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Changes in the course of the spring generative phenological phases in manna ash (Fraxinus ornus L.) in dependence on the air temperature conditions

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Abstract

Manna ash (*Fraxinus ornus* L.) is the small tree of warm and dry localities with the center of geographic distribution in Mediterranean and the northern border of its native area in southern regions of Slovakia. The course of the spring generative phenological phases of this species was studied in allochthonous population in Central Slovakia (Radvaň – Vartovka in the vicinity of Banská Bystrica) during two vegetation periods with significantly different air temperature conditions. In the first season of our investigations (2008), the winter and early spring months were, from the viewpoints of air temperatures, only slightly above the long-term average at most. In most of the observed individuals, the end of the flower bud burst fell on 28th April. The start of the stigma receptivity and the start of the pollen release were mostly registered in 4th May and 10th May, respectively. In 2014, after the extremely warm winter and early spring, the advance of the generative bud burst was as high as 11–14 days and the advances of the start of the pollen release/receptivity of stigmas involved 6 and 7 days, compared to 2008. The achieved results are discussed in context of the reproductive biology of manna ash, as well as in relation to the older phenological data from two autochthonous localities of manna ash in southern Slovakia.

Key words: Phenology, changing climate, flowering

Introduction

The woody plants of warm and dry localities are the frequent objects of phenological studies, carried out in context of the climatic changes (Walkowszky 1998, Llorens *et al.* 2004, Škvareninová 2013). The research of such plant species is, in addition to their importance as bioindicators, related to the assumed shift or enlargement of their areas due to the increase of the average air temperature, changes of water regime, increase of the frequency of meteorological extremes and the shifts of the whole climatic regions or subregions (Ogaya, Peñuelas 2004, Bertin 2008, Škvareninová *et al.* 2009).

One of the woody plants, tolerating the high temperatures and shortage of water, is manna ash (*Fraxinus ornus* L.), small tree or higher shrub from the family of olives (Oleaceae), native to Mediterranean and southern Europe. The northern border of its natural distribution reaches the southern parts of Slovakia. Due to its frequent artificial planting in the past (Bertová 1984, Dostál 1989, Manica, Slobodník 2008), as well as its expansive properties, that express extraordinarily markedly out of the borders of its native area (Thébaud, Debussche 1991, Gojdičová *et al.* 2002, DAISIE 2009), however, according to our opinion there exists the possibility of its spontaneous spreading, in consequence of changing climate as well.

The studies on manna ash, aimed preferably at the impact of meteorological extremes on its phenological traits, will thus help us to assess its response to the intensive changes of outer environment in context of changing climate.

Material and methods

Characteristics of studied species

Manna ash (*Fraxinus ornus* L.) has its natural range, above all, in northern Mediterranean from the eastern part of Spain (Valencia) through the south-eastern France, Italy and Balkan Peninsula to Turkey and Middle East (north-western Syria and Lebanon). The southernmost parts of its natural distribution involve Hungary and south of Slovakia (FRAXIGEN 2005).

It differs from the other European ashes (*Fraxinus* L.) not only by its lower habitus, but also by an atypically smooth bark, pubescent grayish bud scales and much bigger flowers. These are, unlike the flowers of common ash and narrow-leaved ash, aggregated in rich terminal panicles and have four whitish leaflets of corolla. They are

hermaphrodite or male and these two types of flowers never occur together within the same individual. From the viewpoint of reproductive biology, manna ash is thus characterized as the morphologically androdioecious species (Dommée *et al.* 1999). Nevertheless, newer studies confirmed the functional dioecy of manna ash. This means that, despite the coexistence of male and hermaphrodite individuals in common populations, the paternal function in the sexual reproduction is really effective only in males. The decisive role in elimination of the male function of the morphological hermaphrodites is played by postzygotic factors, above all, by a much higher viability of the progenies, sired by the pollen of male individuals (Verdú *et al.* 2004). An eventual importance of prezygotic mechanisms in this process, e.g. the phenological advance of male individuals, remains still unknown.

In terms of reproductive phenology, manna ash belongs to the woody plant species with the late start of flowering. The exact data are available only from autochthonous localities in southern Slovakia. Due to the relatively frequent reforestations of abandoned and degraded biotopes in the past, however, there exist many scattered allochthonous localities of manna ash, situated in western, central and eastern regions of Slovakia as well (Bertová 1984, Dostál 1989, Manica, Slobodník 2008). The fact, that manna ash is well-adapted or even spontaneously expands in many sites with its allochthonous distribution, accounts for its high ecological plasticity. That could even mean that the area with the secondary occurrence of manna ash might further enlarge due to its expansive traits and global climatic changes, i.e. without a direct contribution of human. The last mentioned fact even more enhances the importance of further studies on the biological and ecological properties of this species, including monitoring of the time course of the phenological phases not only in its natural range, but also on the allochthonous localities.

Description of locality

In the presented paper, the flowering of manna ash is observed on its allochthonous locality Radvaň – Vartovka in the immediate vicinity of Banská Bystrica (region of Central Slovakia). The artificial planting of manna ash carried out here in late 1950s after the marked devastation by pasturing and the following erosion of soil (Midriak, Lipták 1965, Hladká 2010). At the present, manna ash is very well adopted here, regenerates naturally and even spontaneously expands (Manica, Slobodník 2008).

The locality is situated on the south-western slope of the Vartovka hill in Bystrická vrchovina Mts. and its altitude is about 450 m a. s. l. The bedrock is formed by dolomites and the most frequent soil type is rendzina (calcisol). The soil is flat, stony and, although the locality is characterized by the perhumid climate ((Midriak, Lipták 1965), also considerably dry. The extremity of site is even enhanced by the maximum slope of approximately 65 %.

The main native forest tree species are sessile oak – *Quercus petraea* (Matt.) Liebl. and common beech – *Fagus sylvatica* L. Nevertheless, the forest stands were markedly negatively influenced by human activity and their contemporary character is significantly determined not only by manna ash, but also by other allochthonous or originally only admixed species, e.g. Scots pine – *Pinus sylvestris* L., black pine – *Pinus nigra* Arnold, black locust – *Robinia pseudoacacia* L., common hornbeam – *Carpinus betulus* L. etc. Due to the intensive shading by the dense stand by manna ash, the herbal layer is relatively poor, with the occurrence of calciphytes, e.g. white sedge – Carex alba Scop., hairy violet – *Viola hirta* L., branched St. Bernard's lily – *Anthericum ramosum* L. and sword-leaved helleborine – *Cephalanthera longifolia* (L.) Fritsch, accompanied by some species of sessile oek stands, e.g. cypress spurge – *Tithymalus cyparissias* (L.) Scop., swallow-wort – *Vincetoxicum hirundinaria* Medik., and some of the species of forest-steppes, e.g. purple gromwell – *Buglossoides purpurocaerulea* (L.) I. M. Johnst. and wall germander – *Teucrium chamaedrys* L. From among the species of common beech forests, only the rare occurrence of Early dog-violet – *Viola reichenbachiana* Jord. ex Boreau was registered (Miňová 2012). The locality is also characterized by the occurrence of lady orchid – *Orchis puspurea* Huds.

Temperature conditions

Our research on the described locality was carried out during two vegetation periods with the markedly different air temperature conditions. While in the first season of our investigations (2007/2008) the winter and spring months from this point of view were only slightly above the long-term average at most, in the second season of our research (2013/2014) the monthly average values were much higher. According to the data from the near meteorological station (Sliač), in winter 2013/2014 all the monthly average temperatures of air were higher than the freezing point and the extremely high air temperatures were also registered during early spring (Fig. 1).

The highest difference of monthly average temperatures of air between the seasons of investigations (3.6 °C in 2008, 7.7 °C in 2014) is characteristic of March, i.e. the month that precedes the flowering of manna ash. This difference is even enhanced due to the relatively small precipitations in March 2014 (35.2 mm vs. 76.5 mm in March 2008).

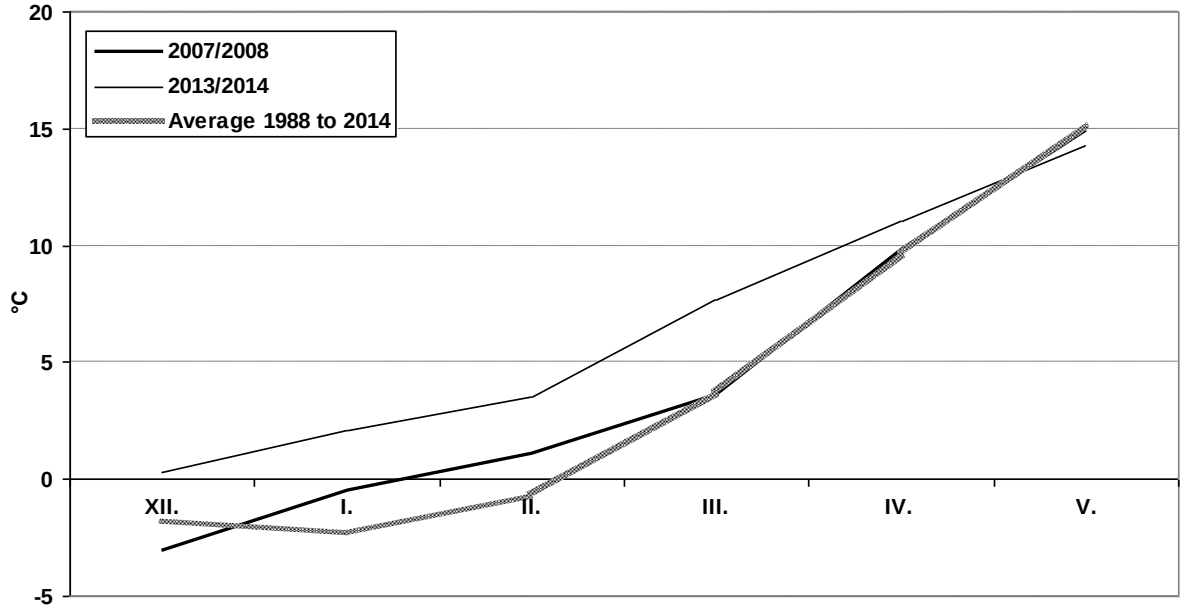

Fig. 1: Average monthly air temperatures during the winter and spring periods (December to May) of 2007/2008 and 2013/2014, and the long-term averages of the monthly air temperatures from 1988 to 2014, achieved from the near meteorological station Sliač.

Methods of field observations

Before the first season of our investigations, 60 individuals of manna ash from the studied locality were randomly chosen and tagged by numbers. Their morphological sexual type or gender (hermaphrodite, male) was estimated on the basis of presence or absence of fruits from the previous vegetation periods. Later, at the time of the full flowering, the sexual type (hermaphrodite, male) was determined definitely on the basis of presence or absence of pistils.

The course of the spring generative phenological phases of the chosen and tagged individuals was observed and recorded at the intervals of 3 to 4 days. We evaluated the course of the flowering according to the methodology, which had already been used in our previous research (Slobodník *et al.* 2006). This methodology is based on

the detailed assessment of each observed individual (phenological phases are recorded for each individual separately), as well as the separate assessment of male and female generative organs, i.e. stamens and pistils.

The used methodology enables the exact comparison of the achieved data with the results of the previous research, carried out on the other localities. In addition, the finding of eventual phenological differences between the sexual types (hermaphrodites and males) could contribute to the improvement of our knowledge of the biological properties of the studied species. Numbers and descriptions of the assessed spring generative phenological phases are summarized in Tab. 1.

Tab. 1: Numbers and descriptions of the assessed spring generative phenological phases in manna ash. Note: Course of the phenological phases 2, 2/3 and 3 is assessed separately for male generative organs (stamens) and female generative organs (pistils).

Number	Description	
0	Closed generative buds	
0/1	Start of the bud burst (opening of the generative bud scales)	
1	Opened generative buds with non-receptive flowers (butonization)	
2	♂: Start of the pollen release	♀: Start of the stigma receptivity
2/3	♂: Peak of the pollen release	♀: Peak of the stigma receptivity
3	♂: End of the pollen release	♀: End of the stigma receptivity

Results

Sexual structure of population

From among 60 individuals of manna ash, chosen and tagged at the beginning of our observations in 2008, 27 were determined as males. The morphological hermaphroditiism was ascertained for the same number of individuals, 27. The rest 6 individuals did not flower in 2008 and were classified as sterile.

In 2014, the flowering of the manna ash on the studied locality was much poorer: 18 flowering individuals were classified as males, i.e. they contains exclusively male flowers and 17 flowering individuals were classified as morphological hermaphrodites, i.e. their flowers were complete and contained stamens and pistils. The rest 25 tagged individuals were in 2014 sterile.

Thus, the male/hermaphrodite ratio of studied population is considered balanced. Eventual changes of the sexual type (gender) were not observed. Thus, this trait of the individuals of manna ash could be considered stable.

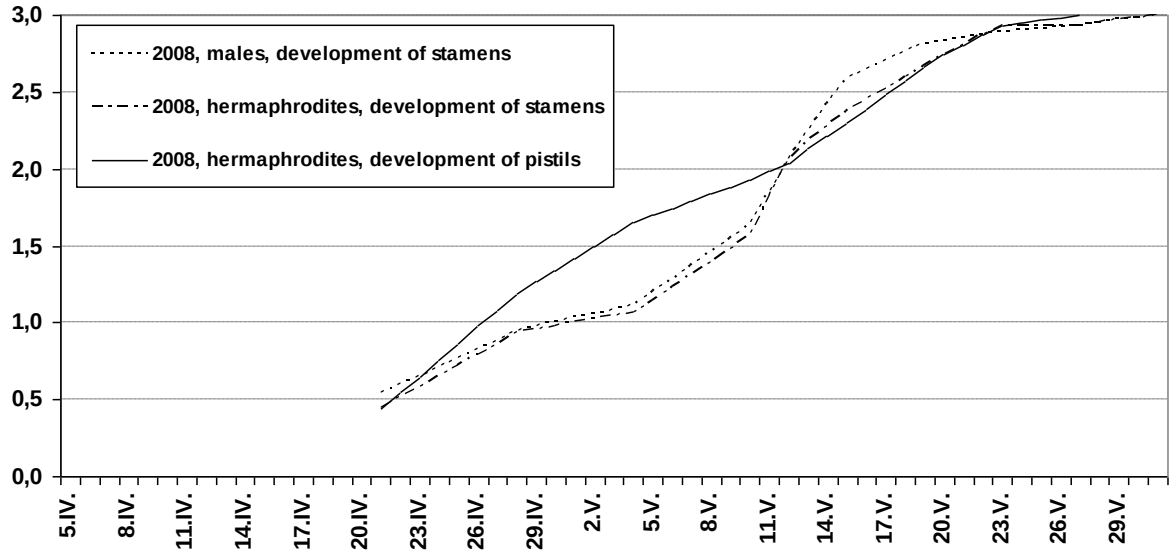

Fig. 2: Average number of achieved phenological phases, recorded during the observations of manna ash on the locality Radvaň – Vartovka in 2008.

Course of the spring generative phenological phases

The first of the main assessed phenological phases, opened generative buds with the non-receptive flowers, i.e. the phenological phase 1 was in 2008 in most of the observed individuals registered on 28th April, without the apparent differences between the hermaphrodite individuals and males. In 2014, when the start of our observations was preceded by the winter months with abnormally high monthly average temperatures, this phase was in most of the males registered as early as on 14th April, i.e. two weeks earlier than in 2008. In most of the morphological hermaphrodites, this phenological phase was achieved on 17th April, i.e. 11 days earlier than in 2008.

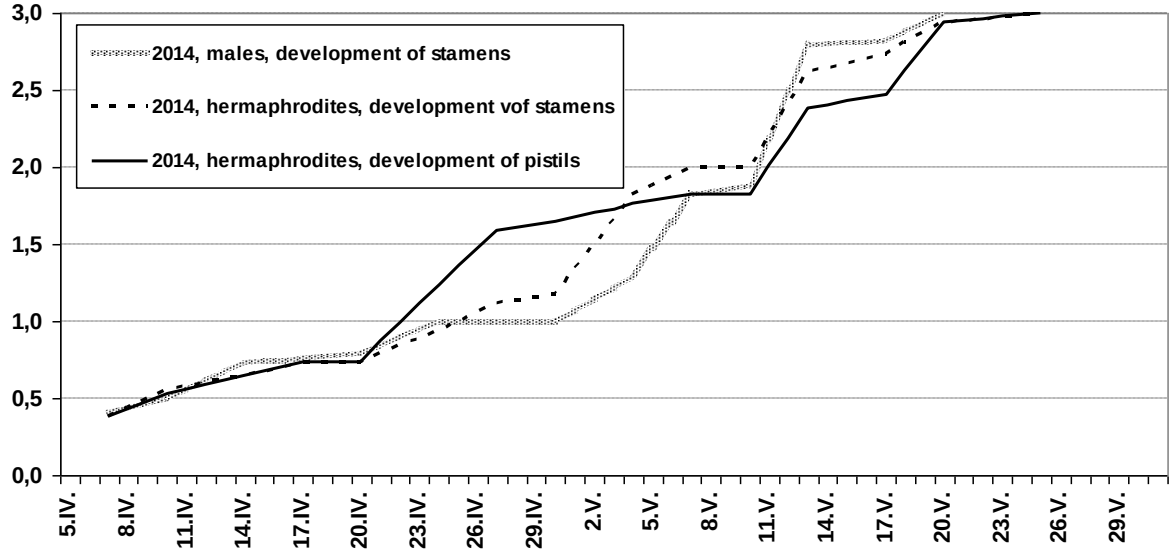

Fig. 3: Average number of achieved phenological phases, recorded during the observations of manna ash on the locality Radvaň – Vartovka in 2014.

Achieving phenological phase 2, i.e. the start of the release of pollen and the start of the receptivity of stigmas, respectively, fell on the different dates in the different years, as well as in the different types of generative organs (pistils, stamens).

In 2008, the start of the release of pollen fell, in the majority of the observed individuals, on 10th May, without apparent differences between morphological hermaphrodites and males.

The start of the receptivity of stigmas was in the majority of morphological hermaphrodites observed 6 days earlier, i.e. on 4th May. This fact is giving the evidence for protogyny, i.e. the phenological advance of female generative organs (pistils) in comparison with the male generative organs (stamens).

In 2014, the start of the pollen release was observed on 4th May, i.e. 6 days earlier than in 2008 in most of the observed individuals (hermaphrodites as well as males). The same date fell on the median of the start of the pollen release in morphological hermaphrodites. In the majority of males, however, this phase was registered a little later, on 7th May. Protogyny of manna ash was demonstrated in 2014 too, because the median of the start of the receptivity of stigmas fell on 27th April.

Unlike the previous phenological phases, the phase 3 (end of the release of pollen and end of the receptivity of stigmas, respectively) was achieved on the very similar

dates in both seasons of investigations. This fact is perhaps connected with the very similar average monthly temperature of air in May 2008 and May 2014 (Fig. 1). In 2008, this phase was in most individuals achieved on 15th May (end of the pollen release in males) and 19th May (end of the stigma receptivity and end of the pollen release in morphological hermaphrodites). In 2014, it fell on 13th May (end of the release of pollen in males), 17th May (end of the release of pollen in hermaphrodites) and 20th May (end of the stigma receptivity in hermaphrodites).

The mean numbers of achieved phenological phases, recorded during our observations in 2008 and 2014, are shown on Fig. 2 and Fig. 3.

Discussion

In general, flowering period of manna ash starts relatively late, at latest from among the European species of *Fraxinus* L. Under conditions of Sicily, Wallander (2001) observed the most intensive flowering of manna ash approximately at the turn of April and May. Even later flowering (turn of May and June) was characteristic of the population of relative, also androdioecious and partly insect-pollinated Japanese species *Fraxinus lanuginosa* Koidz, without apparent differences between male individuals and hermaphrodites (Ishida, Hiura 1998). According to the recent knowledge (Bolmgren *et al.* 2003), the late flowering period of ash species from section *Ornus* (Boehm.) DC. is perhaps a result of the partial adaptation to the pollination by insects.

Under conditions of Slovakia, phenological observations of manna ash were carried out by Slobodník *et al.* (2006) on autochthonous localities near to the border with Hungary. Their results are following:

(1) Median value for the achieving of the phenological phase 1 (opened generative buds) fell in the studied year (2003) on 16th April in case of the very warm locality in one of the southernmost regions of Slovakia (Kováčovské kopce) and on 23rd April in case of slightly cooler locality (Príbelce). Presented results from Central Slovakia (year 2014) are thus, from this point of view, very similar to the achieved data from the vicinity of Hungarian border (year 2003).

(2) On the southern border of Slovakia, phenological phase 2 fell in most of the observed individuals on 29th April (start of the receptivity of stigmas) and on 2nd and 4th May (start of the pollen release in males and hermaphrodites, respectively). On

the second locality (Príbelce), phenological phase 2 was achieved in the majority of individuals on 3rd May (start of the stigma receptivity) and on 5th and 7th May (start of the pollen release in males and hermaphrodites, respectively). The values, recorded in Central Slovakia after the extremely warm winter and early spring in 2014 (27th April, 4th May and 7th May, respectively) are thus, also for this phenological phase, very similar to the phenological data, achieved on the much warmer localities 11 years ago.

(3) On average, the anthers of the male individuals started to open 2 days earlier than the anthers of the morphological hermaphrodites.

(4) The end of the receptivity of stigmas was observed about 10th May (medians represented 8th May for the warmer locality Kováčovské kopce and 12th May for a little cooler locality Príbelce). On average, the stigmas were receptive more than 8 days. On both localities, the end of the pollen release was in male individuals recorded several days earlier than the end of the release of pollen in morphological hermaphrodites. In the male individuals, the total length of the period of the pollen release was thus longer.

Nevertheless, the last mentioned facts (paragraphs 3 and 4) were not demonstrated in case of the allochthonous population of manna ash. The problems of an eventual prezygotic reproductive advantage of males (and an eventual prezygotic elimination of the male function of the hermaphrodites) are therefore still under debate. Nevertheless, the experimental studies of common ash (*Fraxinus excelsior* L.) demonstrated the importance of the time advance of pollination and the relation between the phenological advance of the pollen donors and their paternal reproductive success (Bochenek, Eriksen 2011).

Conclusion

The results of the phenological observations of manna ash (*Fraxinus ornus* L.) from Central Slovakia suggest the possible shift in the time course of its spring generative phenological phases in case of the expected increase of the frequency of the extremely warm periods, similar to the winter 2013/14 and early spring 2014. In comparison with 2008, we recorded as high as 11 to 14 days advance in the opening of buds and 6 to 7 days advance in the start of the release of pollen and the receptivity of stigmas, respectively. Such phenological advance means an imaginary

movement of studied locality from Central Slovakia to its southernmost regions, where the spring generative phenological phases were investigated in 2003 (Slobodník *et al.* 2006).

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Summary

Jaseň mannový (*Fraxinus ornus* L.) je nízky strom teplých a suchých lokalít s ťažiskom zemepisného rozšírenia v Stredomorí a s výrazne vysunutou severnou hranicou svojho areálu, prechádzajúcou južnými regiónmi Slovenskej republiky. Priebeh jarných generatívnych fenofáz tejto dreviny bol sledovaný pri umelo založenej populácii v centrálnej časti Slovenska (Radvaň – Vartovka pri Banskej Bystrici) počas dvoch vegetačných období s výrazne odlišnými teplotnými pomermi.

V prvej sezóne našich pozorovaní (2008), keď boli zimné a skoré jarné mesiace z hľadiska teplotných pomerov nanajvýš iba mierne nadpriemerné, pripadlo ukončenie otvárania kvetných púčikov pri väčšine pozorovaných jedincov na 28. apríl a začiatok štádia receptivity blizien, resp. uvoľňovania peľových zŕn bol pri väčšine sledovaných indivíduí zaznamenaný 4., resp. 10. mája. V roku 2014, ktorý bol charakteristický extrémne teplou zimou a začiatkom jari, sme v porovnaní s rokom 2008 zaznamenali až 11–14-dňový predstih v otváraní púčikov a 6–7-dňový predstih pri začiatku uvoľňovania peľu, resp. začiatku receptivity blizien.

Dosiahnuté výsledky naznačujú možný posun v časovom priebehu jarných generatívnych fenofáz jaseňa mannového pri predpokladanom náraste frekvencie extrémne teplých období, podobných zime 2013/14 a začiatku jari 2014. Fenologický predstih, zaznamenaný v roku 2014 oproti roku 2008, predstavuje pomyselný posun sledovanej lokality zo stredného Slovenska na úroveň jeho najjužnejších častí, v ktorých sa jarné generatívne fenofázy jaseňa mannového sledovali v roku 2003 (Slobodník *et al.* 2006).

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