Abstract. At the northern borders of the peach-growing zone, low temperatures during winter are the critical factors for the survival of the trees and for the reliability of production. Our aim was to carry out detailed analysis of the hardening and dehardening processes of flower buds of three peach cultivars with contrasting frost tolerance and to evaluate the effects of environmental factors and of genotypic differences in two consecutive winters with very diverse weather conditions. Based on our results, the hardening process takes place in two phases in peach flower buds. In the first phase, gradual cooling is essential if the level of frost resistance characteristic of the genotype is to develop, but in the second phase, it is a prerequisite that the external temperature drop consistently below zero for reaching the maximum frost tolerance. The maximum level of frost resistance developed by peach flower buds was only maintained for a limited time and the differences between the cultivars gradually decreased as flowering time approached. At the time of leaf fall in the fall and before flowering, the difference between the mean frost tolerance values for flower buds of the extremely frost-tolerant and frost-sensitive cultivars was only 2 °C, whereas in midwinter, it was 5 to 5.5 °C.

The zone in which peaches can be economically grown is limited to both north and south by the temperature. In the northern hemisphere, the winters become too mild for peach as we go south and too cold as we go north. Hungary is located on the northern borders of the peach-growing zone, so low temperatures in the dormant season are the critical factors for the survival of the trees and for the reliability of production. The various overwintering organs of the trees have very different levels of frost resistance, which also vary greatly over time. The experiments carried out in apricot and peach chiefly examined changes in the frost resistance of the flower buds, but there is information on the frost tolerance of the vegetative buds and the twigs as well (Guerrero, 1982; Hatch and Walker, 1969; Hewett, 1976; Layne and Gadsby, 1995; Miranda et al., 2005; Proebsting and Mills, 1978; Quamme, 1974; Szabó, 1992; Werner et al., 1993). Farm experience shows that during dormancy, it is the flower buds that most frequently suffer frost damage (Nyeki and Szabo, 1989; Szabo, 2002; Szabó and Nyeki, 1988, 1991, 1998; Timon, 2000). The vegetative buds are usually damaged at lower temperatures (4 to 5 °C) than the flower buds, although it has been reported that for some genotypes, the vegetative buds are more sensitive to frost than the flower buds in the first half of the winter (Szalay, 2001).

This can be explained by the diverse developmental rates of the two types of buds and by their differing responses to changes in environmental conditions. The flower buds play a key role in yield stability, because damage to these organs leads directly to yield losses. If the vegetative buds on the nodes are destroyed by frost, they can be partially replaced by the latent buds on older branches. From a practical point of view, the frost resistance and winter-hardiness of the flower buds thus deserves more detailed study.

In preparation for the winter, the flower buds gradually develop frost resistance as a result of the joint effects of inherited genotypic traits and environmental factors. This process begins long before frost is actually experienced, probably in response to the shortening of the days and the gradual decline in the temperature (Ashworth et al., 1983; Ashworth and Wisniewski, 1991; Flore, 1994; Westwood, 1993). Investigations on the vegetative organs of apple trees and forest trees indicated that the frost tolerance of overwintering organs developed in several stages (Howell and Weiser, 1970; Tromp, 2005). Studies on the frost tolerance of the overwintering organs of woody plants demonstrated that the hardening processes taking place during the first half of dormancy could be divided into several stages (Tromp, 2005). Two stages could be distinguished for fruit trees in the temperate zone and three for trees in the northern boreal zone. In the case of apple trees, the first stage of hardening was found to start well before the trees shed their leaves in fall and continued until the external temperature dropped consistently below 0 °C. Temperatures below 0 °C were required if the frost tolerance of the tissues was to increase. If this condition was not satisfied, the second stage of hardening failed to take place (Howell and Weiser, 1970).

In addition to genetically determined traits and ecological factors, other factors also influence the frost resistance and winter-hardiness of overwintering organs. These include the training system, the cultural practices, and the yield in the previous year (Byers and Marini, 1994; Cser et al., 1983, 1998; Timon, 2000). Frost resistance also depends on the health status of the trees, because many pathogens, particularly bacteria, may cause severe reduction in frost resistance (Gross, 1984; Lindow et al., 1982).

Because considerable differences have been observed between the frost resistance levels of various peach accessions, one of the most important tasks facing breeders at the northern limit of the production zone is to obtain precise knowledge on the frost resistance and winter-hardiness of the genotypes and to breed resistant cultivars (Layne, 1989, 1996). Thus, the development rate of the overwintering organs of peach and changes in their frost resistance during the dormancy period have been regularly investigated in recent years in the gene bank collection of Corvinus University of Budapest.

The present article provides a detailed analysis of the hardening and dehardening of flower buds, of the effects of environmental factors, and of the genotypic differences in two consecutive winters with very diverse weather conditions.

Materials and Methods

Six trees of each of Venus, Redhaven, and Piroska peach cultivars were assessed. The trees were grown at the same location in the experimental orchard in Soroksár on the outskirts of Budapest. The cultivars were chosen for the present study on the basis of previous research on the frost resistance of the flower buds in 12 peach cultivars (Szalay, 2001; Szalay et al., 2000). ‘Venus’ is the most frost-tolerant peach cultivar in the gene bank collection. It is a late-maturing, yellow-fleshed nectarine, bred in Italy, and is popular in the Mediterranean region. It is grown in less exposed locations in Hungary but often suffers frost damage. In the international literature, ‘Redhaven’ is frequently used as a reference cultivar for the medium frost resistance category (Layne 1989, 1996), whereas ‘Piroska’ is the most frost-tolerant peach cultivar in the collection. This cultivar is little known internationally, because it is only grown in Hungary and in the neighboring countries. It is a downy, white-fleshed landrace developed in the Carpathian Basin and selected for the strongly continental climate of the Great Hungarian Plain. It was state-registered in Hungary in 1973.

The trees were grafted onto peach seedling rootstocks (‘C 2630’) and trained to a slender spindle shape with a spacing of 4 × 2 m. Integrated plant protection was applied in...
the LT50 values (the temperature at which aged brown tissues). At each sampling date, the tissues (green living tissues versus damaged lengthwise and observing the discoloration of the discoloration of the tissues) was scored by cutting the flower buds in half room temperature, the extent of frost damage was reduced by 2°C/h and the samples were kept at the desired freezing temperature for 4 h, after which the temperature was raised by 2°C/h. At each sampling date, the effects of three to five freezing temperature levels in 2°C decrements were examined. After 1 d at room temperature, the extent of frost damage was scored by cutting the flower buds in half lengthwise and observing the discoloration of the tissues (green living tissues versus damaged brown tissues). At each sampling date, the LT50 values (the temperature at which 50% of the flower buds were damaged) were calculated from the regression curves ordered to the percentages of bud damages of the six branches of each cultivar measured at the three to five freezing regimes to obtain comparable data (Hatch and Walker, 1969; Proebsting, 1970; Proebsting and Sakai, 1979; Quamme, 1974). In addition to field sampling, a 3-year-old potted tree of ‘Redhaven’ was placed into a room in early October with controlled temperature conditions (15 ± 2°C), a temperature level found to be neutral from the aspect of chilling unit accumulation according to Richardson et al. (1974) with 60% to 70% relative water content and under natural light derived through windows. The LT50 values for its flower buds were also evaluated regularly from October to January. The statistical analyses (one-way and two-way analyses of variance) on the data matrices of the LT50 values were carried out using the program package of Statistica 6.0 for Windows (StatSoft, Tulsa, OK). The results obtained during the last two winters (2006–2007 and 2007–2008) are analyzed in this article.

Results

The effect of the sampling date on the LT50 was the highest and most significant factor accounting for 90.6% of the total variance. This was followed by the cultivar effect, which explained 5.9% of the total variance at the P = 0.001 level. The year effect, although also significant at the P = 0.001 level, contributed only a low portion to the total variance (1.8%), whereas the two-way interactions and the within-group variance were not significant components. The winter season of 2006–2007 was significantly milder than the averages of the last 15 years (Fig. 1); it was the mildest winter in the last decades. This in general has led to significantly higher LT50 values irrespective of the cultivars. The temperature profile during the winter season of 2006–2007 was close to the averages of the last 15 years, making it possible to compare the effects of an average Hungarian winter temperature profile on the hardening and dehardening processes of peach trees with the effects of an extremely mild winter (Fig. 1).

Irrespective of the year, the cultivars could be characterized with similar LT50 curves during the dormant seasons and at each sampling date, their ranking based on the frost tolerance was always the same; ‘Venus’ was the most frost sensitive followed by ‘Redhaven’ and the most frost-tolerant ‘Piroška’. When examining changes in the level of frost tolerance, there were two distinct parts in the LT50 curves (Figs. 2 and 3). The hardening process taking place during fall and early winter could be characterized with the gradually increasing frost tolerance of the flower buds, which occurred in parallel with the decrease in the daily temperature. During the second half of the winter, the frost resistance gradually declined, a process known as dehardening. The results showed that the maximum level of frost resistance developed by peach flower buds was only maintained for a limited time and the differences between...
the cultivars gradually decreased as flowering time approached.

**Hardening.** During hardening, two phases were observed in the flower buds. The first lasted until the external temperature dropped consistently below 0 °C. In an average winter season (2007–2008), the mean frost tolerance value of the flower buds at the end of the first period of hardening was –16.0 °C for ‘Venus’, –19.5 °C for ‘Redhaven’, and –21.0 °C for ‘Piroska’ (Fig. 3). These values were recorded in mid-October. This was followed by a few days of very mild weather, leading to a slight reduction in the frost resistance, but when the external temperature dropped consistently below 0 °C, the hardening of the overwintering tissues continued, and by late December, the buds reached their highest levels of frost tolerance, LT50 being between –21 and –26 °C.

In September, at the beginning of the hardening process, there was only a 2 °C difference between the LT50 of ‘Piroska’ (the most frost-tolerant) and of ‘Venus’ (the most frost-sensitive). This difference gradually increased during the first half of dormancy, being 5 °C by late December or early January.

In the extremely mild winter (2006–2007), with the exception of 2 d, the value of the daily temperature minimum did not drop below 0 °C until early December, and there was only a short spell of cold weather before the temperature rose above 0 °C again. At the end of the first phase of hardening, in the middle of October, the LT50 values were –13.8 °C for ‘Venus’, –15.5 °C for ‘Redhaven’, and –16.8 °C for ‘Piroska’ (Fig. 2). The maximum frost tolerance of the cultivars was very similar to that recorded in the colder winter but was reached much later and at a much slower rate. At the end of December, when the flower buds were at the most frost-resistant stage, values of –19.5 and –25 °C were recorded.

The hardening process in the flower buds of the potted tree of ‘Redhaven’ grown at 15 °C slowed and finally stopped. Although the LT50 value of flower buds in the orchard reached –20 °C in mid-November, those kept indoors showed a value of only –16.5 °C (Fig. 4). The second phase of hardening did not take place in the indoor buds, and their frost resistance slowly declined.

**Dehardening.** Like in the case of hardening, the external temperature was crucial during the dehardening period, exerting a considerable influence on the rate at which the frost resistance of the overwintering organs declined. From January onward, the flower buds responded sensitively to warming, and the frost resistance of the buds decreased rapidly in response to mild weather. Substantial differences in the frost resistance of the flower buds were thus observed between the years. In the case of the colder winter (2007–2008), the 5 °C difference noted between the LT50 of the most frost-sensitive and most frost-tolerant flower buds in early January dropped to 2 °C by the second half of April, i.e., the difference was the same as that recorded in the fall, at the beginning of hardening (Fig. 3). In the milder winter, the frost resistance of the flower buds declined more rapidly (Fig. 2).

**Discussion**

The hardening processes of overwintering organs are fundamentally determined by environmental factors, particularly the temperature. Thus, even at the same location, the development rate of the flower buds and the development of frost resistance may differ from year to year. In the present investigations, carried out in 2 consecutive years, two stages could be distinguished in the hardening of flower buds of the three peach cultivars. The first stage lasted until the external temperature dropped consistently below 0 °C. The findings of Howell and Weiser (1970), that below-0 °C temperatures were essential for further hardening after this first stage, was confirmed in an experiment on the flower buds of ‘Redhaven’. The second stage of hardening failed to take place in the flower buds of a tree taken at 15 °C from mid-October, and even during the first stage, the buds hardened to a lesser extent than those of trees in the orchard. Gradual cooling in the first half of the winter is thus essential if the level of frost resistance characteristic to the genotype has to develop. This is confirmed by the fact that in the milder winter of 2006–2007, the mean frost tolerance (LT50) values for the flower buds of the cultivars tested were 1 to 1.5 °C higher than in the year with average weather conditions.
In the second half of the winter, during the ecodormancy period, there was a gradual decline in the frost tolerance of the tissues, the rate of which was greatly dependent on the external temperature. The response of dormant flower buds to above-freezing temperatures becomes more sensitive as the flowering period approaches. When the frost resistance of the flower buds was examined in the cultivar Elberta every 5 to 6 d and was compared with changes in the external temperature, it was found that when the winter temperature exhibited great fluctuations, the frost resistance of the buds followed the external temperature within certain limits. In response to mild weather, there was a rapid decrease in frost tolerance, but renewed cooling caused readhering. Flower buds with reduced frost resistance were thus able to readhere to a slight extent if the external temperature declined, but the loss of frost resistance proceeded at a faster rate than readhering, and the process was also influenced according to the given part of the winter it occurred (Proebsting, 1970). This phenomenon was demonstrated in the second half of Jan. 2007 in the cultivars tested in the orchard of M. T. Cultivars of peach exhibit considerable variability with respect to frost resistance and winter-hardiness, but few data are available on the real level of frost resistance in the overwintering organs of different cultivars.

Although the determination of the maximum frost resistance is genetically attainable, the description of changes in frost resistance is only possible in a series of experiments covering several years as a result of the strong environmental influence. The largest body of data is available for the cultivar Elberta, in which the frost resistance of the flower buds has been examined throughout dormancy (Hatch and Walker, 1969; Proebsting, 1970; Proebsting and Mills, 1966; Quamme, 1974). The level of frost resistance differed greatly at diverse locations in various years with maximum values between −24 and −27 °C recorded at the end of endodormancy. It is clear from the data of other authors, who investigated a number of cultivars, that year to year differences during the winter are greater (Smith et al., 1994; Szabol and Nyéki, 1988, 1991), that differences between the cultivars are far greater than the beginning and end of dormancy than in the middle. This was confirmed by the present results. At the time of leaf falling in the fall and before freezing, the difference between the mean frost tolerance values for flower buds of the extremely frost-tolerant and frost-sensitive cultivars was only 2 °C, whereas in midwinter, it was 5 to 5.5 °C.

Based on the official measurements of the Hungarian Meteorological Service (http://www.met.hu), the yearly average temperature level in Hungary has increased by 0.76 °C during the last 100 years. This value presently is between 10 and 11 °C for the most part of the country (with the exceptions of the higher mountainous peaks). The level of warming up is, however, not linear; it shows a more dramatic increase in the last 40 years compared with the earlier periods (Bartholy et al., 2007; Dunkel, 2005; Mersich et al., 2002). The various climatic scenarios established for Hungary calculate with further warming up and predict the increased occurrences of weather extremities as a result of the special location of the country at the borderlines of three larger climatic zones (Atlantic, Mediterranean, and Continental; Bartholy et al., 2007; Mika, 2005). The climatic changes affect the life functions of peach trees (and the other temperate zone deciduous trees) unfavorably. These species have developed their adaptation strategies to the gradual cooling during the beginning of winter and to the gradual warming during the end of winter. The more frequent occurrences of the temperature extremities instead of the gradual changes may exert a strong negative influence on the hardening and the deepening processes, leading to the increased frequencies of serious frost damages and to disturbed floral development. Our results listed here show that the impacts of the unusual temperature extremities during the winter seasons can already be detected, and this necessitates a more rigorous choice of cultivars and areas when newer orchards are planned for ensuring economical peach production in the future also. It is hoped that the present work will facilitate this choice. However, the research project can by no means be regarded as complete, because newly bred cultivars regularly need to be subjected to thorough examination before they can be recommended for general cultivation.

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