardening in selected red raspberry cultivars. *Journal of the American Society for Horticultural Science* 124: 341–346.

Pesola, V.A. 1932. Vehnän jalostustyöstä ja sen tuloksista. *Valtion Maatalouskoetoiminnan julkaisuja* 43: 1–87.

Pietilä, M. & Karvonen, J. 1999. Tyrni viljelykasvina – mahdollisuuksia ja haasteita. *Puutarha&kauppa* 3, 19: 15–17.

– , Karvonen, J. & Aflatuni, A. 1999. Talviharson käyttö lisää mansikan satopotentiaalia. *Puutarha&kauppa* 3, 23: 8–9.

Pihakaski-Maunsbach, K., Griffith, M., Antikainen, M. & Maunsbach, A.B. 1996. Immunogold localization of glucanase-like antifreeze protein in cold acclimated winter rye. *Plant Physiology* 191: 115–125.

– & Puhakainen, T. 1995. Effect of cold exposure on cortical microtubules of rye (*Secale cereale*) as observed by immunocytochemistry. *Physiologia Plantarum* 93: 563–571.

Pohjakallio, O., Salonen, A. & Antila, S. 1960. Päivän pituuden vaikutuksesta apilan talvenkestävyyteen (Summary: The effect of day length on winter hardiness of clover). *Maatalous ja koetoiminta* 14: 104–111.

Pohjanheimo, O. 1959. Syysvehnän talvenkestävyydestä maamme viljelysoloissa. *Maatalous ja Koetoiminta* 13: 98–109.

Pulli, S.K. 1986. Climatic factors in relation to winterhardiness. *Landbruksväxternas övervintring*, NJF Seminar No. 84, Jokioinen. p. 48–58.

– , Hjortsholm, K., Larsen, A., Gudleifsson, B., Larsson, S., Kristiansson, B., Hömmö, L., Tronsmo, A.M., Ruuth, P. & Kristensson, C. 1996. *Development and evaluation of laboratory test methods for winterhardiness breeding*. Nordic Gene Bank, 68 p.

Putievsky, E., Ravid, U., Dudai, N., Katzir, E., Galambosi, B., Aflatuni, A., Pessala, R. & Hupila, I. 1998. Yield potential and essential oil content of *Origanum vulgare, Artemisia dracunculus* and *Melissa officinalis* grown at different sites in Israel and Finland. *Drogenreport* 11, 20: 3–11.

Repo, T., Halonen, P., Leinonen, I. & Hänninen, H. 1998. Frost hardiness in oak (*Quercus robur*), maple (*Acer platanoides*), elm (*Ulmus glabra*) and silver birch (*Betula pendula*). *Biotieteen päivät*, Helsinki, Finland. p. 49.

– & Pulli, S. 1996. Application of impedance spectroscopy for selecting frost hardy varieties of English ryegrass. *Annals of Botany* 78: 605–609.

Rikala, R. & Repo, T. 1997. The effect of late summer fertilization on the frost hardening of second-year Scots pine seedlings. *New Forests* 14: 33–44.

Seppänen, M.M., Cardi, T., Borg-Hyökki, M. & Pehu, E. 1999. Characterization and expression of cold-induced glutathione S-transferase in freezing tolerant *Solanum commersonii*, sensitive *S. tuberosum* and their interspecific somatic hybrids. *Plant Science* (in press).

– , Majaharju, M., Somersalo, S. & Pehu, E. 1998. Freezing tolerance, cold acclimation and oxidative stress in potato. Paraquat toleance is related to acclimation but is a poor indicator of freezing tolerance. *Physiologia Plantarum* 102: 454–460.

Sorvari, K. 1998. Onko ranskalaisesta rakuunasta viljelykasviksi Pohjois-Suomeen? *POHERIKA (Pohjoisen Erikoiskasvit 1996–1999) -seminaari*, Sotkamo 23.11.1998. p. 20–23.

Suojala, T. & Lindén, L. 1997. Frost hardiness of *Philadelphus* and *Hydrangea* clones during ecodormancy. *Acta Agriculturae Scandinavica, Section B, Soil and Plant Science* 47: 58–63.

Säkö, J. 1958. Eräiden suvuttomasti ja siemenistä lisättyjen perusrunkojen vaikutuksesta omenapuiden menestymiseen Suomessa (Summary: The influence of some vegetatively raised and seedling rootstocks upon apple trees in Finland.) *Valtion maatalouskoetoiminnan julkaisuja* (*Publications of the Finnish state agricultural research board*) 165: 1–90.

– 1970. Inverkan av B-995 på äppleträdens vinterhärdighet. *Nordisk Jordbruksforskning* 52: 118–119.

– 1985a. Winter hardiness problems in fruit growing in Finland. *Acta Horticulturae* 168: 31–36.

– 1985b. Perusrungon merkitys omenapuiden talvehtimisessa. 1983–84. *Maatalouden tutkimuskeskus, Tiedote* 17/85: 17–20.

– & Hiirsalmi, H. 1980. Winterhardiness and productivity of the red raspberry in Finland. *Acta Horticulturae* 112: 221–227.

– & Laurinen, E. 1986. Apple trees in ridge planting. *Acta Horticulturae* 160: 285–292.

– & Lundén, K. 1988. Talven 1986–87 tuhot hedelmä- ja marjatarhoissa. *Maatalouden Tutkimuskeskus, Tiedote* 14/88: 1–34.

– & Meurman, O. 1960. Kestävien välirunkojen merkityksestä omenapuille. *Maatalous ja Koetoiminta* 14: 171–181.

– & Yli-Pietilä, M. 1987. Winter injury to Finnish apple orchards in 1984–85. *Annales Agriculturae Fenniae* 26: 251–260.

Uosukainen, M. 1992. *Rhododendron brachycarpum* subsp. *tigerstedtii* Nitz. – a transmitter of extreme frost hardiness. *Acta Horticulturae* 320: 77–83.

– & Tigerstedt, P.M.A. 1988. Breeding of frost hardy rhododendrons. *Journal of Agricultural Science in Finland* 60: 235–254.

Vaarama, A. 1941. Helsingin yliopiston kasvitieteellisessä puutarhassa talven 1939–40 aikana puille ja pensaille aiheutuneet pakkasvauriot. *Annales Botanici Societatis Zoologicae Botanicae Fennicae Vanamo* 16, 6: 1–48.

Valmari, A. 1959. Väkilannoituksen vaikutuksesta ohran, kauran ja perunan hallankestävyyteen. (Summary: The effect of fertilization on the frost resistance of barley, oats, and potato.) *Maatalous ja Koetoiminta* 13: 54–63.

Valo, R. 1996. Uudet Piikkiön omenalajikkeet menestyvät Etelä-Savossa. *Koetoiminta ja Käytäntö* 53: 20.

Varis, E. 1965. Winter hardiness as a breeding problem of winter wheat in Finland. *Acta Agralia Fennica* 107:320–336.

Vuorinen, J. 1958. Maaperän merkityksestä omenapuiden talvenkestävyydelle (Summary: On the influence of soil properties on the winter resistance of apple trees). Maatalouden tutkimuskeskus, Maantutkimuslaitos. *Agrogeological publications* 69: 1–32.

Väinölä, A. 1992. Atsaleoita Suomenkin puistoihin – jalostus alkaa lajiristeytyksillä (Summary: Azaleas for Finnish parks – Breeding work starts with interspecific crosses). *Sorbifolia* 23: 133–142.

– 1999. Atsalean jalostuksen kuulumisia (Summary: Progress in azalea breeding). *Sorbifolia* 30: 45–47.

– & Junttila, O. 1998. Growth of *Rhododendron* cultivars as affected by temperature and light. *Journal of Horticultural Science and Biotechnology* 73: 812–821.

– , Junttila, O. & Rita, H. 1999. Cold hardiness of rhododendron cultivars grown in different photoperiods and temperatures. *Physiologia Plantarum* 107: 46–53.

– , McNamara, S. & Pellett, H. 1997. Stem and bud hardiness of deciduous azalea. *Journal of Environmental Horticulture* 15: 45–50.

– & Repo, T. 1999. Cold hardiness of diploid and corresponding autotetraploid rhododendrons. *Journal of Horticultural Science and Biotechnology* 74: 541–546.

Yao, Y. & Tigerstedt, P.M.A. 1995. Geographical variation of growth rhythm, height, and hardiness, and their relations in *Hippophaë rhamnoides*. *Journal of the American Society for Horticultural Science* 120: 691–698.

Yli-Pietilä, M., Säkö, J. & Kinnanen, H. 1987. Puuvartisten koristekasvien talvehtiminen talvella 1984–85. *Maatalouden tutkimuskeskus, Tiedote* 9/87: 1–38.

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SELOSTUS

Pelto- ja puutarhakasvien kylmänkestävyystutkimus Suomessa

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Riittämätön kylmänkestävyys rajoittaa monien kasvilajien viljelyä Suomessa. Tämä artikkeli käsittelee suomalaisia pelto- ja puutarhakasvien talvehtimiseen ja kylmänkestävyyteen liittyviä tutkimuksia. Perinteisesti talvenkestäviä lajikkeita on valittu jalostusaineistosta pitkäaikaisten kenttäkokeiden perusteella. Sittemmin on kehitetty laboratoriossa tehtäviä kylmänkestävyystestejä nopeuttamaan ja tehostamaan valintaa. Viime vuosina tutkimus on lisäksi pyrkinyt selvittämään peltokasvien karaistumisen ja kylmävaurioiden taustalla olevia molekyylitason mekanismeja. Tässä artikkelissa käsitellään peltokasveista syysviljoja, nurmia, apilaa, perunaa sekä rypsiä. Puutarhakasveista mukana ovat omena, mansikka, vadelma, herukat, mustikka, tyrni, yrtit sekä koristepuut ja pensaat. Niiden osalta käsitellään talvehtimishavaintojen ja lajikevalinnan lisäksi viljelytoimenpiteiden vaikutusta talvenkestävyyteen. Kontrolloidut kylmätestit ovat mahdollistaneet myös puutarhakasvien kylmänkestävyysmekanismien tarkemman tutkimuksen.