



## Analysis of chosen growth and reproductive traits of manna ash (*Fraxinus ornus*) with regards to its expansive properties

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Manna ash (*Fraxinus ornus* L.) is a Mediterranean shrub or a small tree with the northern limit of its natural range in central Europe. At the same time, it is also a tree species which, due to its considerable tolerance to high temperatures and lack of moisture, as well as some expansive properties, could be expected to increase its range in the coming decades as a result of the changing climate and the associated spontaneous spread. The paper summarizes the results of several years of our research, during which we evaluated the following growth and reproductive characteristics: (1) phenological traits and the length of the growing season, (2) the intensity and evenness of fruiting, and (3) the numbers of individuals and stems according to the height categories. In addition, the species composition of vegetation cover was analysed on the sites with the occurrence of manna ash. Observations were made in two autochthonous populations of manna ash in Southern Slovakia and one allochthonous population in its central region. The onset of spring vegetative and generative phenophases showed a noticeable latitudinal trend during our observations (2015–2019). In Central Slovakia, flowering and leafing of manna ash occurred on average more than two weeks later than in its southernmost region. The “Central Slovakian” population of manna ash was also characterised by the earliest onset of autumn vegetative phenophases and the lowest total length of the growing season. Despite these trends, flowering and fruiting in this population were relatively regular – in contrast to the other two sites, it was observed every year. In this locality, we also observed the highest total numbers of individuals and stems in all the height categories and the markedly decreased occurrence of competing species. The achieved results point out to the considerable vigour and high reproductive ability of the allochthonous population of manna ash outside its natural range and the natural range of its most important competitors.

**Keywords:** woody plant; phenology; vegetation period; reproduction; regeneration; spread; expansion.

### Introduction

Manna ash (*Fraxinus ornus* L., Oleaceae) is a deciduous woody plant, native to Southern Europe (Eastern Spain, South-Eastern France, Italy and Balkan Peninsula) and Western Asia (Boshier et al., 2005). The northern limit of its natural distribution reaches Hungary (Csontos et al., 2001; Kalapos & Csontos, 2003) and Southern Slovakia, where it grows in warm and dry localities (Bertová, 1984; Dostál, 1989).

It is characterised by its lower habitus, smooth bark and rich terminal inflorescences of whitish, fragrant, partially insect-pollinated flowers. Manna ash forms two types of flowers (hermaphrodite and male) and its individuals always bear only one flower type (Dommée et al., 1999).

Manna ash is a woody plant commonly found in Mediterranean regions. However, it is a highly adaptable species that tolerates a variety of ecological conditions. *Fraxinus ornus* is primarily adapted to a climate which is characterised by hot, dry summers and mild, rainy winters. However, it can also grow in regions where temperatures are more extreme, including a large scale of different altitudes. Due to its ability to spread spontaneously, it even shows apparent expansive properties (Thébaud & Debussche, 1991; Gojdičová et al., 2002).

In the light of the global climate change, many relevant publications also deal with the possible shifts of the plant species distribution into the higher elevations and higher latitudes (Bertin, 2008; Feehan et al., 2009; Garamvölgyi & Hufnagel, 2013). According to the predictions of Feehan et al. (2009), even several hundred kilometres shifts of the European plant species ranges in a northern direction are probable during the next decades. The climate is changing in Slovakia and Central Europe too.

Many publications draw attention to the rising trend in temperatures and to the declining trend in the humidity of air (Brázdil et al., 1996; Lapin, 2004; Labudová et al., 2015). Based on their data, since the 1990s the climatic conditions of Southern Slovakia have been considerably similar to those of the regions around Mediterranean Sea.

Škvarenina et al. (2018) predict that at the end of this century, the existence of typical Central European broadleaved forests will not be more possible at lower elevations due to the lack of humidity as a consequence of high air temperatures. Their decline will be probably connected to the expansion of the forest-steppe ecosystems and the xerothermic shrub vegetation. The similar scenarios were published not only for the territory of Slovakia, but also for the neighbouring region of Central Europe (Mačhar et al., 2017). Nevertheless, some species can adapt to the new conditions and start to expand. One of the other risks of the changing climate is therefore the risk of the biological invasions (Walther et al., 2002; Morellato et al., 2016).

Under the conditions of Slovakia, manna ash is a part of the xerothermic vegetation of lower trees and shrubs. Nevertheless, due to its ability to rapidly colonize disturbed areas and produce a dense canopy, this species was planted frequently in the past (Bertová, 1984; Dostál, 1989; Manica & Slobodník, 2008). It has been even listed among the expansive native vascular plant species (Gojdičová et al., 2002).

In our studies, we examined the variability of the following growth and reproductive traits of manna ash that may affect (positively or negatively) its expansive behaviour and spreading:

- 1) phenological traits and the length of the growing season;
- 2) the intensity and evenness of fruiting;

3) the numbers of individuals and stems according to the height categories.

Besides that, we assessed the species composition of vegetation cover in all three studied localities with the occurrence of manna ash.

## Materials and methods

The growth and reproductive characteristics of manna ash were studied in three different locations (Fig. 1). From among them, there is one locality with a clearly autochthonous population in the southernmost region of Slovakia (Kováčovské kopce), one locality where manna ash is autochthonous with high probability (Príbelce) and one allochthonous locality, where manna ash was planted in the past to strengthen a slope threatened by erosion (Radvaň – Vartovka).

The first of these sites (Kováčovské kopce) is characterized by a combination of xerothermic oak forests and enclaves of rocky forest-steppe and represents the area with the richest xerothermic flora in Slovakia. The bedrock is formed by andesites and andesite tuffs. The second site (Príbelce) is located north-east of the first one. The parent rock is andesite tuff. The habitats in this locality are rock forest-steppe formations with (in all probability) natural occurrence of manna ash. The last locality repre-

sents an allochthonous population of manna ash in Central Slovakia. Unlike the previous sites, the main parent rock is dolomite. The afforestation with manna ash, Scots pine and Austrian pine has occurred due to significant devastation caused by grazing and subsequent erosion of soil. The basic geographical and climatic characteristics of the studied sites are summarised in Table 1.



Fig. 1. Position of the studied localities on the territory of Slovakia

Table 1  
Geographical and climatic characteristics of studied localities

Locality	Coordinates		Elevation, m a. s. l.	AVG temperature, °C			AVG precipitation, mm
	Latitude	Longitude		Year	January	July	
Kováčovské kopce	47°50'	18°49'	180	10.2	-1.4	20.4	551
Príbelce	48°12'	19°15'	370	9.4	-2.4	19.7	631
Radvaň – Vartovka	48°43'	19°09'	450	8.0	-1.2	15.8	682

Our studies on the populations of manna ash included:

1) phenological observations and assessing the length of the vegetation periods;

2) evaluation of fruiting intensity and evenness;

3) counting the numbers of stems depending on the height category.

Studies on phenology and the length of the vegetation period (Ad 1), as well as the assessment of fruiting (Ad 2) included a five-year period of the investigations (2015–2019). Counting and evaluating the numbers of stems in individual height categories was related to the vegetation periods of 2015 and 2016.

Ad 1: On each of 60–65 of manna ash in each population, phenophases were scored according to the methodology of the Slovak Hydrometeorological Institute (Slovak Hydrometeorological Institute, 1984). Observations were carried out two times a week with a special emphasis on initial leafing and initial leaf fall, i.e. the phenological phases that represent beginning and end of the vegetation period. Assessed individuals were chosen randomly and were marked and numbered for the purpose of the assessment of fruiting, as well as for the repeated investigations in the following years.

Ad 2: After the assessing the sexual type of manna ash, (hermaphrodite, male), the flowering hermaphrodite individuals were counted and their percentage was calculated. Later (in autumn), the rate of the fruiting hermaphrodites was calculated. All the cases of the sporadic flowering and fruiting were excluded from the calculations.

Ad 3: Three 5 × 5 m plots were established and staked at each of the three sites. In each of these plots, the numbers of manna ash individuals and stems were recorded in the following height categories, corresponding to the different stages of individual development:

- under 25 cm (seedlings and young suckers);
- 25–50 cm (saplings and juvenile sprouts);
- 51–100 cm (outgrowths and outgrowing suckers);
- 101–300 cm (adolescents and tillers);
- above 301 cm (mature individuals and stems).

In each of two years of these measurements, the stems were counted in May–June, i.e. in the first half of the growing season.

Differences in the numbers of stems in each height category were tested by standard ANOVA, designed by the following model: Locality, Plot (Locality), Year, Year × Locality, Year × Plot (Locality). In all cases of the absence of normal distribution of values, which is a prerequisite for

the use of this method, it was necessary to perform their logarithmic transformation.

Besides that, we assessed the vegetation cover by phytosociological relevés, prepared by the standard Braun-Blanquet method. Three relevés from the plots of 5 × 5 m were made at each locality.

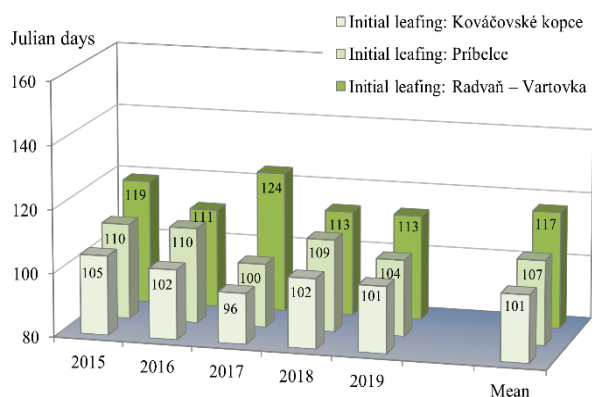
## Results

*Onset of phenophases and length of the vegetation period.* On average, the start of the vegetation period, i.e. onset of the phenophase of initial leafing, fell in the studied sites on the 101th Julian Day (April 11) in the southernmost locality) and the 117th Julian day (April 27) in the locality in Central Slovakia. The mean time difference between the two “South-Slovakian” localities (Kováčovské kopce and Príbelce) represented 7 days and as many as 16 days between the southernmost and the northernmost site (Kováčovské kopce and Radvaň – Vartovka, respectively). The time difference between the onsets of the initial leafing in the last mentioned sites was the lowest (9 days) in 2016 and the highest (no less than 28 days) in 2017 (Fig. 2).

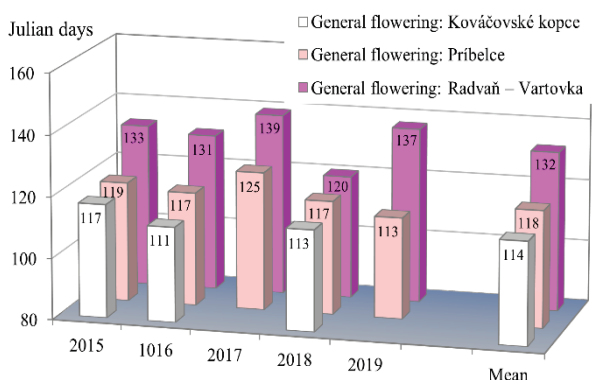
As follows from Figure 3, achieving generative phenological phase of full flowering (connected with the release of pollen and the receptivity of stigmas) occurred between the 111th (April 20 in the southernmost locality in 2016) and 139th (May 19 in the northernmost locality in 2017) Julian days. Analogous to the leafing, the time differences among localities show a marked latitudinal trend, representing, on average, 4 days between two localities in Southern Slovakia and as many as 18 days between the southernmost and northernmost situated populations. In all three localities, the start of the pollen release was almost always observed several days later than the start of the receptivity of stigmas. In two years of our investigations (2017 and 2019), flowering was fully absent in the southernmost studied site (Kováčovské kopce).

The total length of the vegetation period (bordered by the initial leafing and the initial leaf fall) ranged between 155 days (in the northernmost locality in 2017) and 190 days (in the southernmost site during the same year). In total, the vegetation period was the shortest (159 days on average, 155–168 days in individual years) in the northernmost site (Radvaň – Vartovka in Central Slovakia) and the longest (182 days on average, 175–190 days in 2015–2019) in the southernmost locality on the border with Hungary. The third locality (Príbelce) was characterised by the mean

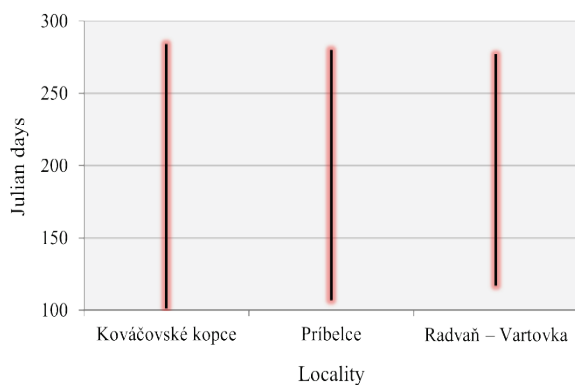
length of the vegetation period of 174 days (161 in 2016 to 188 in 2018). The time ranges and mean lengths of the vegetation periods of manna ash in all three localities are compared in Figure 4.



**Fig. 2.** Onset of initial leafing (leafing of 10% of observed individuals – start of the vegetation period) in the studied localities in 2015–2019



**Fig. 3.** Onset of general flowering (full flowering in 50% of observed individuals) in the studied localities in 2015–2019; in 2017 and 2019 flowering absent in Kováčovské kopce



**Fig. 4.** The time ranges and mean lengths of the vegetation periods of manna ash in the studied sites

**Table 2**

The mean numbers and standard deviations for individuals and stems of manna ash per area unit (1 m<sup>2</sup>) according to sites, height categories and years, and chosen parameters of ANOVA

Site/Height category	<25 cm		25–50 cm		51–100 cm	101–300 cm	>301 cm
	2015	2016	2015	2016	2015–16	2015–16	2015–16
Kováčovské kopce	2.09 ± 1.69	4.08 ± 2.15	0.34 ± 0.20	0.60 ± 0.23	0.00 ± 0.00	0.03 ± 0.00	0.03 ± 0.02
Pribelce	0.76 ± 0.47	1.13 ± 0.70	0.32 ± 0.25	0.21 ± 0.21	0.12 ± 0.05	0.16 ± 0.08	0.10 ± 0.07
Radvaň – Vartovka	14.67 ± 13.07	8.10 ± 7.95	2.90 ± 2.14	2.16 ± 1.56	0.76 ± 0.22	0.73 ± 0.08	0.73 ± 0.08
F	4.86		3.99		47.96	30.10	13.40
P	0.0555		0.0790		**0.0002	**0.0007	**0.0061

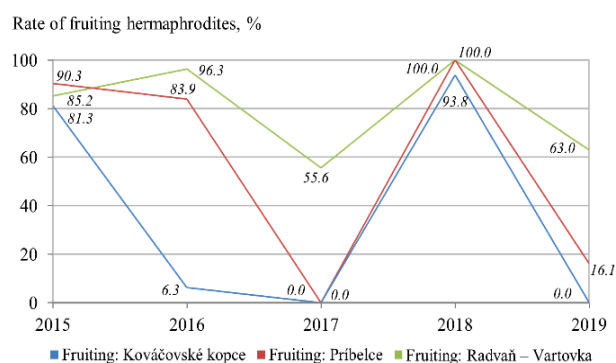
Notes: F – testing characteristics, P – critical probability; related to testing the differences between localities; at each site, three plots were analysed in two consecutive years; in the height categories 51–100, 101–300 and above 301 cm, there were only minimum differences between the years of investigations.

**Intensity and evenness of fruiting.** As Figure 5 shows, in both localities in Southern Slovakia, the fruiting of manna ash was characterised by a significant irregularity. In Kováčovské kopce, only two vegetation periods (2015 and 2018) were characterised by rich fruiting, when in 2015 81.3% and in 2018 93.8% of hermaphrodite individuals flowered and bore fruits. In 2017 and 2019 flowering and fruiting were absent in this locality (see also Figure 2) and in 2016, flowering and fruiting of hermaphrodite ashes was only very poor.

A similar situation was observed in Pribelce. Only male individuals flowered in 2017 (percentage of the individuals with fruits was therefore equal to zero) and only a poor fruiting was registered two years later. In 2015, 2016 and 2018, the flowering and fruiting were rich.

Contrariwise, in Radvaň – Vartovka (i.e. the locality in Central Slovakia with the allochthonous population of manna ash) the flowering and fruiting of this species were observed every year. Even in 2017 and 2019, when at the other two sites its flowering and fruiting were absent or very poor, flowers and fruits were here found in 55.6% and 63.0% of hermaphrodite individuals, respectively. In the other three years (2015, 2016 and 2018), percentage of the hermaphrodite individuals with fruits was here even higher than 90% (Fig. 5).

As the individuals with a sporadic flowering were excluded from our calculations, percentages of the flowering and fruiting hermaphrodite individuals of manna ash from the same locality and year were equal.



**Fig. 5.** Percentages of fruiting hermaphrodite individuals of manna ash depending on the locality and year in 2015–2019

**The numbers of individuals and stems according to the height categories.** In all the height categories (under 25 cm, 25–50, 51–100, 101–300 and above 301 cm), the numbers of juvenile and mature individuals, suckers, sprouts and mature stems of manna ash per area unit were clearly highest in the “Central-Slovakian” locality Radvaň – Vartovka with its allochthonous, spontaneously expanding population. The calculated mean values and standard deviations, as well as the chosen parameters of ANOVA, are briefly summarised in Table 2.

However, we also registered a high degree of variability between plots within the same site and, in cases of “lower” height categories (under 25 and 25–50 cm), between the years of investigations as well.

The results of ANOVA demonstrate the high significance of the differences between the compared sites in the height categories 51–100, 101–300 and above 301 cm, where. Contrariwise, the differences between the years and plots were significant in “lower” height categories (under 25 and 25–50 cm).

*Assessment of the vegetation cover.* The tree layer of the southernmost locality, Kováčovské kopce, is characterised by the combination of *Fraxinus ornus* L., *Quercus pubescens* Willd. and *Q. cerris* L. The shrub layer is here composed, besides the lower and younger individuals of the above mentioned woody plants, by *Cornus mas* L., *Sorbus aria* Crantz and *Acer campestre* L. The typical species of the herb layer (apart from the seedlings and saplings of the woody plants) are *Festuca valesiaca* Schleich. ex Gaudin, *Galium glaucum* L., *Verbascum phoeniceum* L., *Lithospermum purpureocaeruleum* L., *Eryngium campestre* L., *Hylotelephium telephium* (L.) H. Ohba, *Tanacetum corymbosum* (L.) Sch. Bip., *Erodium cicutarium* (L.) L'Hér. ex Aiton, *Stipa* spp. and *Iris pumila* L.

At the second site, Pribelce, the tree layer is (in addition to manna ash) is formed by *Quercus cerris* L. and *Q. petraea* (Matt.) Liebl., the shrub layer also by *Ulmus minor* Mill., *Ligustrum vulgare* L., *Viburnum lantana* L., *Sorbus torminalis* (L.) Crantz, *S. aria* and *Acer campestre*. The herb layer consists, above all, of *Festuca pseudovina* Hack. ex Wiesb., *Melica transilvanica* Schur, *Eryngium campestre* L. and *Silene coronaria* (L.) Clairv.

The northernmost, allochthonous locality of the manna ash (Radvaň – Vartovka) has the tree layer composed by *Pinus sylvestris* L., *P. nigra* J. F. Arnold and by the tallest individuals of manna ash. In the lower layer, the thick stands of manna ash almost fully dominate over the other shrubs like e.g. *Berberis vulgaris* L., *Sorbus aria* or *Cornus mas*. The herb layer is here relatively poor and consists mainly of *Carex alba* Scop., *Vincetoxicum hircundinaria* Medik. and *Anthericum ramosum* L. A special feature is the occurrence of the remarkable native orchids *Cephalanthera longifolia* (L.) Fritsch, *Orchis purpurea* Huds. and rarely, *Ophrys insectifera* L.

The herb species that occurred in all three compared localities were *Teucrium chamaedrys* L. and *Euphorbia cyparissias* L.

## Discussion

It is known that the flowering period of manna ash starts relatively late, the latest from among the European species of *Fraxinus* L. (Wallander, 2001). According to the opinion of Bolmgren et al. (2003), the late flowering period of ashes from section *Ornus* (Boehm.) DC. could be a result of the partial adaptation to the pollination by insects.

Another phenomenon, related to the phenology of manna ash, is protogyny, i.e. the phenological advance of female generative organs (pistils), compared to the corresponding male structures (stamens). As a part of the self-pollination-preventing reproductive strategy, it was referred to for all the European ashes (Boshier et al., 2005).

From the viewpoint of its reproduction system, manna ash was originally characterised as an androdioecious species with a balanced male/hermaphrodite ratio. However, the studies of Verdú et al. (2004) confirmed that manna ash is functionally dioecious, because the male function of morphological hermaphrodites is eliminated by postzygotic factors. The sexual dimorphism of the manna ash was studied by Verdú et al. (2007). According to their findings, the male individuals are characterised by a quicker growth and better regeneration ability due to their lower reproduction costs.

The manna ash has all the characteristics of a pioneer woody plant. It is characterised by a high resilience, rapid growth, early maturation, strong vegetative reproduction ability, and is considered to be relatively resistant to biotic pests (Piškur, 1999).

Nevertheless, the generally reported information about the annual production of large quantities of seeds requires some corrections. According to our findings, the flowering and fruiting in autochthonous Slovak populations of manna ash seems to be rather irregular, similarly to the populations of *Fraxinus excelsior* L. (Tapper, 1992; Tapper, 1996). Unfortunately, the causes of this irregularity (and concurrently, the relative evenness of the flowering and fruiting of manna ash from the allochthonous “Central Slovakian” population) remain unknown.

As mentioned above, the areas with the most abundant natural occurrence of manna ash are the Apennine and Balkan Peninsulas. As reported by Amiraglio et al. (2006), in Northern Italy it forms stands with Scots pine (*Pinus sylvestris* L.) and Scots hombeam (*Ostrya carpinifolia* Scop.). In the Central Apennines, i.e. in warmer and drier conditions, it is most often found in combination with *Ostrya carpinifolia* and *Acer opalus* Mill.

(De Sillo et al., 2012). From the Balkan Peninsula, data on the co-occurrence of manna ash with holm oak (*Quercus ilex* L.) are available. In particular, the association *Fraxino ornio-Quercetum ilicis* is known from Istria in Croatia (Baričević & Šapić, 2011).

From the hilly limestone areas of Hungary, the *Cotino-Quercetum pubescentis* association is known with *Pinus nigra* J. F. Arnold and *Quercus cerris* L. in the upper tree layer, *Fraxinus ornus* L. and *Quercus pubescens* Willd. in the lower tree layer, and with a rich shrub layer with the typical occurrence of *Cotinus coggygria* Scop. (Csontos et al., 2001).

Regarding its high resistance and resilience, manna ash was planted frequently in the past in various types of disturbed areas in various parts of Europe (Csontos et al., 2001; Kalapos & Csontos, 2003; Zagas et al., 2010) including Slovakia (Bertová, 1984; Dostál, 1989; Manica & Slobodník 2008).

Manna ash is also able to colonise new areas spontaneously. Therefore, it is a frequent component of the secondary succession of disturbed agricultural areas and disturbed forests (Giovannini et al., 1992).

However, the above mentioned characteristics of manna ash also represent a strong potential for its undesirable expansion. This undesirable expansive behaviour of manna ash has already been studied in several regions of Europe (Thébaud & Debussche, 1991; Giovannini et al., 1992; Wallnofer et al., 2008) including South-Western Slovakia (Hegedúsová & Senko, 2011).

The most striking example of the expansive behaviour of manna ash is probably its expansion along the Hérault River in Southern France (Thébaud & Debussche, 1991). Here, manna ash spreads along the watercourse and outcompetes most of the other, native species. Thus, its fruits are dispersed by water, analogous to the fruit and seed of many harmful invasive plants (Richardson et al., 2007; Aguiar & Ferreira, 2013).

In Slovakia, manna ash occupies steep, warm and dry slopes. Its spreading by watercourses is therefore improbable. Nevertheless, flowing water could play a role in the dispersal of its fruits towards the bases of the exposed slopes, where manna ash occasionally expands (e.g. on the locality Radvaň – Vartovka in Central Slovakia). However, the extent of this expansion depends on a variety of factors, e.g. interspecific competition and the specific climatic conditions of the locality.

At both studied sites in Southern Slovakia (Kováčovské kopce and Pribelce), manna ash is present in combination with several other lower trees and shrubs with very similar ecological requirements (*Quercus pubescens*, *Q. cerris*, *Cornus mas* and *Sorbus aria* in Kováčovské kopce and *Quercus cerris*, *Q. petraea*, *Ulmus minor*, *Viburnum lantana* and *Sorbus torminalis* in Pribelce). All these species can be considered the potential or real ecological competitors of manna ash and for some of them, Southern Slovakia represents the northern limit of their natural distribution. On the third, northernmost situated site (Radvaň – Vartovka), which was for a longer time a bare, deforested slope almost without any woody plants, the allochthonous population of manna ash forms a homogenous shrub layer in the understory of the thin, artificially established pine stand. The occurrence of competing species is here greatly reduced or even prevented, as many of them are not native to Central Slovakia. This could be (at least) one of the main reasons for the fact that manna ash has become perfectly established here and continues to regenerate and rejuvenate, and thus has a strong potential for the continuing spontaneous expansion.

## Conclusion

Despite the latest start of the spring phenophases and the shortest vegetation period from among populations from the three different studied sites, it was confirmed that the allochthonous population of manna ash from the northernmost situated locality Radvaň – Vartovka has the highest vigour and the strongest potential for the continuing spontaneous spread. This population is characterised by a relatively regular flowering and fruiting (in contrast to the populations from the other two studied sites), high total numbers of individuals and stems in all the height categories, and the markedly decreased occurrence of competing species.

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