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Seed propagation in four perennial species of *Astragalus* (Leguminosae, Papilionoideae, Galegeae): productivity, non-random seed abortion and germination rate

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Summary: The largest angiosperm genus *Astragalus* exhibits a wide range of morphological variation regarding flowers, inflorescences and especially pods. As a result, some of its species are widely distributed, while others are local endemics and often threatened. It is of significant interest to trace features which provide a higher success for some species under conditions, where their relatives are depressed. Four perennial species of *Astragalus* from central Russia served as models for this comparative survey, viz. *A. cicer*, *A. glycyphyllos*, *A. arenarius*, and *A. danicus*. The two former species are widely distributed and rarely included into the regional Red Lists, while the two latter are comparatively rare and considered endangered in several regions. Only a relatively small fraction of ovules develops into fully mature seeds in all four species. Basing on the results of comparative study, it was hypothesised that the main sources of prosperity are a high potential productivity (measured as a number of ovules per seasonal shoot) and pronounced seed dormancy, typically physical. A number of produced ovules is substantially dependent on synflorescence morphology. The feature common for all examined species of *Astragalus* and distinguishing of the whole genus is an unusual biseriate arrangement of ovules in an ovary, which is probably adaptive for many-seeded fruits exhibiting non-random seed abortion.

Keywords: conservation, flower, hard-seededness, inflorescence, ovule, pod

The rates of diversification and underlying reasons have been debated for long (see Sanderson & Wojciechowski 1996 for review). The largest angiosperm genus *Astragalus* (Leguminosae) demonstrates the exceptional diversity with respect to lifespan (annual or perennial), life forms and morphology of flowers, inflorescences and especially fruits (Barneby 1964). Its worldwide diversity is hardly possible to be reviewed and analysed in a single work, even in narrow ranges of conditions one can find the remarkable variation of adaptations. As a result, some *Astragalus* species are very widely distributed and easily introduced beyond their primary habitats, while others are local endemics and endangered. It is of special interest to trace key features which provide an adaptive success to some species in comparison with their relatives, sometimes even cohabitants.

The key set of adaptations is associated with reproduction to any extent. As for *Astragalus*, the amount of literature devoted to its reproductive biology (phenology, pollinators, seed set etc.) is very impressive – and, proportionally to the number of species in this genus, probably yet insufficient to make any genus-wide conclusions. Recent reviews by Soltani et al. (2020, 2021) update the current state of this problem. Very many papers focus on endangered species to characterise their mode of reproduction and work out recommendations for conservation strategy.

This paper aimed at the characterisation of reproductive biology of four species of *Astragalus* more or less commonly found in central Russia. Of these four, two are more or less commonly distributed, while a certain conservation status is more often attributed to the other two. In

Table 1. Plant material used for analysis.

Species	Collection site	Voucher specimen
Astragalus arenarius L.	Moscow 55.792484 N, 37.441216 E	MW 1066277
A. cicer L.	Moscow 55.707269 N, 37.521078 E	MW 0568650
	Kaluga region 54.739244 N, 37.180522 E	MW 1066274
A. danicus Retz.	Moscow 55.793277 N, 37.443303 E	MW 1066276
A. glycyphyllos L.	Moscow region 55.705786 N, 36.685739 E	MW 1066281
	Kaluga region 54.739244 N, 37.180522 E	MW 1066282

addition to a broadening of available knowledge on reproductive biology of *Astragalus*, it was of special interest to find, which features provide more adaptive success to their owners.

Materials and methods

Plant material and morphological observations. Four species of *Astragalus* served as material for this survey (Table 1). They are found more or less on the entire territory of the temperate European Russia, although in some regions they are included into the regional Red Lists (Red Data Books, Fig. 1). The populations of *A. cicer* and *A. glycyphyllos* in Kaluga region (Tarusa) were observed in 2020 and 2021. The voucher specimens from studied populations were deposited in the Moscow University Herbarium [MW, see Table 1].

The plant material (flowers, inflorescences) was collected in natural populations (Table 1) and preserved in 70% ethanol solution for subsequent morphological analysis. To count ovules, 10–20 ovaries of each species' flowers were dissected under a stereomicroscope. Photo images were captured with an Olympus SZ61 stereomicroscope (Olympus Corp., Japan) equipped with a UHCCD05000KPA camera (ToupTek Photonics, Zhejiang, China).

For scanning electron microscopy (SEM) studies, ethanol-fixed material was dissected, then dehydrated in an ethanol series with a final dehydration in acetone and dried using a HCP-2 (Hitachi, Japan) critical point dryer. Specimens were mounted onto metal stubs using nail polish, coated with Pd in an Eiko IB-3 (Eiko, Japan) sputter coater and then visualised under CamScan-S2 (Cambridge Instruments, UK) microscope in Secondary Electron Image (SEI) regime with an accelerating voltage of 20 kV.

Analysis of non-random seed abortion. In *A. cicer* and *A. glycyphyllos*, seed abortion was scored with respect to the position of ovules in a pod. For this purpose, 100 almost mature pods of each species from Kaluga region (Table 1) were dissected under a stereomicroscope. As carpels of *Astragalus* produce opposed ovules in two parallel rows (Fig. 2, see Discussion), each ovule was numbered beginning from the proximal end of a pod in two rows independently. As seeds were sometimes damaged by insects, only pods/rows in which the precise number of seeds could be estimated were included in the analysis.

Each species exhibited a certain level of variation of ovule number per pod, viz. 9–14 in *A. cicer* and 14–23 in *A. glycyphyllos*. To unify these data, the method of transformation suggested by Hossaert & Valéro (1988) was applied. However, to avoid statistical artifacts, the real number of ovules in a row was normalised with respect to the maximum (not 'typical' or average) number

Figure 1. Selected federal subjects of the European Russia (continental temperate part); those which have the investigated species of *Astragalus* included into the regional Red Lists are shaded with grey. Dot = Moscow (55.752220 N, 37.615560 E). AR – *A. arenarius*, CI – *A. cicer*, DA – *A. danicus*, GL – *A. glycyphyllos*. Numbers indicate the category or rareness: 1 – 'endangered', 2 – 'decreasing number', 3 – 'rare', 4 – 'uncertain status', asterisk – 'requires special attention' (see Khapugin et al. 2020a for descriptions of categories).

of ovules per row. This means that the normalised number of ovule comprised $7f/n$ in *A. cicer* and $11f/n$ in *A. glycyphyllos*, where f stands for the former ovule position and n for the exact number of ovules in a given row. The resulting ratios were rounded to the nearest integer.

The described algorithm enables to estimate the absolute position of each ovule, which, however, is not convenient for a comparison between different species. For this purpose, the ordinal number of each fully developed seed in a row was divided by the number of ovules in this row. The resulting ratios exceeded zero and had its maximum value of 1 (if the distal-most ovule produced mature seed). For example, if a row consisted of eight ovules and 2nd, 3rd and 8th of them developed into seeds, the resulting ratios comprised ⅜, ⅜ and ⁸⁄₈, i.e. 0.250, 0.375 and 1.000. The whole set of data from all rows of all pods was merged and their distribution was divided into five equal intervals. This distribution represents the relative positions of mature seeds with respect to their position.

Study of germination rate. Seeds of all four species were collected in natural populations (Table 1) in August 2020 and stored in paper envelopes at room temperature. The first trial was conducted in April 2021. The samples of 25 fully mature and visually undamaged seeds of each species (for *A. cicer* and *A. glycyphyllos* seeds from populations of Moscow and Kaluga region were chosen, respectively) were washed with a liquid soap and then either left intact or scarified using nail clipper. Totally, two samples of each species were included into the experiment. The seeds were placed onto wet filter paper in Petri dishes and stored in a dark thermostat at 21–22°C for 30 days. A number of germinated seeds (with at least 1 mm of growing radicle visible) was scored regularly.

The second trial was conducted in September 2021 using the same collection of seeds and the same experimental design.

Figure 2. Alternate (A: *Pisum sativum*, lateral view, one of carpel valves removed) and opposite (B: *Astragalus glycyphyllos*, inner view from the removed dorsal suture's side) arrangements of ovules in the leguminous ovaries. A longitudinal septum is seen in B.

Results

Potential and realised seed productivity in four species of *Astragalus*. The primary results of field observations are available in Table 2. All indicators of post-fertilisation reproductive success (such as numbers of seeds and pods) were found remarkably variable, with a coefficient of variation (standard deviation/average) often exceeding 50%. In *Astragalus* (as well as in most of legumes), flowers, which produce no seeds, shed, while a pod may develop containing only a single seed. As a result, the number of seeds per pod varied strongly (Table 2). Similarly, the number of pods produced by a single axillary inflorescence (for sake of uniformity and brevity, this inflorescence is further called raceme, although in some species it may be a spike) also ranged widely.

Moreover, the features of potential productivity exhibited a certain level of intraspecific variation between populations, individuals or even within a single individual. The perennial species of *Astragalus* develop a caudex (see Barneby 1964 for terms) which in its turn gives rise to seasonal shoots. In three species (*A. arenarius*, *A. danicus* and *A. glycyphyllos*), this caudex is relatively compact, so it was rather easy to recognise an individual in a population. However, a number of aerial shoots produced by a single caudex varied significantly, probably depending on the certain individual's age. In *A. cicer*, an underground part represents a long branching rhizome, so it was very difficult to define which aerial shoots belonged to a solitary plant, especially in a dense stand. Some of the seasonal shoots produced paracladia (see below), while others did not. Number of flowers borne by axillary racemes was usually larger at the first flowering nodes than in the distal part of a shoot.

For this reason, it is most reliable to evaluate productivity of a single aerial shoot rather than of a whole individual. A simple multiplication of average values ('number of axillary racemes × number of flowers per raceme × number of ovules per flower' vs 'number of fruiting racemes × number of pods per raceme × number of seeds per pod') gives only rough estimates weakly reflecting the pronounced variation of studied parameters. These values are presented in Table 3.

Non-random seed abortion. In both *A. cicer* and *A. glycyphyllos*, patterns of seed abortion appeared non-random, although differently (Fig. 3). While the highest frequencies of seed maturation are confined more or less to the middle part of the pod in *A. glycyphyllos*, the distal-most ovule was the most successful in *A. cicer*.

Table 2. Values of quantitative reproductive traits in examined species of *Astragalus* represented as average ± standard deviation and minimum–maximum interval in parentheses.

Species locality	Year	Ovules per flower	Seeds per pod	Seeds to ovules ratio[1]	Shoots per plant	Racemes per main shoot + paracladia	Flowers per raceme	Pods per raceme	Pods to flowers ratio[2]
A. arenarius	2020	16.1 ± 1.1 (15–18)	3.7 ± 1.9 (1–7)	0.23	2.0 ± 1.6 (1–6)	5.4 ± 2.6 (3–9)	6.8 ± 0.8 (6–8)	2.7 ± 1.00 (1–5)	0.40
A. cicer Moscow	2020	12.0 ± 0.9 (10–13)	3.8 ± 1.4 (1–7)	0.32	–	–	–	–	–
A. cicer Kaluga region	2020	9.5 ± 0.6 (9–10)	4.6 ± 2.8 (2–9)	0.49	–	–	21.3 ± 1.5 (20–23)	17.3 ± 8.9 (4–22)	0.81
	2021	10.9 ± 1.1 (9–14)	4.5 ± 2.6 (1–12)	0.41 ± 0.24 (0.08–1.00)	–	14.3 ± 7.2 (8–26) 9.5 ± 3.9[3] (6–15)	27.7 ± 7.4 (21–41)	12.3 ± 5.1[5] (5–20) 12.8 ± 7.3[5] (1–22)	0.44
A. danicus	2020	15.9 ± 1.4 (14–17)	3.4 ± 2.4 (1–11)	0.22	–	1–3[4]	11.6 ± 3.7 (7–19)	8.2 ± 3.4 (1–16)	0.71
A. glycyphyllos Kaluga region	2020	18.2 ± 1.0 (17–20)	17.1 ± 1.3 (15–19)	0.94	–	–	15.2 ± 2.9 (12–19)	11.3 ± 1.2 (10–12)	0.75
	2021	18.0 ± 1.9 (14–23)	15.3 ± 4.0 (3–23)	0.88 ± 0.14 (0.21–1.00)	7.4 ± 3.1 (3–11)	10.8 ± 4.0 (5–21) 6.2 ± 2.5[3] (3–12)	–	–	–
A. glycyphyllos Moscow region	2020	20.3 ± 1.9 (16–23)	–	–	–	–	17.7 ± 2.9 (14–23)	–	–

Notes. [1] ratio between average numbers of seeds and ovules per raceme except for observations of 2021 in Kaluga region, from where data of individual pods are available and presented as average ± stand. dev.; [2] ratio between average numbers of pods and flowers per raceme; [3] number of racemes producing mature fruits; [4] min–max range; [5] for two subpopulations; dash, data absent.

Germination rates. There are numerous approaches to analyse germination patterns (Ranal & Santana 2006), but this work focused exclusively on the characterisation of germination rate on qualitative level. As observations indicate, all species possess a pronounced physical dormancy which was easily overcome by mechanical scarification (Fig. 4). In all species except for *A. glycyphyllos*, 100% of scarified seeds germinated rapidly. In *A. glycyphyllos*, only a part of

Table 3. Potential productivity and seed set in examined species of *Astragalus* calculated for a seasonal shoot.

Species, locality, year	Ovules per shoot	Seeds per shoot	Seeds to ovules ratio
A. arenarius, Moscow, 2020	591.2	53.9*	0.09
A. cicer, Kaluga region, 2021	4317.6	525.8	0.12
A. danicus, Moscow, 2020	368.9	55.76*	0.15
A. glycyphyllos, Kaluga region, 2020–2021	2954.9	1195.2	0.40

Note. * a proportion of racemes producing fruits was not scored, so this calculation is based upon the assumption that all racemes were productive (and hence is overestimate).

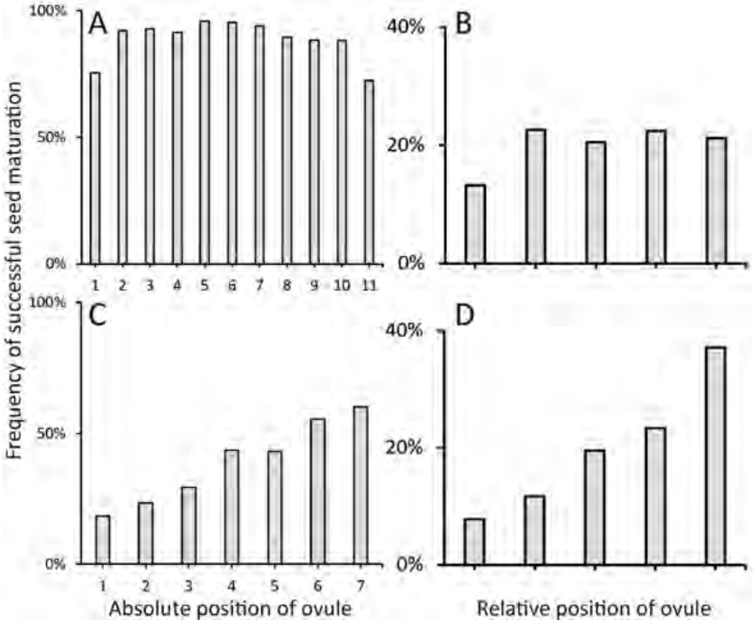

Figure 3. Patterns of non-random seed abortion in *Astragalus glycyphyllos* (A, B) and *A. cicer* (C, D) represented as frequencies of seed maturation with respect to the absolute (A, C) and relative (B, D) position of ovules. The minimum of horizontal axis corresponds to the proximal portion of a pod.

scarified seeds exhibited features of germination, although they all imbibed water. In *A. arenarius* and *A. danicus*, both producing smaller seeds (Fig. 5C, D), there was a certain percentage of seeds which germinated even without scarification. During observations in a natural population in 2020, several individuals of *A. danicus* were recorded with seeds germinating in wet indehiscent pods, i.e. prior to dispersal.

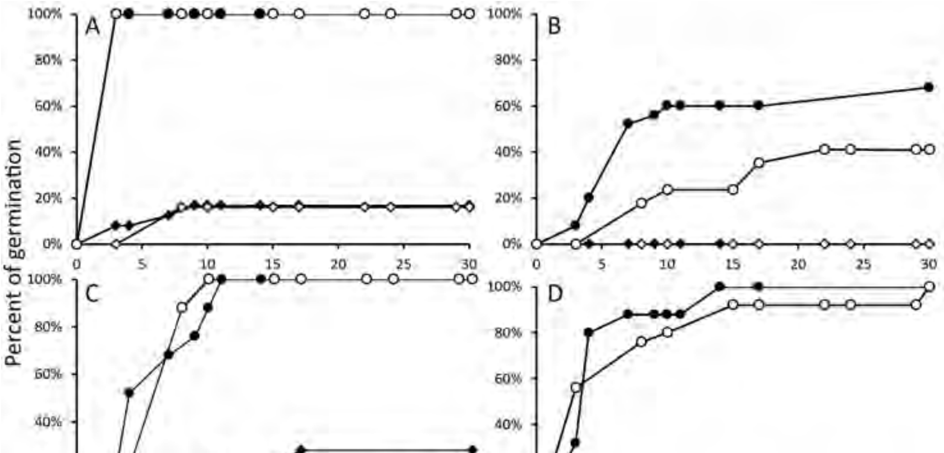

Figure 4. Dynamics of seed germination in *Astragalus arenarius* (A), *A. glycyphyllos* (B), *A. danicus* (C) and *A. cicer* (D). Dots designate data for scarified seeds, diamonds stand for unscarified control, colour distinguishes two trials (black for spring, white for autumn).

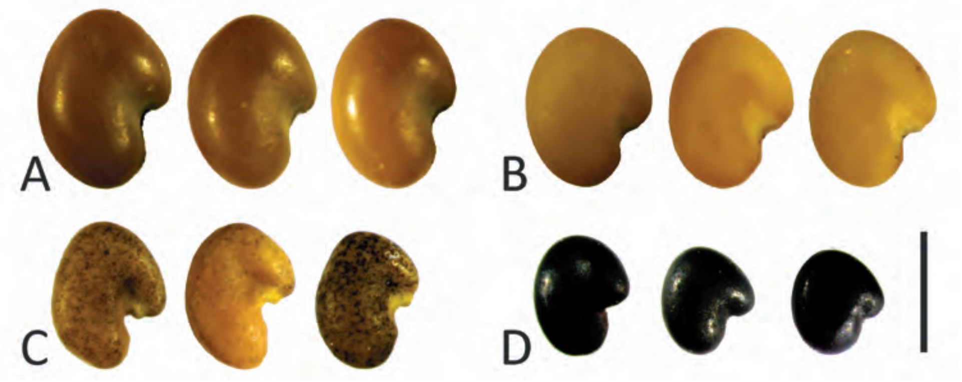

Figure 5. Seed morphology in studied species of *Astragalus*. A – *A. glycyphyllos* (Kaluga), B – *A. cicer* (Moscow), C – *A. arenarius*, D – *A. danicus*. Scale bar = 2 mm.

Patterns of germination were similar in both spring and autumn trials almost in all cases. Rate of germination of scarified seeds of *A. glycyphyllos* appeared lower in autumn, for which no reasonable explanation could be found at the moment.

Discussion

Only the smaller part of flowers produces mature fruits. In legumes, the flowers to fruits ratio is usually lower than 100%, which is especially pronounced in perennials (Hossaert & Valéro 1988; Ehrlén 1992; Kang 1996; Soltani et al. 2021). The data presented here provide the material for some conclusions on patterns of flower abortion in *Astragalus*.

- The distal-most (i.e. later flowering) axillary racemes often fail to produce fruits. This feature is remarkable for *A. glycyphyllos* with its shoots producing axillary racemes during the whole flowering period. As a result, a compound raceme emerges with an uninterrupted floral zone (Fig. 6C). The distal-most racemes hence begin flowering, when the basal-most ones already produce pods. In the examined population of *A. glycyphyllos* from Kaluga, little more than 50% of initiated axillary racemes were fruiting. A similar pattern was reported for other species of *Astragalus* (e.g. Kudo & Molau 1999) as well as for genera with a similar synflorescence structure, such as *Vicia* (Kang 1996) and *Lathyrus* (Ehrlén 1992).

  However, in some species of *Astragalus* the structure of synflorescence is somewhat more 'parsimonious'. It is the case of *A. cicer* and *A. danicus*, in which only few (often one in *A. danicus*) successive leaves bear racemose partial inflorescences in their axils. In axils of upper leaves, vegetative buds unfold, so the flowering zone is therefore intercalary (Fig. 6B). In *A. cicer*, there is no pronounced pattern, in which positions the axillary racemes fail to produce mature fruits. As Kuznetzova (1989) hypothesised, the former type (Fig. 6C) may be derived from the latter (Fig. 6B), although there is no clear correlation between taxonomical position of species and its synflorescence structure. The observations in natural populations do not give enough data to define, which type *A. arenarius* belongs to.

- In each axillary raceme, the distal flowers usually fail to produce mature pods. Earlier, Kudo & Molau (1999) discovered that *A. alpinus* exhibited a 'gradient of masculinity' along an axis of axillary racemes, so that the upper flowers had larger stamens and higher pollen viability than the lower ones, but they produced fewer pods and seeds. Ehrlén (1992)

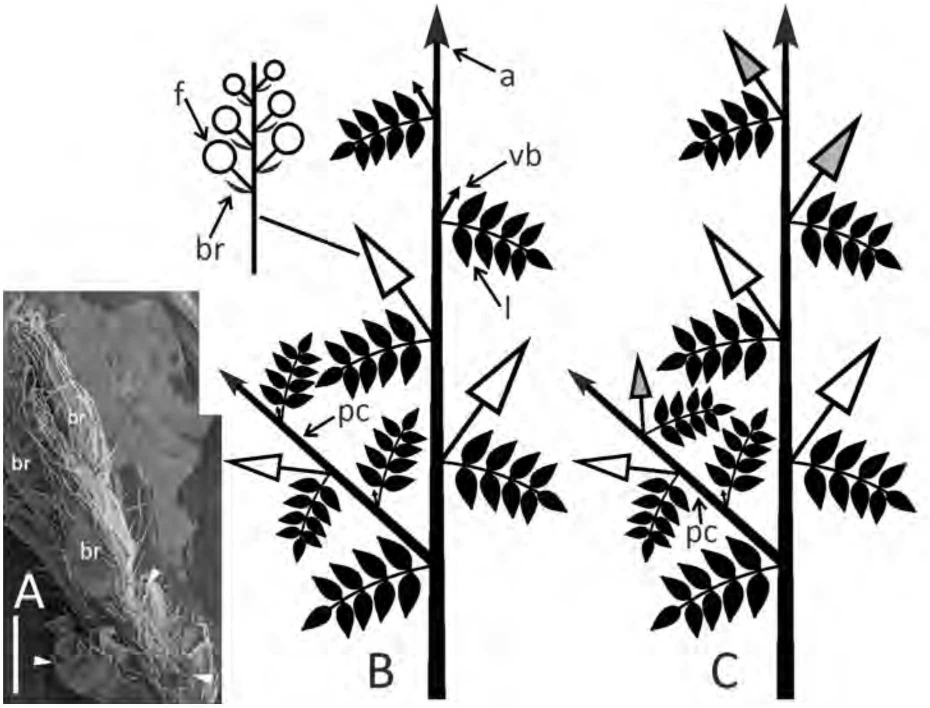

Figure 6. Morphology of raceme tip of *Astragalus cicer* (A, SEM image) and schematic representations of synflorescences in *Astragalus*. B – type with an intercalary floral zone, C – true compound raceme. a = apex of a seasonal shoot, br = bract, f = flower, l = leaf, pc = paracladium, vb = axillary vegetative bud, arrowheads = sites of attachment of lower flowers. The axillary racemes, which are least probable to produce fruits, are shaded with grey. Scale bar (A) = 1 mm.

suggested that excessive (non-fruiting) flowers of *Lathyrus* might serve preferentially as a source of pollen but in some circumstances also for providing reserve ovaries. Additionally, these flowers increased the attractiveness of the whole synflorescence for insect pollinators.

In many-flowered racemose partial inflorescences, such as those of *A. cicer* and *A. glycyphyllos*, the distal-most flowers sometimes remain underdeveloped and wither before opening (Fig. 6A). Possibly all initiated flowers may reach full anthesis under certain weather conditions. Otherwise, the initiation of these flowers may represent an ontogenetic 'overshoot' which brings no adaptive benefits.

- Flowers on paracladia, if developing, often do not produce pods. No paracladia were recorded in *A. danicus*, while synflorescences of other species (especially *A. cicer*) were often highly ramified. The paracladia are elements which develop only under certain conditions and can remain unfolded in other cases. One may suggest that paracladia, if emerging, may either serve to enhance attractiveness of the whole synflorescence or/and provide a pollen, but only under favourable conditions they produce fruits and seeds.

Arrangement of ovules in ovaries of *Astragalus* may offer the advantage against position-dependent seed abortion. The phenomenon of position-dependent (non-random) abortion of ovules and seeds has been repeatedly investigated in different plant species, including legumes (Hossaert & Valéro 1988; Kang 1996; Susko 2006). As Hossaert & Valéro (1988) demonstrated in their work on species of *Lathyrus*, ovules at the basal portion of the carpel have lower probability of fertilisation, while seeds at the distal (stylar) part of the maturing pod more often fail to develop due to imperfect resource allocation. As a result, maximum likelihood of successful seed maturation is observed in the middle part of the pod. In some legumes, however, this pattern is diverse, with the maximum frequency of successful seed maturation at the distal end of a pod (Susko 2006). Kolyasnikova (2004) discovered that in some species of *Astragalus* ovules in the middle of the ovary developed somewhat faster than those at proximal and distal positions.

In two species examined with respect to this feature, *A. glycyphyllos* and *A. cicer*, patterns of non-random seed abortion were different (Fig. 3). In *A. glycyphyllos*, the maximum probability of full seed maturation was confined to the middle part of the pod, while in *A. cicer* this probability reached its peak at the distal-most ovule.

As Barneby (1964) figuratively stated considering *Astragalus*, “no other genus of flowering plants exhibits greater variety in the form of the fruit”. Pods of all four examined species, although differing in size, shape, colouration and texture, possess two remarkable features of this genus. These are a longitudinal endocarp-derived septum produced from the dorsal suture and seeds borne in two distinct rows separated by this septum (Fig. 2B). The first peculiarity may hypothetically prevent developing seeds from being damaged by semenivorous insects: if one of the pod locules is infested by larvae, they may have difficulties penetrating the septum, especially lignified. Additionally, the presence of the septum and patterns of its lignification and fusion with the ovary wall define the mode of pod dehiscence (e.g. Holden 1952).

The second characteristic feature of fruits of *Astragalus*, i.e. the opposed arrangement of ovules, may contribute to the frequency of seed abortion. Among Leguminosae of temperate European Russia, species of *Astragalus* belong to those with the highest number of ovules, comparable with those of some *Lathyrus*, *Robinia* (introduced) and *Lotus* species. However, in three listed genera the proportion of ovules reaching the fully mature seeds rarely exceeds ⅓ (Dobrofsky & Grant 1980; Hossaert & Valéro 1988; Susko 2006). As summarised in a recent metastudy of Soltani et al. (2021), there is a significant variation in seeds/ovules ratios among different species of *Astragalus* mostly depending on self-compatibility. Surprisingly, *A. glycyphyllos* with the largest number of ovules among examined species exhibited the highest seeds/ovules ratio during two years of observations (Table 3). It is not a necessary feature of this species, as Mamedova (2020) reported its relatively low seed productivity.

Data on seeds/ovules ratio should be treated with caution, as seed productivity depends on numerous factors, such as weather conditions of a given season, availability of pollinators and the ratio between self- and cross-pollination in a certain population as well as frequency of deleterious mutations causing seed abortion irrespectively of ovule position. For example, Kolyasnikova (2004) reported a certain frequency of sterile ovules and anomalies of embryonic development in several species of *Astragalus*. This may suggest the numerous embryonic lethal mutations in the corresponding populations, a phenomenon probably more inherent to perennials than to annuals.

However, if the fate of each ovule is dependent on its position with respect to the proximo-distal axis of a carpel, then species of *Astragalus* have a certain advantage, as their ovules are arranged in an opposite, not alternate, manner. That is why in each position chances of successful seed production are theoretically twice as high as in more ‘convenient’ pods, which explains a high overall seeds/ovules ratio compared to other leguminous genera having similar (high) numbers of ovules but in the alternate arrangement (Fig. 2A). If one assumes that the angiosperm carpel is homologous to a phyllome bearing megasporangia along its margins, then theoretically a switch between opposite and alternate arrangement of ovules can be regulated as easy as switches between alternate (relatively rare in Leguminosae) and opposite position of leaflets of a pinnate compound leaf.

The examined species possess varying degrees of a physical seed dormancy. Due to their unparalleled variation and wide distribution, numerous species of *Astragalus* were repeatedly studied for the features of seed germination (reviewed by Soltani et al. 2020). The data reported here indicate that three examined species of *Astragalus* (except for *A. glycyphyllos*) exhibit a physical dormancy, which was easily broken by mechanical scarification (Fig. 4), so after a treatment all seeds germinated rapidly. Nikolaeva et al. (1985) stated that immature seeds of *Astragalus* spp. imbibed water and germinated more readily than mature ones, the latter possessing hard-seededness. As data presented here indicate, a certain percentage (ca 20–30%) of seeds of *A. arenarius* and *A. danicus* imbibed water and germinated even without any pretreatment. Several previously published papers are dedicated to the germination of the same species (Nikolaeva et al. 1985; Statwick 2016; Kornievskaya 2021 and references found in Soltani et al. 2020) and can be compared with the data presented here. As distinct from the newly obtained data (Fig. 4), Kornievskaya (2021) never recorded 100% of germination of seeds of *A. cicer* under three tested temperature regimes, which may be connected with differences in experimental design: Kornievskaya (2021) scarified seeds with a concentrated sulphuric acid and a percentage of germinated seeds was evaluated at 7th day after beginning of germination rather than in long-term dynamics. Statwick (2016) reported a maximum of ca 30% of germination of intact seeds of *A. cicer*, which may indicate that in some populations the physical dormancy may be not as deep as in the Russian ones. The hard-seededness is heritable in legumes (e.g. Keim et al. 1990) and hence may vary in different populations.

A somewhat different pattern was observed in *A. glycyphyllos*, as only ca 70% of scarified seeds germinated (Fig. 4B). It agrees with the observations of Nikolaeva et al. (1985) that seeds of this species germinated after being stratified at 4°C for one month and scarified. There are not so many species of *Astragalus* which exhibit the combinational (i.e. both physical and physiological) dormancy (Soltani et al. 2020), and *A. glycyphyllos* seems to belong to this type.

The type of seed dormancy may partly contribute to the efficiency of reproduction. A deep physical or combinational dormancy probably extends germination over a longer period of time and hence maintains the persistent seed bank. Two out of four examined species, *A. arenarius* and *A. danicus*, have a relatively low percentage of hard-seededness and at the same time are more often included into the regional Red Lists (Fig. 1).

Conclusion

Although growing in similar habitats (and often cohabiting), four investigated species of *Astragalus* possess different strategies of seed propagation. The principal drivers of extinction of plants in Russia are anthropogenic, such as habitat degradation, grazing or urbanisation (Khapugin et al. 2020b), but some *Astragalus* species are obviously more resistant against them, which is reflected in a frequency of inclusion into the regional Red Lists (Fig. 1). Basing on the results reported here, the following components of success can be listed.

- A higher potential productivity, i.e. the number of ovules produced by an individual plant and capable of fertilisation. Although *A. cicer* exhibits a relatively low seeds to ovules ratio

(Table 3), the resulting seed set is significant and probably can be even higher under favourable conditions.

- The morphology of synflorescence. The uninterrupted terminal floral zone, such as in *A. glycyphyllos* (Fig. 6C), is associated with a relatively high level of flower abortion, especially in distal positions. The intercalary floral zone (Fig. 6B) seems more 'parsimonious', and there is no clear position-dependent effect on flower abortion within a seasonal shoot. However, in *A. danicus* this floral zone is very short (one to three axillary racemes), which, together with an absence of paracladia, results in a low potential productivity.
- A pronounced seed dormancy, either physical or combinational. The seed bank in soil can be built up only with species with a delayed germination. However, this relation requires a closer investigation including the direct analysis of seed bank content.

One of the features potentially advantageous in most species of *Astragalus* compared with the majority of legumes is the biseriate arrangement of ovules which (probably under certain conditions) may increase the chances of successful seed maturation in the face of position-dependent seed abortion. The reproductive features of *Astragalus* should be a subject of a closer examination (involving wider range of species, especially annuals) to get deeper into the reasons of striking evolutionary success of the largest angiosperm genus.

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