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Heritability of Flowering Time within Apple Progeny

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Abstract

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The flowering onset of 19 apple progeny was evaluated in 2005–2014 on a total number of 715 seedlings in comparison with their parents and grandparents. A very low flower set delays generally the onset of flowering by one day in comparison with a higher flower set. The maximum span between the first flowering onset and the last one within all the progeny of the study was 11 days. With one exception, the incidence of the first flowering dates of all the progeny fluctuated only within four days – April 28 and May 1. Among them, the great majority of the seedlings had the first flowering date span of not more than ± one day. The progeny of Pink Lady × Discovery was the most exceptional having the mean day on the April 17 and the span about two days longer. The means of the first flowering dates within seedling populations and corresponding dates of both their parents and grandparents were very highly correlated (r = 0.926 for parents and r = 0.877 for grandparents). The incidence of flowering onset dates in almost all progeny followed a typical Gaussian distribution, in which the majority of seedlings start flowering within 3 or 4 days. The maximum difference between both extremes (found only in one progeny) was 11 days. The share of seedlings in both extremes was, however, very small – less than 2%.

Keywords: apple breeding; flower set; *Malus* × *domestica*; progeny segregation; onset of flowering time

The time of flowering is an important characteristic of each apple cultivar and therefore it is included in the introductory description of each novelty recommended to fruit growers in connection with the use of a proper pollinator for flowering at the same time (Blažek 2001, 2007).

In the past, an apple breeding programme focused on the late time of flowering was performed at the East Malling Research Station, England, with the aim to reduce the risk of crop loss by late spring frosts (Tydeman 1958). Nearly two decades later, a programme of apple breeding focused on late flowering was recommended at the New York State Agricultural Experiment Station in Geneva, USA, in connection with reducing the risk of fire blight (*Erwinia amylovora*) spread (Aldwinkle *et al.* 1976). Subsequently, a correlation was found between the time of seedling leafing and the time of its flowering that could be utilized for pre-selection of late flowering genotypes (Mehlenbache & Voordeckers 1991).

In Australia, information on the flowering period and choice of suitable pollinators for commercially grown apple cultivars were included in a special publication issued for fruit growers (Lace & Antoine 2006).

A recent study from France was aimed at improving the modelling of flowering time in fruit trees and at understanding to what extent global warming affected this trait since the end of the 1980s. The onset of flowering time in apple trees advanced by 7 days since the late l980s (Legave *et al.* 2008).

One of the latest studies of flowering time (Celton *et al.* 2011) explores the genetic determinism of bud phenological traits using two segregated apple progenies. Phenological trait variability was dissected into genetic and climatic components using mixed linear modelling, and estimated best linear unbiased predictors were used for quantitative trait locus (QTL) detection. For flowering dates, year effects were decomposed into chilling and heat require-

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ments based on a previously developed model. Both 'chilling requirement' and 'heat requirement' periods influenced flowering dates, although their relative impact was dependent on the genetic background.

General information on the regulation of seasonal flowering in the *Rosaceae* is provided by a very recent paper (Kurokura *et al.* 2013). Detailed data on the flowering time of *Malus domestica*, wild apple species (*Malus* sp.), and *Malus* hybrids maintained in a large apple germplasm collection in Geneva, USA, were published at the same time (Gottschalk & Nocker 2013). Information on the heritability of flowering time in other fruit species has been recently published in a number of papers (Jung & Müller 2009; Campoy *et al.* 2011; Sanchez-Pere *et al.* 2014).

The aim of the study was to find out differences between apple progenies in the time and length of flowering and to reveal variation in these values.

MATERIAL AND METHODS

The experimental material originated from crossings of selected cultivars and genotypes that were done in 1999. In the next year, stratified seeds were sown in a plastic greenhouse, where grown up seedlings were selected according to their resistance to diseases (e.g. scab, powdery mildew). Selected seedlings were grafted on the M9 rootstock and the subsequently grown 2-years-old trees were planted at the spacing of 4 × 1m in an experimental orchard located in Holovousy in the spring of 2004. The locality is characterised by an average annual temperature of 8.4°C, average rainfall of about 663.5 mm and altitude about 300 m a.s.l. A broad spectrum of characteristics was evaluated in the genotypes. This paper, however, is focused on the time of their flowering onset defined by the calendar day of the year when at least 5% of the flowers are open. The number of evaluations of particular genotypes varied between the years 2005 and 2014, depending on the length of their juvenile phase and regularity of their cropping. Therefore, for a mutual comparison these data from different years were converted into overall means from all years of the study. These fluctuated within a total span of 16 days in the evaluated period of 10 years.

Another characteristic assessed every year was the flower set expressed by values of the commonly used rating scale 1–9 (1 – no flower set, 9 – maximum flower set). These data were used to evaluate whether or not the flower set influences the flowering onset of particular genotypes. For the purpose of evaluating the influence of the flower set on the flowering onset, data of particular parental progenies were transferred from all the years of their evaluation into a single mean onset of the phase. This made it possible to analyse this phenomenon in a single comparison using a maximum amount of data.

The data on the flowering time of parental cultivars or genotypes and their grandparents were taken from observations either on other breeding plots or from gene bank collection orchards. All the places are located in the same climatic, site and soil conditions, and therefore they can be fully comparable.

The standard correlation analysis was done for the assessment of relationships between the first flowering days within seedling populations and corresponding days of both their parents and grandparents. Flowering time was expressed as days from January 1st.

RESULTS AND DISCUSSION

Influence of flower set on the start of flowering. The data summarizing this phenomenon from the present study are presented in Table 1. Among these data the flower set seems to be the most important feature. The majority of the progeny seedlings having a very low flower set (classification degree 2) started flowering one day later than in all the years of their better cropping. In the case of the Pink Lady × Discovery progeny, the delay was even two days, and one-day delay was observed also in the flower set classified by number 3.

The opposite effect was the effect of a very high flower set observed in six progenies (Braeburn × Angold, HL 665 × HL 782, HL 665 × Pink Lady, Pink Lady × Discovery, Resista × HL 447 and Resista × HL 75-26-18). Among them, flowering started one day earlier if their flower sets were maximum ones. The behaviour of seedlings in the progeny of Resista × Rucla was completely opposite. There, the seedlings with the highest flower set started flowering one day later.

Distribution of flowering time in evaluated progenies. A survey of the first flowering dates in the 19 evaluated progenies is given in Table 2. According to the mean values, the earliest in this characteristic was the progeny of Pink Lady × Discovery, having the mean day on the 27.4. The second earliest was the HL 782 × Topaz progeny, having the mean day of flowering one day later (28.4.). In the following order, 8 progenies had a date of one day later (29.4.)

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Table 1. Effect of the flower set on mean dates of the first flowering (expressed as days from January 1st)

Cross	Total No. of observations	Mean dates of first flowering according to flower set value*						
		2	3	4	5	6	7	8
Braeburn × Angold	69	122	122	122	122	122	121	–
HL 665 × HL 782	366	122	121	121	121	121	121	120
HL 665 × Pink Lady	140	123	122	122	122	122	122	121
Pink Lady × Discovery	87	121	120	119	119	119	118	118
Resista × HL 2219	173	123	121	121	121	121	121	121
Resista × HL 447	235	122	121	121	121	121	121	120
Resista × HL 75-26-18	138	123	123	122	122	122	121	121
Resista × Karmína	92	123	121	121	121	121	121	121
Resista × Rucla	89	122	122	122	122	122	123	123

*1–9 scale; 1 – no flower set; – not evaluated

and another 8 progenies two days later (30.4.). Three progenies (Rubinstep × HL 665, Resista × Pink Lady, Resista × Karmína) having the mean day on the first of May were the latest ones. Therefore, a difference between both extremes of the characteristic is 4 days.

The earliest seedling from the progeny of Pink Lady × Discovery started flowering on average on April 24, and the latest in this respect was the seedling from the HL 1737 × Pink Lady progeny, having the mean day as late as on May 5.

A difference between both extremes within one progeny equals 11 days and it was observed in the parental combination of HL 1737 × Pink Lady. In the case of the progeny, only 16 seedlings were evalu-

Table 2. Distribution of the first flowering dates in evaluated progenies (flowering time was expressed as days from January 1st)

Cross	No. of genotypes	Mean	Min	Max	LSD
Braeburn × Angold	33	122	119	125	1.6
HL 1737 × Pink Lady	16	122	116	127	2.7
HL 665 × HL 782	119	121	117	127	1.8
HL 665 × Pink Lady	45	122	118	126	1.8
HL 665 × Rosana	34	121	119	123	1.2
HL 782 × HL 665	30	121	117	124	2.0
HL 782 × Pink Lady	40	121	118	125	1.8
HL 782 × Topaz	17	120	117	123	1.3
Pink Lady × Discovery	25	119	116	124	2.1
Resista × HL 2219	66	121	117	127	1.7
Resista × HL 447	73	121	117	124	1.4
Resista × Pidi (HL 75-26-18)	56	122	118	126	1.6
Resista × Karmína	37	123	120	126	1.6
Resista × McIntosh Wijcik	18	122	119	126	1.6
Resista × Pink Lady	16	123	121	126	1.5
Resista × Rubinola	18	122	119	126	2.2
Resista × Rucla	30	122	120	126	1.5
Rubinstep × HL 665	21	123	118	126	2.3
Rucla × Rosana	21	121	119	125	1.6
Total	715	121	116	127	1.7

LSD – least significant difference, based on using Fisher's Least Significant Difference test

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Table 3. The flowering onset (days from January 1st) of parents and grandparents

Parental cultivars	Start of flowering	Female grandparent	Start of flowering	Male grandparent	Start of flowering
Angold (HL 362)	121	HL A 28/39 (Antonovka o.p.)	121	Golden Delicious	123
Braeburn	121	Granny Smith	120	Lady Hamilton	123
Discovery	118	Worcester Pearmain	119	Beauty of Bath	118
HL477	119	A18/74 (Hedvábné p. × Krátkostopka K.)	120	Alkmene	123
HL665	122	Spartan	120	HL A28/39 (Antonovka o.p.)	121
HL782	120	Rubín	120	Priscilla	122
HL1737	123	HL 231 (Starkrimson D. × Glockenapfel)	123	Honey Gold	122
HL2219	122	HL 237 (Starkrimson D. × Glockenapfel)	123	26 TRS 29 T-26 TE (ŠS Těchobuzice)	120
Karmína	123	Karmen	122	UEB 1725/6/PŘI 370-15 × Spartan	120
McIntosh Wijcik	119	Fameuse	118	O.P.	
Meteor (HL 704A)	124	Megumi	122	Melrose	120
Pidi (HL75-26-18)	120	McIntosh Wijcik	119	Florina	120
Pink Lady	121	Lady Williams	120	Golden Delicious	123
Resista (HL 835)	121	Prima	123	NJ 56	120.
Rosana	121	Jolana	122	Lord Lambourne	116
Rubinola	121	Prima	123	Rubín	120
Rubinstep (HL 164)	119	Clivia	118	Rubín	120
Rucla (HL 251)	120	Clivia	118	Rubín	120
Topaz	122	Rubín	120	Vanda	121

ated. Therefore it is possible to anticipate that the difference between both extremes could be larger if the size of the progeny were much greater.

Impact of parents and grandparents. The flowering onset in parents and grandparents with regard to the evaluated progenies is presented in Table 3. Among the parental cultivars, the cv. Discovery is characterized by the earliest time of flowering, having the mean date on April 25. Its parents (Worcester Pearmain and Beauty of Bath) have the flowering time on average only one day later. On the other hand, the latest time of flowering was found in the parental cultivar Meteor, having the mean date on May 2. Its predecessors – cultivars Megumi and Melrose – started flowering on average 3 days earlier. It seems to be rather an exception because these differences between other parents and grandparents were one or two days at maximum.

The means of the first flowering days within seedling populations between all the evaluated parental combinations and corresponding days of both their parents and grandparents were very highly correlated. The correlation between the mean first flowering days of progenies and parents was equal to $r = 0.926$, and between the means of progenies and grandparents to $r = 0.877$.

Segregation patterns of flowering onset in progenies. The incidence of flowering onset days in the progeny of parents having the same date had a typical pattern of the Gaussian distribution

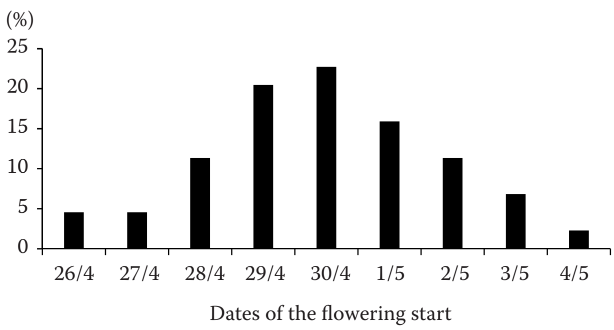

Figure 1. Distribution of flowering onset time in the progeny of HL 665 and Pink Lady cross

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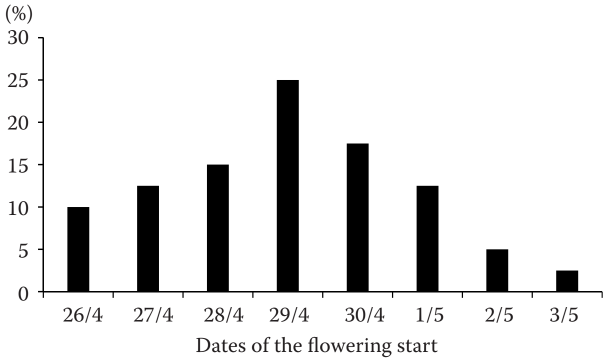

Figure 2. Distribution of flowering onset time in the progeny of HL 782 and Pink Lady cross

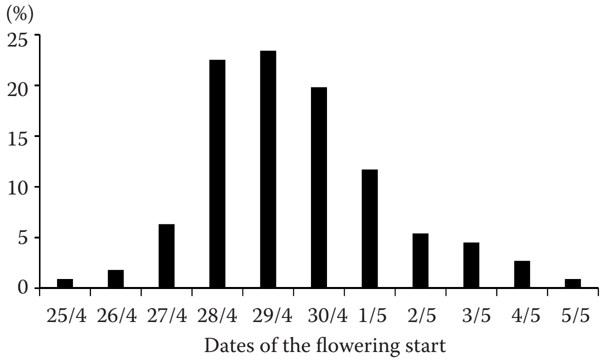

Figure 3. Distribution of flowering onset time in the progeny of HL 665 and HL 782 cross

(Figure 1). Nearly 60% of seedlings start flowering within 3 days – from April 29 to May 1. On the other hand, the share of both extremes, corresponding to April 26 and May 4, was less than 7%. Similar patterns of flowering time distribution were also found in progenies of parental combinations, where differences in the time between parents were equal to one or two days (Figures 2–4). Among them, the highest number of seedlings (119) was evaluated in the progeny of the cross between HL 665 and HL 782 (Figure 3). In this progeny, the difference between both extremes was equal to 11 days (April 25 and May 5). The share of seedlings in both extremes was, however, very small – less than 2%. The profile of distribution within the Resista × HL 2219 progeny (Figure 4) was also characterized by minimum differences. This was based on the evaluation of 66 seedlings. The greatest difference between all the other progenies was found in the progeny of Pink Lady and Discovery (Figure 5). The peculiarity of the progeny is a large difference between the flowering times of parental cultivars, which corresponded to 5 days. The distribution of frequency of the flowering onsets is characterised by two peaks – the first on April 25 and the second on April 29. Each of them is close to the time of flowering of the parents. Unfortunately, the size of the progeny (25 items) was relatively small. It would be very interesting to analyse this progeny with 100 or more genotypes.

Final comments and recommendation. Timing of flowering is a very important characteristic of apple cultivars, which has a great impact on their selection in particular growing conditions. Floral tissues are easily damaged by freezing temperatures, and freeze injury is especially problematic in years when abnormally warm temperatures in early spring lead to rapid floral development (Gottschalk & Nocker 2013). Therefore, it seems necessary also in the Czech Republic that the cultivars of a later time of flowering should be preferred.

The results of the present study are generally in good agreement with recent findings on the subject (Jung & Müller 2009; Celton *et al.* 2011; Gottschalk & Nocker 2013) and could be applied in future breeding programmes focused on the development of new apple cultivars characterized by very late time of flowering.

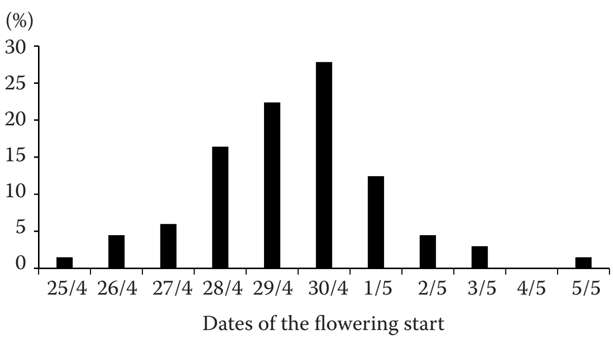

Figure 4. Distribution of flowering onset time in the progeny of Resista and HL 2219 cross

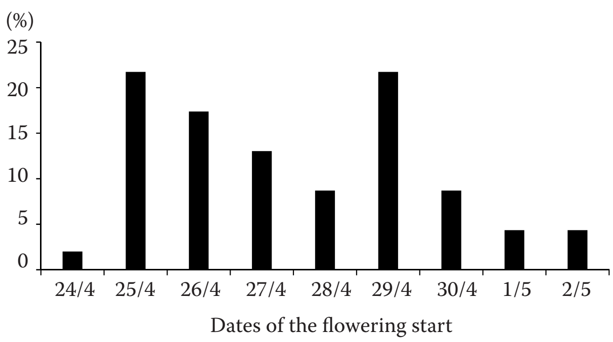

Figure 5. Distribution of flowering onset time in the progeny of Pink Lady and Discovery cross

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CONCLUSION

The results obtained in this study can be useful for the planning of future breeding programmes aimed at the development of new apple cultivars possessing a significantly delayed time of flowering. Such cultivars should be very useful for growing apples in regions with high incidence of late spring frosts. It is clear that such programmess would require huge numbers of seedlings in selected progenies to provide a chance to combine the late flowering with other important characteristics, especially very good fruit quality, that are necessary for obtaining any new apple cultivars. Possible pre-selection of the material for late flowering, however, could make it possible to reduce in time the total quantity of the finally evaluated material to a reasonable extent.

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