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Bio-Morphological Characters of Alien Legume Species, Influencing Their Invasion in Natural Plant Communities

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Abstract

Five alien legume species, actively invading in natural plant communities in European part of Russia, were studied—*Lupinus polyphyllus* Lindl., *Galega orientalis* Lam., *Robinia pseudoacacia* L., *Amorpha fruticosa* L. and *Caragana arborescens* L. Distribution ranges (considering their invasive status) were mapped. Not a single bio-morphological character to forecast invasion success in natural plant communities within secondary distribution range was found. The data of key value/importance for explaining invasive success of the species studied were obtained. Two hypotheses—Propagule Pressure and Evolution of Invasiveness—were critically analyzed in view of the received data.

Keywords

Alien Species, Weeds, Legumes, Lupinus, Galega, Robinia, Amorpha, Caragana, Invasion, Propagule Pressure Hypothesis, Evolution of Invasiveness Hypothesis

1. Introduction

Human activity seriously transformed natural ecosystems particularly in consequence of intentional transfer of plant species from their natural distribution range to new habitats. Many of the most aggressive alien plant species invaded in natural communities and caused significant changes in structure and functioning of the latter. Those species are treated as invasive group of species. There are many hypotheses which attempt to explain the phenomenon of invasiveness [1] [2].

Invasive species influence natural plant communities in different ways. They could reduce a number of indigenous species and their abundance, change soil and hydrogeological conditions; invasive species often hybridize with natural ones, etc.

Full and detailed classifications, defining the impact of non-native species were recently published [3] [4]. The following impact classes were designated: competition, hybridization, transmission of the diseases to natural species, poisoning/toxicity, bio-fouling, etc. Thus, in majority of cases the influence of an alien species in natural communities is a complex phenomenon, comprising a few impact factors simultaneously.

Legumes (Fabaceae/Leguminosae) are one of the leaders in harmful consequences of plant invasions. The family is on 4th place in Europe in number of alien species (323 in total, 181 naturalizing [5]). In the Middle Russia legumes occupy the 5th place in a number of alien species (79 in total, 43 naturalizing [6]). Aggressiveness of the legume species could be explained by their mass usage in agriculture as forage grass/soilage as well as soil fertility boosters. Benevolent intentions soon demonstrate the opposite side of "environmental improvement": invading in a habitat, lacking nitrogenous compounds, the legume species fertilize soil with nitrogen, making it suitable for other alien weeds. Since all the changes occur at the level of ecosystem even a complete elimination of the invasive legume species wouldn't return the community to its initial ("before-invasion") status.

Within the last 20 year the alien fraction of flora of the Middle Russia gained 80 new species of Fabaceae. About 20 of them were brought purposeless/accidentally, 30 are increasing their natural distribution range to the North, the other 30 are represented by the species escaped from cultivation. The most aggressive invasive legume species belong to the third group—*Lupinus polyphyllus* Lindl., *Galega orientalis* Lam. and *Robinia pseudoacacia* L., as well as actively naturalizing and potentially invasive *Amorpha fruticosa* L. and *Caragana arborescens* L. Those five species are still widely cultivated so we expect a further increasing of their secondary distribution range and invasive status [6].

In this paper the results of biological study of the most aggressive alien legume species in the Middle Russia are presented. We undertook an attempt to explain a success of those species' invasion in natural and semi-natural plant communities of the region.

The following tasks were accomplished: a) trends in changes of status for model species were revealed; b) schemes of distribution ranges were compiled to forecast the species' further expansion; c) a comparative analysis of bio-morphological characters of the model invasive and closely-related non-naturalizing species was performed; d) the hypotheses, explaining invasive success of plants species within secondary distribution range were tested; the arguments in favour of Propagule Pressure and Evolution of Invasiveness hypotheses are presented.

2. Material and Methods

According to invasive potential of the species the following four groups are recognized [7] [8] [9]:

- Status 1. Transformers;
- Status 2. Alien species, actively spreading and becoming naturalized within disturbed, semi-natural and natural habitats;

- Status 3. Alien species, spreading and undergoing naturalization in disturbed habitats; in the course of further naturalization, some of them will apparently be integrated in semi-natural and natural communities;
- Status 4. Potentially invasive species, capable of reproduction in impact habitats or demonstrating invasive potential in adjacent regions.

It is worth mentioning, that one and the same species could be attributed to different statuses in different regions (Figure 1).

Data on the mentioned above invasive statuses are provided by the local researchers from 25 administrative regions of the European territory of Russia. Territory area is 3,960,000 km^2 (40% of all Europe)-from 70˚00'N to 41˚13'N and from 19˚38'W to 66˚11'W.

Characters' detecting was carried out in two directions: 1) comparison of bio-morphological characters of the invasive and closely-related non-naturalizing species; 2) comparison of bio-morphological characters of one and the same species in within natural and secondary distribution ranges. The first route comprised comparisons of the invasive species from North America *Lupinus polyphyllus* with the cultivated *L. angustifolius* L.; the naturalizing *Caragana arborescens* with the cultivated *C. laeta* Kom., the invasive *Galega orientalis* with the cultivated *G. officinalis* L.; the invasive (in many regions) *Robinia pseudoacacia* with the cultivated *Robinia × ambigua* Poir. The second route is presented by comparison of *Galega orientalis* characters within natural and secondary distribution ranges. All species were identificated by the author of this article.

For each species 10+ populations from secondary distribution range were studied. Detailed data on individual populations were published earlier [6]. In this paper we present averaged data in table form for all the species, also indicating morphometric amplitudes of the characters.

The following characters were studied:

– biomass of above-ground organs and assimilating surface; leaves' surface; number of leaves per shoot and number of shoots per plant;

– permanent flowering/fruitng capacity

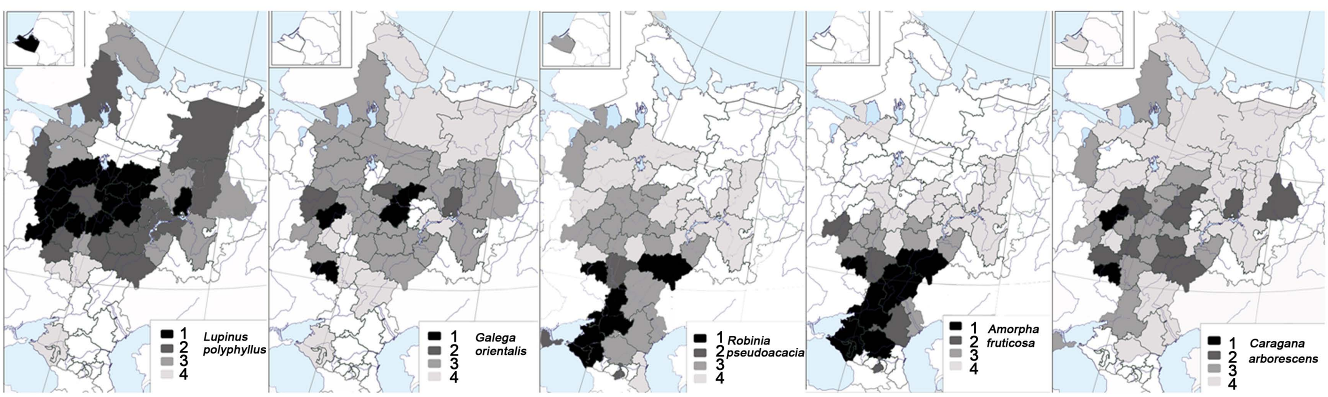

Figure 1. Secondary distribution ranges in different regions of the European territory of Russia. 1: Status 1, 2: Status 2, 3: Status 3, 4: Status 4.

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- androecium capability, allowing/not allowing two anthesis periods for individual flower;
- morphometric characters: flowers size, beans length, seed weight, pollen-grain size;
- pollen fertility;
- duration of main phenological phases; capability of early seeding/seed production;
- seed production: number of flowers per inflorescence; number of beans per infructescence/per plant; number of fertile seeds per bean;
- germinating capacity of scarified and non-scarified seeds; seedling vigor; seed sprouting duration; seedlings growth dynamics within the first year;
- vegetative propagation capabilities;
- steadiness to pests and diseases;
- population density;
- cultigeneous distribution range.

The morphometric characteristics were determined using a Keyence VHX_1000 E digital microscope. Pollen fertility was detected by staining pollen grains with acetocarmine with insignificant heating with subsequent viewing of slides in five fields of view of the microscope. The results were processed statistically using Microsoft Excel and the Past software package.

3. Results and Discussion

All the five taxa studied are on the list of 50 most actively distributing/naturalizing species in the European part of Russia. *Lupinus polyphyllus* is on 18th place, *Caragana arborescens*—on 28th, *Galega orientalis*—on 32d, *Robinia pseudoacacia* and *Amorpha fruticosa* share 47-48th places (**Table 1**).

An attempt to detect one character, determining invasive activity of alien legume species failed. e.g., *Lupinus polyphyllus* has got a competitive advantage against closely-related *L. angustifolius* in more numerous beans and number of seeds per plant, larger leaf surface (both, of individual leaflet and general surface of compound leaf), more numerous flowers per inflorescence and androecium capability, allowing two anthesis periods for individual flower [8] [9]. *L. polyphyllus* has a vegetative propagation capacity, *L. angustifolius* is an annual. Thus, in another few characters *L. polyphyllus* is inferior to *L. angustifolius,* having smaller beans and seeds, smaller number of lateral shoots and leaves per shoot which results in less assimilating surface. Both species got high pollen fertility and germinating capacity of scarified seeds (**Table 2**).

Table 1. Invasive statuses of 5 legume species in the European territory of Russia.

Status	Number of regions where the species belongs to the status				Total regions number
	1	2	3	4	
Lupinus polyphyllus	10	3	2	4	19 (76%)
Caragana arborescens	2	4	6	5	17 (68%)
Galega orientalis	3	2	9	2	16 (64%)
Robinia pseudoacacia	4	3	4	2	13 (52%)
Amorpha fruticosa	4	2	2	5	13 (52%)

Table 2. Comparison of bio-morphological characters in four herbaceous legume species.

	Lupinus polyphyllus invasive species	*Lupinus angustifolius* cultivated, rarely naturalizing	*Galega orientalis* invasive species	*Galega officinalis* cultivated, rarely naturalizing
Average height, cm	115 (61 - 150)*	53 (36 - 71)	118 (34 - 160)*	40 - 90
Average number of lateral shoots	1.7 (0 - 4)	40 (3 - 151)*	9 (7 - 10)	10 (7 - 11)
Total shoots length	121 (61 - 239)	197 (42 - 594)*	-	-
Number of leaves per plant	7 (3 - 8)	150 (22 - 546)*	29 (20 - 41)	27 (19 - 39)
Leaf surface, sq. mm	8002*	684	-	-
Assimilating surface, sq. cm	560	1027*	-	-
Average stoma square on upper leaf surface, sq. μm	512*	215	167*	99
Average stoma square on lower leaf surface, sq. μm	674*	314	211	283
Permanent flowering/fruitng capacity	yes	no	no	no
Pollination type	cross-pollinating entomophilous, facultative self-pollinating (4% - 5%)	self-pollinating	cross-pollinating entomo-philous, facultative self-pollinating (1.3% - 6%)	cross-pollinating entomo-philous, facultative self-pollinating
Inflorescence length, cm	39 (16 - 60)	3 - 5	29 (15 - 39)	18 (12 - 22)
Flowers number per inflorescence	80*	4 - 7	62 (20 - 76)	35 (21 - 43)
Flower's size (length of standard), mm	14*	10	8,5*	6.9
Several anthesis periods	yes	no	no	no
Average volume of pollen-grain, μm^3	9765	14496*	1750*	1253
Pollen fertility	95%	95%	98%*	88%
Number of beans per infructescence	27 (14 - 59)	11.5	50 (39 - 57)	28 (15 - 41)
Bean's length, cm	2.3 - 4.5	1.6 - 2.0	2.7 (2.4 - 3.1)	2.3 - 3.1
Number of seeds per bean	4.8 (1 - 8)*	3.3	3.4 (2 - 5)*	2.6 (1 - 4)
Number of seeds per plant	103 (49 - 253)*	39	-	-
Weight of 1000 seeds, g	26	53	5 - 9	4 - 7
Germinating capacity of scarified seeds, %	43	80*	5	27*
Germinating capacity of non-scarified seeds, %	90	89	98	98
Vegetative propagation capabilities	Relatively low, caudex particulation	None (annual)	Very high-producing up to 18 long rhizomes (up to 50 cm long). Could form clones, occupying 25 sq. m	Relatively low: nu-merous rhizomes are very short (less than 2 cm long)
Population density, shoots/sq.m	20 - 30	10 - 15	150 - 230	110 - 170
Cultigeneous distribution range in the European part of Russia	Is cultivated in 86% of regions-especially wide in the Nort West provinces	Is meagrely cultivated as forage grass in four provinces only	Is cultivated in 86% of regions-especially wide in the Nort West provinces	Is cultivated as medicinal plant in three provinces only

*characters, proving competitive advantages of the species (statistically significant difference). -: there is no information.

Galega orientalis has got competitive advantage against closely-related *G. officinalis* in more numerous flowers and seeds per inflorescence, higher pollen fertility, vegetative propagation capabilities and higher population density [10]. The main characteristic feature of *Galega orientalis* is its cultigeneous distribution range, far exceeding the one for *G. officinalis.* From the other side *G. orientalis* is inferior to *G. officinalis* in number of lateral shoots per plant and germinating capacity of scarified seeds. There are no significant differences in number of leaves per generative shoot, bean length, number of seeds per bean, structure & development of generative sphere (excluding its smaller sizes in *G. officinalis*) between these species.

Invasive *Robinia pseudoacacia* (**Table 3**) has got competitive advantage against cultivated *R.* × *ambigua* in number of seeds per bean, number of flowers/fruits per inflorescence, slightly larger pollen-grains and significantly (2.5 times) higher pollen fertility [11]. From the other side *R.* × *ambigua* flowers and fruits a few times within one

Table 3. Comparison of bio-morphological characters in six legume species (trees & shrubs).

	Robinia pseudoacacia	*Robinia × ambigua*	*Amorpha fruticosa*	*A. paniculata*	*Caragana arborescens*	*C. laeta*
Flowering behavior	Rare second flowering	*Flowers and fruits few times per season	*Flowers end-June	Flowers mid-July	*Mass flowering	Solitary flowers
Inflorescence length, cm	5.2 - 15.5	5 - 12	11 - 18	9 - 14	In clusters	Solitary flowers
Flowers number per inflorescence	8 - 31	20 - 25	~100*	~40	10*	~0
Flower's size (length of standard), mm	15.4 - 19.5	19.3-22*	6.1 - 6.3	5.2	17-19	28*
Average volume of pollen-grain, μm^3	7484	7854	3089	3259	3239*	1925
Pollen fertility,%	69 - 98*	38	99*	61	93 - 96	96
Fruits number per infructescence	4.4 - 7.8*	1-2	124 (40 - 224)*	19.6	3.9 (1 - 7)*	0
Bean length, cm	4 - 6 (2.1 - 10.7)	5.6 (3 - 8)	0.6-0.8	0.8	4.4 (2.5 - 6)	3.6 (2.6 - 4.6)
Number of seeds per bean	3.8 (1 - 12)*	2.2 (1 - 6)	1	1	2.4 (1 - 8)*	1.6 (1 - 3)
Vegetative propagation capabilities	High-actively producing coppice shoots & root sprouts and forming clones up to 90 sq. m	Weak-producing root sprouts	High-actively producing root sprouts and forming large clones. Adventitious root system well developed	Weak-producing few root sprouts only	High-actively producing root sprouts, but clones are not massive	None-root sprouts not recorded in the Main Botanical Garden)
Population density	2000 trees per hectare	Solitary trees in planting spots	5 shrub per sq. m	Solitary shrubs in planting spots	1 shrub per sq. m	Solitary shrubs in planting spots
Cultigeneous distribution range in the European part of Russia	Mass cultivation in 86% of regions, especially wide in wood lines within South West provinces	Solitaires and parkways in big cities	Mass cultivation in 73% of regions, especially wide in wood lines within South East provinces	Botanical gardens only	Mass cultivation in 83 % of regions, especially wide in wood lines	Botanical gardens only

*characters, proving competitive advantages of the species (statistically significant difference).

season whereas reflorescence occurs in *R. pseudoacacia* not every autumn (and fruit inception does not happen at all).

Amorpha fruticosa has got competitive advantage against cultivated *A. paniculata* and *A. californica* in earlier phenological phases, higher seed production, seed germination capacity, earlier seed sprouting, seedlings growth dynamics within the first year and significantly larger cultigeneous distribution range.

Caragana arborescens has got competitive advantage against closely-related *C. arborescens* f. *lorbergii* and *C. laeta* in larger pollen-grains, more numerous flowers per inflorescence, much higher seed germination capacity and long-standing cultivating tradition, resulting in significantly larger secondary distribution range. Thus, Central Asian *C. laeta* has larger flowers [12].

While comparing the plants of *G. orientalis* from natural and secondary distribution ranges we obtained data, supporting the Evolution of Increased Competitive Ability hypothesis (Evolution of Increased Competitive Ability—EICA; Blossey and Notzold [13]). Invasive phenotype appeared more "powerful" than the natural one: biomass of above-ground organs, inflorescence length, number of flowers/fruits per plant and seed production exceed significantly within the secondary distribution range.

Thus, for all the compared pairs of species the invasive ones have competitive advantage against closely-related non-invasive ones in more numerous flowers/fruits in raceme and denser populations.

Invasive species also far exceed non-naturalizing ones in area of cultigeneous distribution range. Invasive activity of one and the same species in different regions within secondary distribution range varies greatly which is determined by both, the natural and antropogenic factors: species invade more actively in natural plant communities within the regions where they have been widely cultivating for a long period of time.

Therefore I assume that the Propagule Pressure Hypothesis works better for explaining a success of invading the most aggressive legume species in natural phytocenoses. According to that hypothesis some invasive species produce big amount of seeds, which increase the species invasive potential. Thereby already in the next generation after expansion start the species could be qualified as "strong invasive species" [14] and its distribution control becomes extremely difficult task by default.

Although, that would be reasonable to insert additions to statement of the hypothesis, allowing to consider not only seed production of the individual plant but also density of the naturalizing populations and area of cultigeneous distribution range. Reformulated hypothesis could look like follows: "The level of natural communities' invasibility is determined by a number and abundance of invading alien plant species which in its turn depends not only upon the number of diaspores, produced by individual plant but also upon density of the naturalizing populations and area of cultigeneous distribution range".

Besides that, the term "propagule pressure" comprises not only direct meaning—mass invasion of alien plants into natural ecosystems—but also higher probability of new genotypes appearing as a result of mutations and/or recombinations of numerous genomes. Increased genetic diversity in naturalizing populations stimulates appearance of larger number of genotypes, "pressing" the natural communities. In that respect the Propagule Pressure Hypothesis aligns with the Evolution of Invasiveness Hypothesis [13] [15] which considers fast evolution of genetic characters in successful invasive species, tightly connected with natural selection pressure in new environment.

4. Conclusions

There is no single/exclusive bio-morphological character which could be used for predicting invasive success of any alien legume species within the secondary distribution range.

The main reason for invasion of the studied species into natural phytocenoses of the Middle Russia is their wide cultivation, ignoring proper agrotechnology and large waste-lands areas. Thereby, the Propagule Pressure Hypothesis with some additions (population density, area of cultigeneous distribution range) suits best for explaining the invasive species' success.

The Propagule Pressure Hypothesis should be considered in inextricable connection with the Evolution of Invasiveness Hypothesis, because high number of diaspores assumes higher probability of new (and better adapted to new environment conditions) genotypes' appearance as a result of mutations and/or recombinations of numerous genomes

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