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Diversity in honey locust (*Gleditsia triacanthos* L.) seed traits across Danube basin

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Abstract

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Honey locust (*Gleditsia triacanthos* L.), in the past planted as ornamental, technical or forest tree, is presently considered as casually invasive tree in Danube basin. Since plant invasiveness is usually tightly associated with its reproduction biology, in this work we focused on characterization of seeds from honey locust populations across this area. Analysing seed coat colour, thousand seeds weight (TSW), seed projection area, seed thickness, percentage of germinated seeds and their germination energy, as well as portion of seeds infested by honey locust seed beetle (*Megabruchidius tonkineus*), consumed part of seeds and their germination ability in relation to seed characteristics, local temperature means and precipitation sums during vegetation period, we came to the following conclusions: seed coat colour diversity decreases with geographical latitude; TSW, seed projection area and thickness were negatively correlated to mean temperature and positively to precipitation sum; between percentage of naturally germinated seeds and TSW as well as seed thickness we found positive correlations; germination energy showed positive relation to mean temperature and a negative one to precipitation sum; and the same relations were observed for infested seeds percentage and consumed seed part. No infested seed was able to germinate. From these results we can conclude that in colder and wetter conditions higher seed germinability, and in warmer and drier conditions enhanced germination energy of seeds supports spreading of this tree species. However, honey locust seed beetle can significantly affect seed germinability in regions with warm and dry summers.

Keywords

Danube basin, honey locust (*Gleditsia triacanthos* L.), honey locust seed beetle (*Megabruchidius tonkineus*), invasiveness, seed traits,

Introduction

Honey locust (*Gleditsia triacanthos* L., Caesalpinaceae) is a leguminous tree originating in the middle and eastern part of North America, which was in Southern Slovakia and Hungary widely planted in parks as ornamental species, round vineyards, gardens and fruit groves as thorn-hedge, along roads and fields as wind barrier, and as a component of floodplain forests (Chrtková and Jasičová, 1988; György, 2007; Haraszthy, 2001). Into Europe it was introduced in 1700, and its first plantation in the area of present Slovakia was established in 1806 in Dolná Krupá castle (Benčať, 1982).

However, presently this species is ranked as often escaping from culture (Gojdičová et al., 2002) or newly as naturalized in Slovakia (Medvecká et al., 2012) and casually invasive in Hungary (Balogh et al., 2004). It causes extreme complications in Argentinian Pampa grasslands and central natural forests, where a large effort in ecological research has been paid (Chaneton et al., 2004; de Viana and Speroni, 2003; Marco and Paez, 2000). Finally, in 1993 Autralian Queensland

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spent 400,000 $ for eradication campaign ´search and destroy´, stimulated by honey locust infestation of 1,000 ha of Brisbane valley (Csurhes, 2004).

Benčať (1982) classified this tree as very tolerant to industrial and transport emissions; Schindelbeck and Riha (1988) described its relatively high resistance to low soil reaction (up to pH 5). More recent works focus on its extraordinary tolerance to high temperature (Graves et al., 1991; Graves and Wilkins, 1991; Godoy et al., 2011) and drought (Graves and Wilkins, 1991; Burton and Bazzaz, 1991; Burton and Bazzaz, 1995), very helpful for its expansion.

Pyšek and Richardson (2007) summarizing results of 59 studies in 64 alien plant species ordered traits associated with their invasiveness. As expected, features connected to generative reproduction appeared among them. In honey locust, combined clonal and sexual reproduction, short juvenile period, high seed production and high seed germinability were described (Marco and Paez, 2000).

However, there is no reference about changes in this kind of traits with climatic conditions in literature. Therefore, in this work we analysed honey locust seeds from populations across the Danube basin.

Material and methods

Honey locust (*Gleditsia triacanthos* L.) pods from different regions of Slovakia and Hungary (locations with GPS coordinates are listed in Table 1) were collected at the end of November 2011. From each locality three trees were sampled. Trees were determined using determination keys of Rehder (1990) and Krüssmann (1960).

Table 1. Collecting sites of honey locust pods with GPS coordinates

Locality	GPS coordinates
Vieska n/Ž. (SK)	N 48°19´00.6´´ E 18°22´05.4´´
Szirák (HU)	N 47°49´49.4´´ E 19°30´36.4´´
Gyöngyös (HU)	N 47°45´56.4´´ E 19°56´42.3´´
Debrecén (HU)	N 47°34´06.3´´ E 21°35´50.3´´
Mezőtúr (HU)	N 47°00´11.4´´ E 20°38´41.0´´
Békéscsaba (HU)	N 46°40´50.1´´ E 21°02´50.1´´
Szeged (HU)	N 46°22´38.3´´ E 20°02´25.5´´

Pods were stored at 3 °C till seeds were shucked (3 days). Then we let them dry at room temperature (21/17 °C during the day/night). In the course of four months lasting storage in these conditions, adults of honey locust seed beetles (*Megabruchidius tonkineus* Pic, 1904) have enclosed and flied out from seeds. Injured seeds were collected and analysed for weight reduction related to seed beetle life cycle (%) and germination ability (%).

Thereafter, hundred healthy seeds from each tree sample were submitted to multiple analyses:

- Seed coat colour
- Thousand seeds weight (g)
- Seed projection area (mm^2)
- Seed thickness (mm)
- Germinated seeds (%)
- Germination energy (mm d^{-1}).

Seed coat colour was determined visually. Thousand seeds weight (TSW) we calculated from weight of hundred seeds, dried at room temperature. Seed projection area was defined by scanning and area analysis using ImageJ software (ver. 1.46). For seed thickness measuring we utilized a slide calliper. For the latter two tests, seeds have been swelling in water for 1 week, continuously transferred into transparent plastic boxes lined with a water-soaked tissue and analysed for natural germinability. Thereafter, non-swelled seeds were scarified in 93% sulphuric acid for one hour, washed thoroughly in water (Asl et al., 2011), let swell for 24 h and transferred into plastic boxes, as described above. Germination energy was analysed after 4 days of germination as hypocotyl length growth rate. All these procedures were done at 25 °C in constant diffuse light.

Hungarian Central Statistical Office provided us meteorological data (monthly temperature means (°C) and monthly precipitation sums (mm) for year 2011) for most of the analysed collecting sites in Hungary. Mlyňany Arboretum SAS (in Vieska nad Žitavou) dispose of its own meteorological station. From these data we calculated mean temperatures and precipitation sums for a period June–October 2011 (period of flowering, pod/seed establishment, pod/seed growth and ripening; see Table 2).

Experimental data were submitted to statistical analysis of variance (Anova) using Statgraphics Plus v.4.0 software. LSD tests at the 95% confidence level were performed to thousand seeds weight (TSW), seed

Table 2. Average meteorological data for the period June–October 2011 in most of the collecting sites

Locality	Nearest meteo station	Average temperature [°C]	Precipitation sum [mm]
Vieska n/Ž. (SK)	Vieska n/Ž. (SK)	17.4	307
Gyöngyös (HU)	Budapest (HU)	19.5	154
Debrecén (HU)	Debrecén (HU)	18.4	249
Mezőtúr (HU)	Kecskemét (HU)	18.9	212
Szeged (HU)	Szeged (HU)	19.1	116

projection area and thickness as well as germination parameters. Correlation analysis between respective parameters was accomplished using application MS Excell 2010.

Results

Seed coat colour of seeds from two northern collecting sites in Hungary (Szirák and Gyöngyös) showed larger variability than samples from Debrecén, Mezőtúr and Békéscsaba (Table 3). Only trees from alley near Szeged produced seeds uniform in colour. In Vieska nad Žitavou we found green-brown and medium brown seeds.

In weight of thousand seeds (TSW) LSD test distinguished three homogenous groups of samples: 1. with TSW round 220 g (Vieska nad Žitavou, Szirák and Békescsaba), 2. round 175 g (Gyöngyös and Szeged) and 3. intermediate seeds of TSW about 200 g (Debrecén and Mezőtúr).There was no statistical difference in projection area of seeds from respective collection sites. By seed thickness, localities can be ordered this way: 1. Debrecén, 2. Szirák, Gyöngyös, Szeged, 3. Vieska nad Žitavou, Mezőtúr and 4. Békéscsaba.

Naturally germinating seeds represent only a negligible portion from the total number of analysed seeds (Table 4): in Vieska nad Žitavou and Gyöngyösup up to 0.5%, in Debrecén, Mezőtúr and Szeged round 1%, in Szirák 1.35%, and in Békescsaba the portion slightly exceeded 1.5%. One hour pre-treatment by concentra-ted sulphuric acid almost completely released the germination process of any seed sample. We found values ranging from 95 to 98.5%. Only in samples from Debrecén and Békéscsaba less than 95% germinated seeds was identified. Germination energy of most of the samples showed similar level (approximately 9 mm d^{-1}). Extremes were observed only in Vieska nad Žitavou (8.09 mm d^{-1}) and Mezőtúr (10.56 mm d^{-1}).

In samples from Szeged we revealed the highest (9.15%) seed infestation by honey locust seed beetle (Table 5). In those from Békéscsaba almost 7.7%, in Gyöngyös and Debrecéna little more than 4%, in Szirák and Mezőtúr near 2.5% and in Vieska nad Žitavou no infested seeds were found. However, although ranging

Table 3. Parametrization of seeds from respective collecting sites. Abbreviations: TSW, thousand seeds weight; gb, green-brown; mb, medium brown; db, dark brown; lb, light brown. Letters indicate a statistically significant difference at P = 0.05

Locality	Analyzed pods	Analyzed seeds	Seed coat colour	TSW [g]	Seed projection area [mm²]	Seed thickness [mm]
Vieska n/Ž. (SK)	34	562	gb, mb	*221.75 ± 20.51*b*	57.57 ± 3.75*a*	4.04 ± 0.26*bc*
Szirák (HU)	41	575	gb, lb, mb	225.92 ± 29.27*b*	59.64 ± 7.84*a*	3.79 ± 0.26*ab*
Gyöngyös (HU)	33	463	gb, lb, mb	173.49 ± 14.90*a*	48.90 ± 6.97*a*	3.64 ± 0.26*ab*
Debrecén (HU)	33	519	gb, mb	193.61 ± 23.42*ab*	57.07 ± 9.20*a*	3.48 ± 0.37*a*
Mezőtúr (HU)	43	848	gb, lb	202.86 ± 26.37*ab*	51.91 ± 5.92*a*	4.05 ± 0.31*bc*
Békéscsaba (HU)	31	598	lb, mb	217.07 ± 1.06*b*	49.47 ± 3.87*a*	4.35 ± 0.24*c*
Szeged (HU)	44	973	mb	175.96 ± 3.99*a*	50.84 ± 0.84*a*	3.58 ± 0.08*ab*

*Average ± SD.

Table 4. Germination characteristics of honey locust seeds from respective collecting sites in Slovakia and Hungary. Letters indicate a statistically significant difference at P = 0.05

Locality	Germinated seeds [%]		Germination energy [m d^{-1}]
	Non-pretreated	Pre-treated	
Vieska n/Ž. (SK)	0.50	*96.94 ± 4.33*a*	8.09 ± 1.68*a*
Szirák (HU)	1.34	97.97 ± 2.02*a*	9.30 ± 0.30*ab*
Gyöngyös (HU)	0.33	97.29 ± 2.05*a*	9.23 ± 0.35*ab*
Debrecén (HU)	1.07	93.78 ± 7.54*a*	9.00 ± 1.21*ab*
Mezőtúr (HU)	1.00	95.29 ± 4.55*a*	10.56 ± 1.89*b*
Békescsaba (HU)	1.68	92.54 ± 11.13*a*	8.89 ± 0.39*ab*
Szeged (HU)	1.01	98.59 ± 1.22*a*	9.22 ± 0.30*ab*

*Average ± SD.

from 24.5% (Vieska nad Žitavou) to 41.37% (Szeged) in average, no statistically significant difference in consumed part of endosperm across Danube basin was detected. And finally, no infested seed was able to germinate.

Performing correlation analyses, we found that TSW was strongly determined both by seed projection area and seed thickness (r values were a little higher than 0.6; Table 6). However, there was a weak negative relation between the latter two seed characteristics (r = –0.188). We also observed a strong negative correlation between TSW and mean temperature for June–October period (r = –0.897) and a strong positive one between this parameter and precipitation sum for the same period (r = 0.917). Seed projection area was strongly correlated with mean temperature (r = –0.918) and precipitation sum (r = 0.885). For seeds thickness we only observed moderate correlations to these meteorological parameters (r = –0.459 and r = 0.507, respectively). Despite of no relation of the percentage of non-pretreated germinated seeds to seed projection area and mean temperature, moderate positive correlations of this characteristics to TSW (r = 0.449) and seed thickness (r = 0.389) as well as a weak one to precipitation sum (r = –0.117), were revealed. Percentage of pretreated germinated seeds was strongly related to precipitation sum (r = –0.544), moderately related to seed thickness (r = –0.467) but only weakly to the rest of parameters. Germination energy showed a strong correlation with mean temperature (r = 0.633) but a moderate one with precipitation sum (r = –0.434). However, it was not correlated with seeds characteristics. Except of seed thickness (r = –0.105), percentage of seeds infested by honey locust seed beetle was strongly related to all seed/weather characteristics. In the case of seed part consumed by beetle(s) we observed a strong negative correlation to TSW (r = –0.728), seed projection area (r = –0.676) and precipitation sum (r = –0.742). It was moderately related (r = 0.486) to mean temperature and weakly to seed thickness (r = –0.236).

Table 5. Percentage of infested honey locust seeds, consumed part of seeds and germinated infested seeds as influenced by collection locality. Letters indicate a statistically significant difference at P = 0.05

Locality	Seeds infested by seed beetle [%]	Consumed part of seeds [%]	Germinated infested seeds [%]
Vieska n/Ž. (SK)	0.00	–	–
Szirák (HU)	2.61	*24.90 ± 5.73*a*	0
Gyöngyös (HU)	4.54	39.53 ± 4.45*a*	0
Debrecén (HU)	4.05	34.11 ± 3.99*a*	0
Mezőtúr (HU)	2.71	30.32 ± 21.79*a*	0
Békescsaba (HU)	7.69	37.76 ± 9.05*a*	0
Szeged (HU)	9.15	41.37 ± 1.49*a*	0

*Average ± SD.

Table 6. Correlation coefficients (r) of relations between respective seed/weather parameters in honey locust populations for year 2011

	TSW	Seed projection area	Seed thickness	Mean June–October temperature	June–October precipitation sum
TSW	–	0.6***	0.655***	–0.897***	0.917***
Seed projection area	–	–	–0.188*	–0.918***	0.885***
Seed thickness	–	–	–	–0.459**	0.507***
Non-pretreated germinated seeds	0.449**	0.049	0.389**	0.056	–0.117*
Pre-treated germinated seeds	–0.251*	0.172*	–0.467**	0.24*	–0.544***
Germination energy	–0.01	0.03	0.051	0.633***	–0.434**
Infested seeds	–0.512***	–0.659***	–0.105*	0.69***	–0.894***
Consumed seed part	–0.728***	–0.676***	–0.236*	0.486**	–0.742***

*** – strong (1 > r ≥ 0.5), ** – moderate (0.5 > r ≥ 0.3) and * – weak linear regression (0.3 > r ≥ 0.1).

Discussion

Within following locations ordered by lowering geographic latitude we found decreasing diversity of seed coat colour (from green-brown, light brown and medium brown to medium brown). Schoeps (2002) defined that for this pigmentation chlorophylls, carotenes and xanthophylls are responsible. Since sampled trees were components of alleys, and since this species has polygamous character and it is fertilized by insects (Chrtková and Jasičová, 1988; Koblížek, 1995), gene flow between neighbouring individuals was expected. In the work of Schnabel and Hamrick (1995) we can read about 17–30% minimum estimates of pollen gene flow, depending on maternal trees distance (round 100 and 200 m). However, in general seed coat colour is a trait, which is highly influenced by environmental conditions (Souza and Marcos-Filho, 2001).

Ertekin and Kirdar (2010) studied effect of different seed coat colour on other seed characteristics of honey locust. They observed higher hundred seeds weight, seed coat weight, endosperm weight and embryo weight as well as germination in yellow coloured seeds compared with light and dark brown seeds. Despite of different seed coat colour scale, we can see similar trend in TSW but not in the percentage of germinated seeds. According to Asiedu and Powell (1998), slow rates of imbibition, caused by seed shrinkage and greater seed coat adherence to cotyledons during maturation, are associated with pigmentation. As indicated by Geneve (2009), after dormancy release lens and micropyle function as a primary water gap for seed imbibition in honey locust as well as water locust (*Gleditsia aquatica* Marsh.).

Barnabás et al. (2008) summarize that high temperature and water deficit can impair ovary and embryo sac development, cause pollen sterility as well as fruit/seed abortion or reduce their growth by restricted allocation of storage materials in cereals. This is in agreement with a general view of Fenner (2010) and Martre et al. (2011) on seed morphogenesis. Therefore, it is not a surprise that we found negative correlations of TSW, seed projection area and seed thickness with mean temperature as well as positive correlations of these seed parameters with precipitation sum in respective locations of Danube basin for a period from June till October, when reproductive cycle of honey locust has been accomplished. However, even in the warmest and driest regions stress was not enough intense to endanger seed germinability (Gutterman, 1991). Borges et al. (2005) focused on seed maturation process in *Caesalpinia echinata* Lam., a species relative to honey locust, at one place but in two years differing in rainfall during reproduction period. At the full fruit ripeness, seeds differed only in thickness (lower in drier year 2002).

Marco and Paez (2000) present honey locust as a plant species conferring high potential to become invasive: fast growth, clonal and sexual reproduction, short juvenile period, high seed production and high seed germinability. This coincides with a general ranking of plant features associated with their invasiveness (Pyšek and Richardson, 2007). Compared with *Acacia aroma* Hook. et Arn., a native to Argentina, invasive honey locust disposes of higher seed production per plant, percentage of scarified seed germination and density of seedlings around the focal individuals (Ferreras and Galetto, 2010). Herrera and Laterra (2009) show in an ecological study from flooding Pampa grassland that addition of seeds of invasive species promoted seedling emergence, and this effect was higher for large than for small-seeded species. Similar results obtained Eisenhauer and Scheu (2008) stating that established grassland community and invader seed size significantly affected the number of invader plants, while invader biomass was only affected by the established community. Jakobsson and Eriksson (2000) also found that the relative recruitment in undisturbed sward increased with increased seed size, and both recruitment success and seedling size were positively related to seed size. Although it was less strong, we revealed a correlation between the percentage of naturally germinated seeds and their TSW and thickness, as well. It can be explained by rising seed coat impermeability for water, associated with increasing adversity of environmental conditions during later stages of seed maturation (Souza and Marcos-Filho, 2001), responsible also for reductions in seed weight. But since germination energy was positively correlated to mean temperature and negatively to precipitation sum, seedlings of larger vigour can be expected in warmer and drier conditions. It is interesting that dark brown seeds, more frequently produced in such conditions, need much less water for germination than seeds of more lightly toned seed coats (Ertekin and Kirdar, 2010). However, warmer and dried environment was associated with higher seed infestation by honey locust seed beetle (György, 2007; Majzlan, 2011; Jermy et al., 2002), which exclude them from the pool of potentially germinating seeds. So, this is not the case of relative *Bruchidius dorsalis* Fahraeus, considered as a crucial bio-agent providing germination of *Gleditsia japonica* Miq. seeds (Takakura, 2002).

Thus, we can distinguish two different strategies supporting honey locust spreading: i) through higher germinability of larger seeds associated with lower temperatures and higher precipitation, and ii) through higher germination energy of smaller seeds connected with higher temperatures and lower precipitation. These results support the knowledge about high environmental plasticity of honey locust described by Godoy et al. (2011).

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