Acta
Biologica
Szegediensis

Volume 66(2):170-179, 2022
Acta Biologica Szegediensis
http://abs.bibl.u-szeged.hu/index.php/abs
DOI:10.14232/abs.2022.2.170-179

ARTICLE

Frost hardiness of almond flower buds during dormancy

Belay Teweldemedhin Keleta[1,2], Zsuzsanna Békefi[2], József László Bakos[1], Dorottya Örsi[2], László Szalay[1]*

[1] Hungarian University of Agriculture and Life Sciences, Institute of Horticulture, Department of Pomology, Budapest, Hungary
[2] Hungarian University of Agriculture and Life Sciences, Institute of Horticulture, Fruit Research Centre, Budapest, Hungary

ABSTRACT Frost hardiness of flower buds of twenty almond genotypes was investigated in five dormancy periods by determining LT_{50} values after artificial freezing tests. The main aim of our work was modelling the changing of frost hardiness of the observed accessions during dormancy and assessing the potential best frost tolerance of them. The effect of genotype and year had significant impact on frost hardiness of flower buds. The potential frost hardiness of accessions has been characterised by LT_{50} values of flower buds averaged of the bests of the four years. 'Sóskút 96/5' was the most sensitive with -17.16 °C, and 'Tétényi keményhéjú' was the most frost hardy with -21.08 °C in averaged of years, but both showed lower and higher frost tolerance as well in different years. Flower buds were most frost-tolerant in December and January but did not achieve the same frost resistance every year. From this, we conclude that temperature plays an important role in the hardening process of them. From the aspect of safe yield, frost hardiness of flower buds is an important trait of cultivars, because Hungary is situated at the northern part of economical almond growing area. Our work contributes to facilitating practical considerations in orchard planning.

Acta Biol Szeged 66(2):170-179 (2022)

KEY WORDS
artificial freezing tests
frost tolerance
generative organs
LT_{50} values
Prunus dulcis

ARTICLE INFORMATION
Submitted
18 January 2023
Accepted
26 March 2023.

***Corresponding author**
E-mail: szalay.laszlo@uni-mate.hu

Introduction

The primary gene centre of cultivated almonds is in Asia Minor, mostly in arid, subtropical climates. From here it is widespread and has long been cultivated in the temperate zone as well. However, due to its origin, we must count regularly with winter and spring frost damage in these regions, which greatly endangers crop safety.

The efficiency of almond production is greatly influenced by the frost hardiness of the cultivated varieties. Determining this requires several years of research. The frost tolerance of different overwintering organs can be studied in several ways. Indirect laboratory methods can be used to infer the development of frost tolerance of genotypes. By measuring ion efflux, chlorophyll fluorescence assay, and determining the antioxidant capacity of plant organs, many samples can be tested, which provides breeders with useful information during selection (Kodad et al. 2010; Afshari et al. 2011; Moheb et al. 2018). Field frost damage surveys show the differences between the genotypes. Artificial freezing tests can be used to monitor the changes in the frost resistance of cultivars. Even though it is a frost-sensitive species, little data can be found in literature on the actual frost tolerance of almond cultivars in different phenological stages. Hungary is located on the northern border of the economic cultivation of almonds, but unfortunately the Hungarian variety descriptions do not address the issue of frost resistance (Brózik 1998; Tóth 2001; Brózik et al. 2003; Apostol 2013). However, the information gathered on the frost resistance of different genotypes is essential for determining the suitability of the production site and for establishing economic cultivation, so they are all very important from a scientific and practical point of view.

Early literature sources draw attention to the frost sensitivity of almonds and their close relatives, peach, and apricot (Lippay 1667; Bereczki 1882; Mohácsy és Magyar 1936; Wood 1947; Childers 1949; Pejovics 1968). The frost resistance of the vegetative and generative organs of almond cultivars has been studied by several methods in different places. Significant differences were found between the cultivars (Büyükyilmaz and Kester 1976; Rodrigo 2000; Szalay and Fonai 2002, Brózik et al. 2003; Kodad and Socias i Company 2004; Kodad et al. 2010; Afshari et al. 2011; Imani and Mahamadkhani 2011; Imani et al. 2011, 2012; Moheb et al. 2018). Peach is the close relative to almond. The susceptibility of peach cultivars to frost has also been studied and significant differences have been found between cultivars (Hatch and Walker 1969; Proebsting and Mills 1978; Szabó 1992; Nyéki and Szabó 1989; Miranda et al. 2005; Szymajda and Zurawicz 2016; Weaver 1966; Szabó 2002; Childers 1975; Childers and Sherman 1988; Okie 1998; Layne and Bassi 2008; Szabó and Nyéki 1988, 1991; Szabó 1992, 2002; Szabó et al. 1998, Timon 2000; Szalay 2001; Szalay et al. 2010).

Flower buds are the most frost-sensitive overwintering organs of almond. The development of flower buds can be divided into three periods. The first is the paradormancy, lasts from mid-summer to the autumn leaf fall. The second period is the endodormancy, it ends when the flower buds have received the required amount of chilling. Then there is a period of ecodormancy, as third phase, when the flower buds register the heat units (Lang 1987; Lang et al. 1987). During the long development period of flower buds, their sensitivity to frost changes continuously.

Changing of cold hardiness of overwintering organs can be most accurately determined by artificial freezing tests (Pedryc et al. 1999).

There is very little information in the literature about the winter frost tolerance of the flower buds of almond cultivar.

Miranda et al. (2005) examined two almond cultivars by artificial freezing (‘Marcona’ and ‘Ferragnes’) during the ecodormancy period. The critical temperature for frost tolerance of flower buds was -16.3 °C.

The studies were more focused on the flowering period.

Viti et al. (1994) examined frost sensitivity of almond flowers at different phenological stages during flowering time. Based on their experiences, cultivars with late flowering time had higher frost resistance, even if their flowers were in advanced phenological stages. A similar study was published by Snyder and Conell (1996) on the frost tolerance of flowers and fruitlets of Californian almond cultivars. Pink flower buds of the varieties ‘Sonora’ and ‘Price’ were less sensitive, they suffered only 30% frost damage at -5 °C, while the other seven varieties had higher frost damage. In the case of these two varieties, the open flowers were also more frost tolerant: while 100% flowers damaged at -3 °C frost of other varieties, it was -4.5 °C and -5.5 °C in the case of ‘Sonora’ and ‘Price’. Likewise, the differences between several varieties and between various flowering-phenological stages were investigated by Sepahvand et al. (2014). In Spain 12 commercial almond cultivars was observed, and the tolerance to frosts of flowers was evaluation by chlorophyll fluorescence after artificial freezing (Kodad et al. 2010).

The production of frost tolerant and late flowering cultivars is an important breeding aim because almond even at subtropical places can suffer frost damage due to its early flowering time (Daneshvar and Sardabi 2006; Dicenta et al. 2011; García-Gusano et al. 2011; Imani et al. 2011). Research has also begun into the detection of genes responsible for the frost resistance of almonds, so we know more and more about the genetic background of frost tolerance in each variety. (Mousavi et al. 2014; Alisoltani et al. 2015, 2016). Karimi et al. (2016) identified small RNAs that play a role in frost tolerance of reproductive organs in almond. Hosseinpour et al. (2017) identified a cold-shock protein in a frost tolerant genotype which plays role in frost resistance.

In Hungary, almonds are one of the earliest flowerings and most frost-sensitive cultivated fruit species. If we want to establish an economically functioning plantation from almonds, the place of production and the varieties must be chosen very carefully (Mohácsy and Porpáczy 1951; Pejovics 1976; Brózik et al. 2003; Kállay 2003, 2014; Di Lena et al. 2017).

Hungarian University of Agriculture and Life Sciences, Fruit Research Centre in association with Department of Pomology have investigated a research programme to study the frost hardiness of the flower buds of twenty almond accessions by artificial freezing tests. In present article, the results of this study are reported.

Materials and Methods

The samples were collected from the experimental plantation of HUALS, Fruit Research Centre, Érd-Elvira. Our collection includes cultivated varieties and other genotypes as well. All of them are uniformly called accessions in the article. Among twenty accessions analysed five (‘Budatétényi 70’, ‘Tétényi keményhéjú’, ‘Tétényi rekord’, ‘Tétényi bőtermő’ and ‘Tétényi kedvenc’) are commercial almond cultivars in Hungary, the remaining fifteen are landrace selections around the hills of Bakony, collected in the 1960’s. Two-four trees of each of all observed almond accessions were available for research work. The experimental orchard was planted in 1996. The spacing is 7 x 3 meters, the orchard has no irrigation, the trees are on GF-677 rootstock.

Investigations were carried out in the dormant period of the following years: 2016/17, 2017/18, 2018/19, 2019/20 and 2021/22. The experiment could not be carried out in the winter of 2020/21 due to technical reasons. In each dormancy season, the samples were collected 7 times, except the last winter, when there were six sampling dates. Between September and February there was observation in the middle of every month. Occasionally, for technical reasons, this was done in the first or second half of the month. The last sampling day was directly before blooming in March.

The experiments were performed in a Rumed 3301 (Rubarth Apparate GmbH, Laatzen, Germany) climate chamber, in the laboratory of Pomology Department, Hungarian University of Agriculture and Life Sciences. Each time, 4 or 5 freezing temperatures were applied with a difference of 2 °C. To determine the LT_{50} values (the temperature at which 50% of the flower buds were damaged) the treatment temperatures were chosen that all accessions should get frost damage below as well as above 50%. In the chamber initial room temperature 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. After 12 hours at room temperature, the percentage of frost damage was scored by cutting the flower buds in half lengthwise and observing the discoloration of the tissues. Five twigs with 40-60 flower buds from each cultivar per treatments were put into the climate chamber where each twig was considered as a replication for the statistical analysis.

Based on the experimental results, the LT_{50} values were determined by linear regression. Assuming the linear relationship between the treatment temperature and the percentage of frost damage in the range of 20% and 80%. The mean and standard deviation of replications were calculated. Based on the calculated values, the flower bud freezing tolerance profile of each cultivar was outlined during dormancy characterized by LT_{50} values. The potential frost resistance of the observed accessions was determined by variance analysis. For determining year and genotype effect the ANOVA method was applied using SPSS software. At different sampling date the year and genotype effect were examined separately, and the value of eta square was calculated. Daily minimum and maximum temperatures in the almond orchard were recorded by a local automatic meteorological station.

Results

The frost hardiness of flower buds of observed almond accessions is characterized by LT_{50} values. The changing of the LT_{50} values (main frost hardiness values) is shown in Figure 1.

The frost tolerance profile of the examined accessions was different in every year. This is probably due to differences in environmental factors, especially temperature. In all observed years the daily maximum and minimum temperature values showed great daily fluctuations, and the differences between years are also remarkable. The frost hardiness profile of the observed accessions during dormancy were similar. In all five years studied the frost tolerance of flower buds increased gradually in the first half of winter (hardening period), and by increasing outdoor temperature in the second half of winter they gradually lost their frost tolerance (dehardening period). In the winter of 2017/18 and 20021/22, the best frost tolerance values were measured in December, while in the other dormancy seasons, the flower buds reached their best frost tolerance in January. It was not consistent the changing of LT_{50} values during the hardening periods. After the initial fast decreasing, the changing slowed down until a certain point, after it this process was accelerated again, until the lowest value of LT_{50}. So, the hardening period can be divided into two phases as well. The first stage took place at temperatures above freezing. The start of the second, accelerated phase was when the ambient temperature was continuously below freezing point. Based on the results of the five years, the flower buds of the accessions did not achieve their genetically programmed maximum frost tolerance every year. On Figure 2 the best frost tolerance (LT_{50}) values of the flower buds of the studied accessions in the given dormancy period are demonstrated. In our experimental station during the five-year study, the flower buds of the studied varieties reached the most frost-resistant values in 2016/17 winter (Fig. 2.). Further studies are needed to determine whether these values are genetically encoded maximum values. During the study period, flower buds were least hardened in 2019/20 and 2021/22 test season according to cultivar.

During the dehardening period the changing of frost hardiness of flower buds was very different year by year because of different climatic conditions. Due to rapidly rising temperatures, dehardening was very rapid in some periods, such as January, February, and March of 2017 (Fig. 1a), and March of 2019 (Fig. 1c). The slow rise in temperature resulted in slow dehardening, for example in January and February of 2018 (Fig. 1b), 2019 (Fig. 1c) and 2020 (Fig 1d). Recurrent strong cools caused frost damage to flower buds in early March 2018 at the end of the dehardening period (Fig. 1b), and in 2020 during the flowering period (Fig. 1d). There were drastically low temperatures after our observations, during the flowering period in 2022, and it caused severe frost damages in the orchard. An asynchrony was observed between the change in ambient temperature and the frost tolerance profile of flower buds, especially in the last two study periods, when the decrease in frost hardiness was faster than the warming of the plantation (Fig. 1c, 1d).

The sequence of accessions from the aspect of frost tolerance in different sampling dates was not the same (Fig 1.). Based on all of data the 'Sóskút 96/5' was the most sensitive and the 'Tétényi keményhéjú' was the hardiest in general, that is why the values of these two accessions are demonstrated with lines on figures, but there were sampling dates when other accessions represented extreme values.

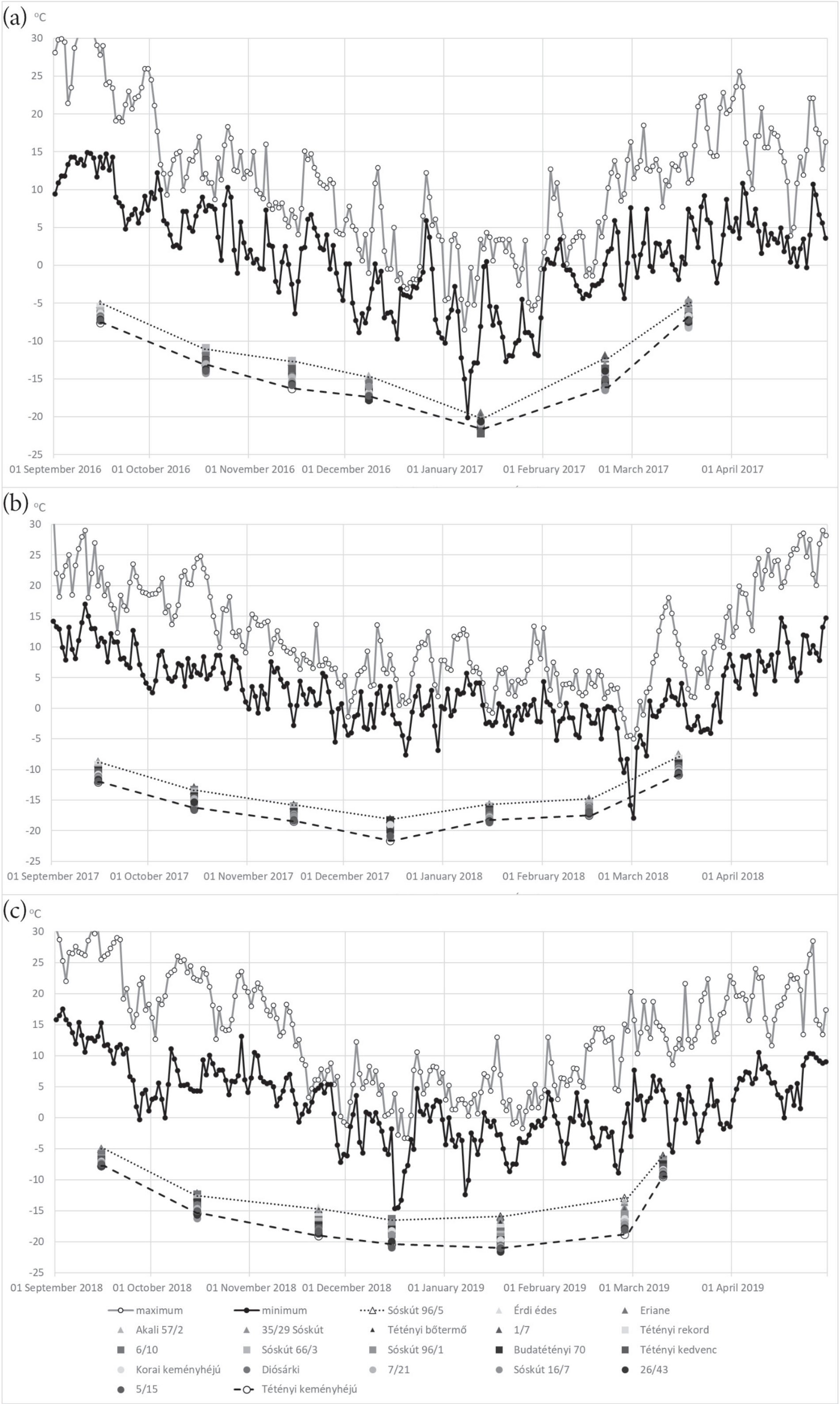

Figure 1. Daily maximum and minimum ambient temperatures, and LT_{50} values of flower buds of the observed almond cultivars based on artificial freezing tests in winter of 2016/17 (a), 2017/18 (b), 2018/19 (c), 2019/20 (d) and 2021/22 (e).

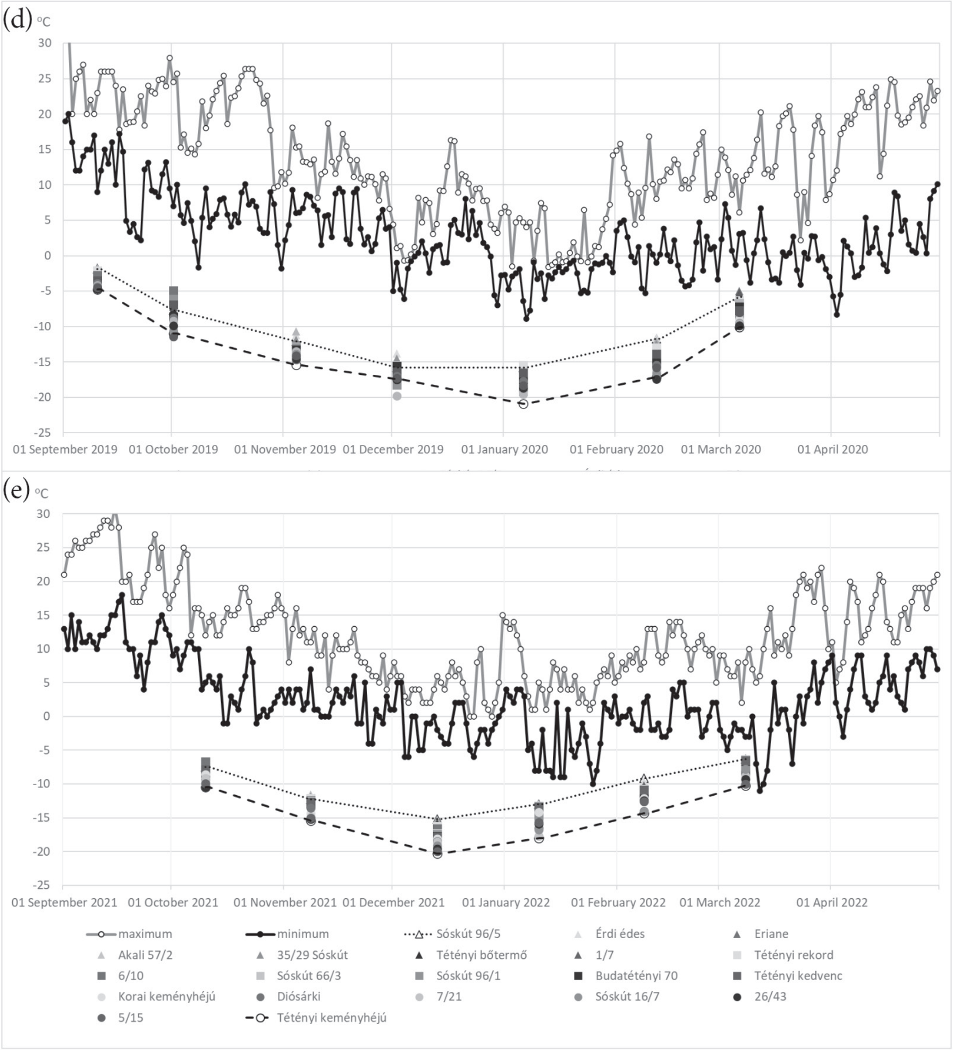

Figure 1. Continued.

Differences between accessions are analysed based on the best frost hardiness values of them achieved in the different test seasons. The statistical analysis distinguished three homogeneous groups (Fig. 3), based on which these groups can be introduced into the group of frost-tolerant, medium-frost-tolerant, and frost-sensitive accessions within the studied cultivar range. ‘Sóskút 96/5’, ‘Érdi édes’, ‘Eriane’ and ‘Akali 57/2’ accessions form the frost-sensitive group. ‘6/10’, ‘Sóskút 66/3’, ‘Sóskút 96/1’, ‘Budatétényi 70’, ‘Tétényi kedvenc’, ‘Korai keményhéjú’ and ‘Diósárki’ belong to the group with medium frost resistance. ‘Tétényi keményhéjú’ alone forms the frost tolerant group. ‘35/29 Sóskút’, ‘Tétényi bőtermő’, ‘1/7’ and ‘Tétényi rekord’ form a transition between the frost-sensitive and the medium-frost tolerant groups, while ‘7/21’, ‘Sóskút 16/7’, ‘26/43’ and ‘5/15’ belong to the transition type between the medium-frost tolerant and frost tolerant groups (Fig. 3).

Discussion

In our present work frost hardiness of flower buds of twenty almond accessions was investigated in five dormancy periods. The frost hardiness profile of the observed almond accessions has been characterised by their LT_{50} values that were calculated based on artificial freezing tests. The present paper is the first report about changes in cold hardiness of flower buds of almond accessions during the whole dormancy period.

Photoperiod and temperature are key environmental factors in cold acclimation of almond trees, like other tem-

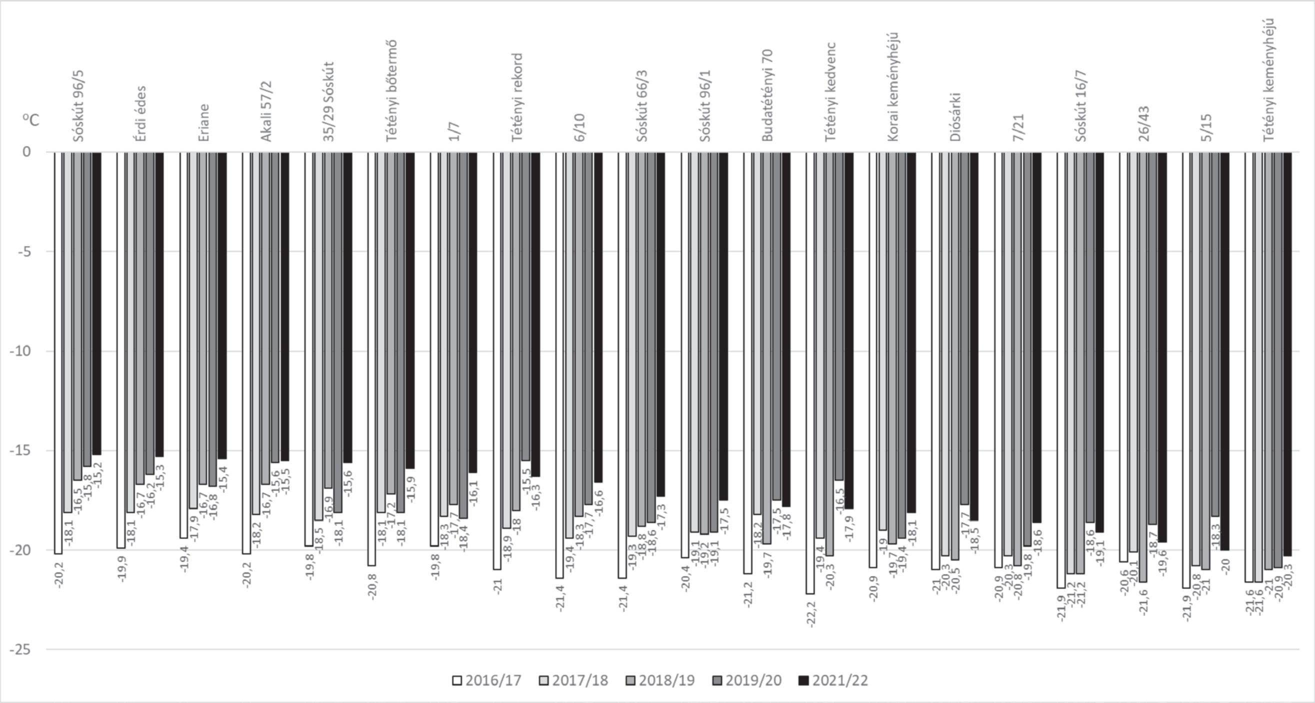

Figure 2. The best frost tolerance (LT_{50} value) of the flower buds of the studied almond cultivars in the given dormancy period based on the results of the climate chamber experiments.

perate fruit species (Faust 1989; Tromp 2005; Heide and Prestrud 2005; Wu et al. 2019). During the dehardening period the temperature is the most important environmental factor affecting the frost hardiness of overwintering organs (Tromp 2005; Quinones et al. 2020). Frost tolerance of trees is also influenced by numerous other factors, such as the cultivar, the rootstock, the cultivation system, the cropping technology, the health status of the trees, the characteristics of the geographical location (Westwood 1993; Faust 1989; Tromp 2005). Due to all these, there are large differences in the development of frost tolerance between cultivars, production sites and years.

In the present experimental work, the frost tolerance of flower buds of different origin almond accessions has been investigated by artificial freezing method for five consecutive years in our experimental plantation, in Central Hungary. The trees stand on the same rootstock and have received the same cultivation technology. Thus, we were mostly able to establish the differences between the accessions. In addition, we were able to describe the course of the change in frost resistance as the tests were performed monthly during the winter dormancy periods. The five years offered only a limited opportunity to determine the impact of environmental factors and years. However, restricted conclusions can be drawn from the differences between the years, based on our results.

The frost resistance of overwintering organs of temperate zone trees develops in two stages in autumn, so the hardening period of them can be divided into two stages. It is experimentally proven in apple vegetative organs (Howell and Weiser 1970). The first stage takes place at temperatures above freezing, but the second stage requires permanently low temperatures. It has been experimentally demonstrated that in the absence of low temperatures different vegetative and generative overwintering organs cannot harden properly in the case of several temperate zone fruit species (Palmer et al. 2003; Szalay et al. 2010; Wu et al. 2019). Our present experimental results suggest this for almond accessions as well referring to the flower buds. In the first part of frost tolerance profile of flower buds of studied accessions a breaking point is observed, after which hardening continues at persistently low temperatures. The role of temperature in hardening is also indicated by the fact that the lowest LT_{50} values of the flower buds of the studied almond accessions were different from year to year. In case of unfavourable weather, the genetically possible level was not reached. Dehardening of flower buds also took place at different rates in the study years, which suggests the role of temperature in this process as well. Further studies are planned to better understand the role of environmental factors in hardening and dehardening of almond flower buds, and to determine the genetically fixed best frost hardiness of genotypes. Climate change

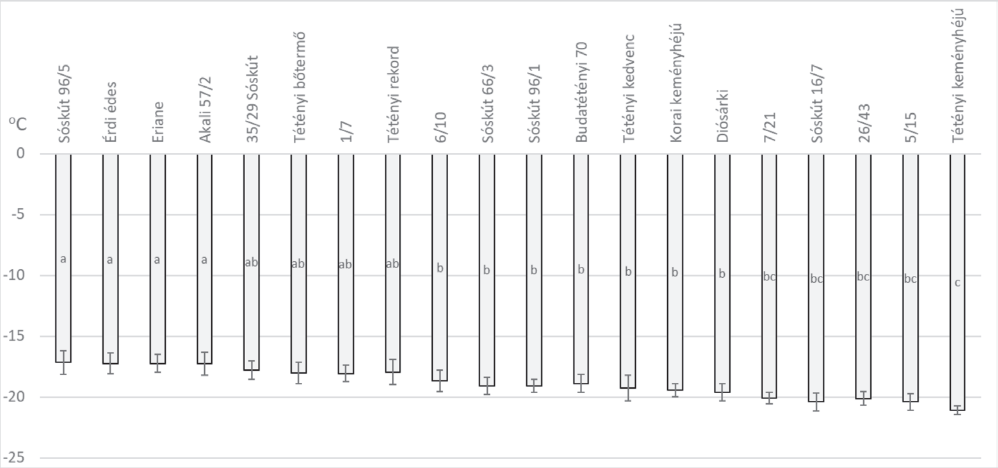

Figure 3. Average LT$_{50}$ values of flower buds of the studied almond cultivars based on the results of artificial freezing tests in December and January of the five test seasons, calculated with the best frost hardiness value in a certain test season; The columns show the mean values, the lines the standard deviation, and the letters the homogeneous groups, the different letters indicate significantly (*P≤0.05*) different values.

results in frequent mild winter temperatures that are not favourable in hardening processes and has impact on the phenological processes of almond genotypes as well, similarly to other fruit trees (Egea et al. 2003; Eccel et al., 2009; Lamp et al. 2001; Kaukoranta et al., 2010; Di Lena et al. 2017; Benmoussa et al 2017; Vitasse et al. 2018; El Yaacoubi et al. 2019).

It is difficult to compare our results with previous research results, as such a systematic study of the frost resistance of flower buds of almond genotypes has not yet been performed.

In this variety range, the best frost tolerance values for flower buds in a certain dormancy period were between -15.2 °C and -22.2 °C, depending on the genotype and year. 'Sóskút 96/5' was the most sensitive, and 'Tétényi keményhéjú' was the most frost hardy.

An asynchrony was observed between the change in ambient temperature and the frost tolerance profile of flower buds, the decrease in frost hardiness was faster than the warming of the plantation. It caused severe frost damages sometimes.

In Hungary, almond growing is limited by ecological conditions, the most risks are winter and spring frosts. When planning an orchard, it is important to harmonise cold hardiness of the selected cultivars and growing site conditions. Based on our results it is not recommended to establish an almond orchard in growing sites where winter temperatures regularly drop below -18 °C. As a conclusion, from practical point of view it is important to have adequate information on the cold hardiness of almond cultivars that should be included into cultivar descriptions, our work hopefully could contribute to this aim. So, we consider our test results to be important, as in the pomological textbooks and variety descriptions the frost tolerance of the varieties we examined either is not mentioned at all or we can only find very incomplete data about them. To accurately describe varieties, determining their frost tolerance is very important, especially for a problematic species such as almonds. This is of great scientific and practical importance. The frost tolerance of the varieties can be determined by several years of research. Field frost damage recordings and artificial freezing experiments together provide adequate results.

Frost tolerance is an important selection aspect in almond breeding as well (Moheb et al. 2018). Research has also begun in the field of physiological and genetic exploration of frost resistance of almond cultivars, and more and more results can be used for practice (Lindow and Connell 1984; Barros et al. 2012; Mousavi et al. 2014; Alisoltani et al. 2015, 2016; Karimi et al. 2016).

References

Afshari H, Parvaneh T, Ebadi AG, Abbaspor H, Arab HA (2011) Studying cold resistance of three commercial cultivars of Iranian almond via ion leakage parameter at different times after chilling. J Food Agr Envir Sci 9:449-454.

Alisoltani A, Shirana B, Fallahi H, Ebrahimie E (2015) Gene regulatory network in almond (*Prunus dulcis* Mill.) in response to frost stress. Tree Genet Genomes 11(100):2-15.

Alisoltani A, Ebrahimia S, Azariana S, Hematyara M, Shirana B, Jahanbazie H. et al. (2016) Parallel consideration of SSRs and differentially expressed genes under abiotic stress for targeted development of functional markers in almond and related *Prunus* species. Sci Hort 189:462-472.

Apostol J (2013) Mandula (Almond). In Soltész M, Ed., Magyar gyümölcsfajták (Hungarian fruit cultivars). Nemzeti Agrárgazdasági Kamara, Budapest, 394-402. [In Hungarian]

Barros PM, Goncalves N, Saibo NJM, Margarida-Oliveira M (2012) Functional characterization of two almond C-repeat-binding factors involved in cold response. Tree Physiol 32:1113-1128.

Benmoussa H, Ghrab M, Ben-Mimoun M, Luedeling E (2017) Chilling and heat requirements for local and foreign almond (*Prunus dulcis* Mill.) cultivars in a warm Mediterranean location based on 30 years of phenology records. Agric For Meteorol 239:34-46.

Bereczki M (1882) Gyümölcsészeti vázlatok (Outline of pomology). Réthy és Gyulai, Arad. [In Hungarian]

Brózik S (1998) Mandula (Almond). In Soltész M, Ed., Gyümölcsfajta-ismeret és -használat (Knowledge and use of fruit varieties). Mezőgazda Kiadó, Budapest, 330-335. [In Hungarian]

Brózik S, Kállay T-né, Apostol J (2003) Mandula (Almond). Mezőgazda Kiadó, Budapest. [In Hungarian]

Büyükyilmaz M, Kester DE (1976) Comparative hardiness of flower buds and blossoms of some almond genotypes in relation to time of bloom and leafing. J Amer Soc Hort Sci 101:344-347.

Childers NF (1949) Fruit Science. J.B. Lippincott Company Press, USA.

Childers NF (1975) The Peach. Horticultural Publications, New Jersey, USA.

Childers NF, Sherman WB (1988) The Peach. Somerset Press, Somerville, New Jersey, Hort Public Gainesville, Florida, USA.

Daneshvar HA, Sardabi H (2006) Variation of flowering period among 60 almond genotypes. Acta Hortic 726:273-278.

Di Lena B, Farinelli D, Palliotti A, Poni S, Theodore M, DeJong TM, Tombesi S (2017) Impact of climate change on the possible expansion of almond cultivation area pole-ward: a case study of Abruzzo, Italy. J Hortic Sci Biotechnol 93(2):209-215.

Dicenta F, Ortega E, Martínez-Gómez P, Sánchez-Pérez R, Martínez-García PJ, Cremades T, Rubio M, García-Gusano M, Egea J (2011) Breeding late-flowering almonds in the Cebas-Csic, Murcia, Spain. Acta Hortic 912:385-389.

Eccel E, Rea R, Caffarra A, Crisci A (2009) Risk of spring frost to apple production under future climate scenarios: the role of phenological acclimation. Int J Biometeorol 53(3):273-286.

Egea J, Ortega E, Martínez-Gómez P, Dicenta F (2003) Chilling and heat requirements of almond cultivars for flowering. Environ Exp Bot 50:79-85.

El Yaacoubi A, Oukabli A, Legave J.-M, Ainane T, Mouhajir A, Zouhair R, Hafidi M (2019) Response of almond flowering and dormancy to Mediterranean temperature conditions in the context of adaptation to climate variations. Sci Hortic 257:108687.

Faust M (1989) Physiology of Temperate Zone Fruit Trees. John Wiley and Sons, New York.

García-Gusano M, Martínez-García PJ, Dicenta F (2011) Seed germination time as a criterion for the early selection of late flowering almonds. Acta Hortic 912:391-394.

Hatch AH, Walker DR (1969) Rest intensity of dormant peach and apricot leaf buds as influenced by temperature, cold hardiness and respiration. J Am Soc Hort Sci 94(3):304-307.

Heide OM, Prestrud AK (2005) Low temperature, but not photoperiod, controls growth cessation and dormancy induction and release in apple and pear. Tree Physiol 25:109-114.

Hosseinpour B, Sepahvand S, Aliabad KK, Bakhtiarizadeh MR, Imani A, Assareh R, Salami SA (2017) Transcriptome profiling of fully open flowers in a frost-tolerant almond genotype in response to freezing stress. Mol Genet Genom 293(1):151-163.

Howell GS, Weiser CJ (1970) The environmental control of cold acclimation in apple. Plant Physiol 45:390-394.

Imani A, Mahamadkhani Y (2011) Characteristics of almond selections in relation to late frost spring. Int J Nuts Rel Sci 2(2):31-34.

Imani A, Mousavi A, Biat S, Rasouli M, Tavakoli R, Piri S (2011) Genetic diversity for late frost spring resistance in almond. Acta Hortic 912:371-375.

Imani A, Ezaddost M, Asgari F, Masoumi SH, Raeisi I (2012) Evaluation the resistance of almond to frost in controlled and field conditions. Int J Nuts Rel Sci 3(1):29-36.

Kállay T-né (2003) A mandula elterjedése és termőhelyigénye (Distribution and site selection of almond). In Brózik S, Kállay T-né, Apostol J, Eds., Mandula (Almond). Mezőgazda Kiadó, Budapest, 21-27. [In Hungarian]

Kállay T-né (2014) Mandula (Almond). In Kállay T-né, ed., Gyümölcsösök termőhelye (Orchard site selection). Mezőgazda Kiadó, Budapest, 147-150. [In Hungarian]

Karimi M, Ghazanfari F, Fadaei A, Ahmadi L, Shiran B, Rabei M, Fallahi H (2016) The small-RNA profiles of almond (*Prunus dulcis* Mill.) reproductive tissues in response to cold stress. Plos One 11(6):e0156519.

Kaukoranta T, Tahvonen R, Ylamaki A (2010) Climatic potential and risks for apple growing by 2040. Agric Food Sci 19:144-159.

Kodad O, Socias i Company R (2004) Differential flower and fruit damages by spring frosts in almond. Nucis-Newslett 12:5-7.

Kodad O, Socias i Company R, Morales F (2010) Evaluation of almond flower tolerance to frosts by chlorophyll fluorescence. 14. GREMPA Meeting on Pistachios and

Almonds, 2008/03/30-2008/04/04, Athens, Greece. 141-145.

Lamp BM, Connell JH, Duncan RA, Viveros M, Polito VS (2001) Almond flower development: floral initiation and organogenesis. J Am Soc Hortic Sci 126:689-696.

Lang GA (1987) Dormancy: A new universal terminology. Hort Sci 22(5):817-820.

Lang GA, Early JD, Martin GC, Darnell RL (1987) Endo-, para-, and ecodormancy: physiological terminology and classification for dormancy research. Hort Sci 22(3):371-377.

Layne DR, Bassi D (2008) The Peach, Botany, Production and Uses. CABI UK.

Lindow SE, Connell JH (1984) Reduction of frost injury to almond by control of ice nucleation active bacteria. J Am Soc Hort Sci 109:48-53.

Lippay J (1667) Posoni Kert. Nagyszombat.

Miranda C, Santesteban LG, Royo JB (2005) Variability in the relationship between frost temperature and injury level for some cultivated *Prunus* species. Hort Sci 40(2):357-361.

Mohácsy M, Magyar Gy (1936) Dió-, mandula-, mogyoró- és gesztenyetermesztés (Cultivation of walnut, almond, hazelnut, and chestnut). Pátria, Budapest. [In Hungarian]

Mohácsy M, Porpáczy A (1951) Dió-, mogyoró-, mandula-, gesztenye termesztés és nemesítés (Cultivation and breeding of walnut, almond, hazelnut, and chestnut). Mezőgazdasági Kiadó, Budapest. [In Hungarian]

Moheb MB, Imani A, Shamili M (2018) The evaluation of almond progenies of cold-susceptible and cold tolerant parents (Filippo-Ceo XShahrood-12). Sci Hortic 234:176-183.

Mousavi S, Alisoltani S, Shiran B, Fallahi H, Ebrahimie E, Imani A, Houshmand S (2014) De novo transcriptome assembly and comparative analysis of differentially expressed genes in *Prunus dulcis* Mill. in response to freezing stress. Plos One 9(8):e104541.

Nyéki J, Szabó Z (1989) Effect of frost damage on peach varieties in Hungary. Acta Hortic 254:255-256.

Okie WR (1998) Handbook of Peach and Nectarine Varieties. United States Department of Agriculture, Washington, USA.

Palmer JW, Privé JP, Tustin DS (2003) Temperature. In Ferree DC, Warrington IJ, Eds., Apples. CABI Publishing, Reading, UK, 217-236.

Pedryc A, Korbuly J, Szabó Z (1999) Artificial frost treatment methods of stone fruits. Acta Hortic 488:377-380.

Pejovics B (1968) A mandula néhány biológiai sajátossága és termesztési sajátosságai (Some biological and cultivation characteristics of almonds) MTA, Doctoral Thesis, Budapest.

Pejovics B (1976) Dió, Mandula, Mogyoró, Gesztenye (Cultivation of Walnut, Almond, Hazelnut and Chestnut). Mezőgazdasági Kiadó, Budapest.

Proebsting EL, Mills HH (1978) A synoptic analysis of peach and cherry flower bud hardiness. J Amer Soc Hort Sci 103(6):842-845.

Quinones AJP, Gutierrez MRS, Hoogenboom G (2020) A methodological approach to determine flower bud vulnerability to low temperatures for deciduous crops in early spring using degree days. Hort Sci 55(5):1-7

Rodrigo J (2000) Spring frosts in deciduous fruit trees – morphological damage and flower hardiness. Sci Hortic 85:155-173.

Sepahvand S, Imani A, Aliabad KK, Hoseinpour B, Abdossi V (2014) Evaluation the resistance of almond cultivars to spring frost at different phenological stages. Adv Biores (Adv Biores) 5:183-190.

Snyder RL, Conell JH (1996) Frost protection. In Micke CM, Ed., Almond Production Manual. University of California, Division of Agriculture and Natural Resources, 155-166.

Szabó Z (2002) Csonthéjas gyümölcsűek termésbiztonságának egyes tényezői (Elements of yield safety of stone fruits). MTA Doctoral Thesis. [In Hungarian]

Szabó Z, Nyéki J (1988) Őszibarackfajták fagykárosodása (Frost damages of peach cultivars). Gyümölcs-Inform, 10(1):15-19. [In Hungarian]

Szabó Z, Nyéki J (1991) Csonthéjas gyümölcsfajok fagykárosodása (Frost damages of stone fruit species). Kertgazdaság (Horticulture) 23(2):9-19. [In Hungarian]

Szabó Z, Nyéki J, Szél I, Pedryc A, Szalay L (1998) Low temperature injury in peach and nectarine cultivars. Acta Hortc 465:399-404.

Szabó Z (1992) Evaluation of cold hardiness of peach cultivars based on freezing injury to twigs. Acta Hortic 315:219-227.

Szabó Z, Nyéki J, Szél I, Pedryc A, Szalay L (1998) Low temperature injury in peach and nectarine cultivars. Acta Hortic 465:399-404.

Szalay L (2001) Kajszi- és őszibarackfajták fagy- és téltűrése (Frost and winter tolerance of apricot and peach varieties). PhD Thesis. Szent István University, Budapest. [In Hungarian]

Szalay L, Timon B, Németh S, Papp J, Tóth M (2010) Hardening and dehardening of peach flower buds. Hort Sci 45(5):761-765.

Szalay L., Fonai L. 2002. Előzetes közlemény a mandulafajták téli virágrügyfejlődésének vizsgálatáról (Preliminary report on the investigation of winter flower bud development of almond varieties). Kertgazdaság (Horticulture) 34(3):21-25.

Szymajda M, Zurawicz E (2016) Tolerance of peach flower buds to low sub-zero temperatures in winter. Hort Sci (Prague) 43(3):126-133.

Timon B (2000) Őszibarack (Peach). 4th Ed., Mezőgazda

Kiadó, Budapest. [In Hungarian]

Tóth M (2001) Mandula (Almond). In Tóth M, Ed., Gyümölcsészet (Pomology). Primom Kiadó, Nyíregyháza, 307-315.

Tromp J (2005) Frost and plant hardiness. In Tromp J, Webster AD, Wertheim SJ, Eds., Fundamentals of Temperate Zone Tree Fruit Production, Backhuys Publishers, Leiden, The Netherlands, 74-83.

Vitasse Y, Schneider L, Rixen C, Christen D, Rebetez M (2018) Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. Agric Forest Meteorol 248:60-69.

Viti R, Bartolini S, Giorgelli F (1994) Effect of low temperatures on flower buds of several almond cultivars. Acta Hortic 373:193-200.

Weaver GM (1966) Response of peach varieties to blossom frost. Fruit Var Hortic Digest 20:66-68.

Westwood MN (1993) Dormancy and plant hardiness. In Westwood MN, Ed., Temperate-Zone Pomology: Physiology and Culture. 3rd Ed., Timber Press, Portland, Oregon, 382-419.

Wood MN (1947) Almond culture in California. Calif Agr Exp Sta Cir 103.

Wu D, Kukkonen A, Luoranen J, Pulkkinen P, Heinonen J, Pappinen A, Repo T (2019) Influence of late autumn preconditioning temperature on frost hardiness of apple, blueberry and blackcurrant saplings. Sci Hortic 258:108755.