

SPATIAL SPREADING OF ROBINIA PSEUDO-ACACIA AND POPULUS ALBA CLONES IN SANDY HABITATS

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Abstract. Invasion of alien species has become a general problem world-wide. Among the shrinking patches of natural vegetation, various human activities create artificial corridors for the migration of species which have been geographically separated, and have had distinct evolutionary histories. The time scale of invasions is much smaller than the evolutionary scale of the traits by which these species have been adapted to their environment. Black locust was introduced to the Hungarian Great Plain in the 19th century.

Its successful invasion nowadays seriously threatens the maintenance of natural communities over large areas, especially in sandy habitats. Our aim was to study the reasons for the rapid invasion of this species. In particular, we focused on its capacity for clonal reproduction.

We investigated the dynamics of ramet production and spatial spreading of *Robinia* clones in sandy habitats. In comparison, we measured the same traits in another clonal tree species, *Populus alba*. White poplar is an element of the natural vegetation in the same area.

Robinia proved to be more aggressive and successful in the occupation of vegetation gaps by strong establishment of brush-wood. Why is the *Robinia* so successful in the occupation of the sandy habitats of Great Hungarian Plain. In this respect, the ability and dynamics of clonal growth seems to be important. We hypothesise that the utilisation of vegetation gap differs in the case of a native and an adventive species

Keywords: growth strategy, competition, invasion, black locust, white poplar.

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Introduction

Degradation and disappearance of natural habitats has become a serious problem to nature conservation. Introduction of adventive plants is another critical phenomenon, because it threatens the integrity of our natural communities. This process is rather conspicuous in the Hungarian Great Plain. The explanation for the present alarming condition of its natural ecosystems over large areas goes back to decades in the history of land use (Hargitai 1940, Kovarik 1995b). Severe deforestation started in the 19th century due to demand for wood (Kertész 1984). As a result of cutting the natural forests, and simultaneously planting *Robinia pseudo-acacia*, some 80-85% of the forests of this region had become black locust stands by the beginning of the 20th century (Kiss 1922). The first appearance of

Robinia in Europe owes to voyagers and horticulturists (Kovarik 1995a). *Robinia* came from the temperate zone of North-America (Kertész 1984), and it found suitable conditions for establishment in Europe. Its invasion has been helped by artificial plantations, but it is spontaneous at a considerable extent. *Robinia* exemplifies those plants which have been introduced from other continents, and started their infamous carriers on the new land by uncontrolled expansion (see Pysek *et al.* 1995, Kovarik 1995a).

Another important factor that promotes unwanted invasion is the increasing size of agricultural and ruderal areas. Disturbed habitats provide suitable sites for the spreading of *Robinia*, and also for weeds, which have been evolutionarily adapted to the occupation newly opened vegetation gaps. The pressure from their seed rain and propagule bank has

also increased on the Great Plain (Halassy and Török 1996). A large set of ruderal species is presented in and around our natural habitats strongly connected to *Robinia*-woods. Therefore, their resistance to disturbance and invasion is a key issue which determines the future of our natural communities.

Continuous or regular disturbance is likely to destroy the natural structure of a community (see Margóczy, Körmöczy and Kincsek 1996). A threat in the expansion of *Robinia* forests is that they accumulate ruderal species in the understorey, therefore, they may become sources for future spreading of these species.

In this paper, we study the clonal expansion of *Robinia pseudo-acacia* stands. Clonality can be essential in reproducing and competing for resources in newly occupied areas (van Groenendaet *et al.* 1996). We investigate how clonality contributes to the successful establishment, growth and competitive dominance of black locust populations on the Great Plain.

Life-form, regeneration cycle and clonal growth habit strongly determine the population dynamics of *Robinia*, and the steps of its invasion. According to our preliminary assumptions, these traits lead to a specific spatial behaviour of this species, which may influence not only the structure of an existing stand, but also the subsequent regeneration of the natural vegetation in its site by secondary succession. Several authors have emphasised the role of clonality in foraging for resources, occupying new habitat patches, tolerance to environmental fluctuations, regeneration after adverse conditions, and defence against herbivores (Oborny and Bartha 1998, Herben *et al.* 1994, Sutherland 1990, van Groenendaet *et al.* 1996). Clonal growth rules can largely determine the long-term pattern of the occupation of habitat space (van Groenendaet *et al.* 1996, de Kroon and Schieving 1990).

The clonal growth form

A cause of the successful invasion of *Robinia* is probably its capability for quick spread by root-buds (Jenik 1994). It is very difficult to eradicate an established tree from the habitat. Developing sprouts, on one hand, is a strategy for growth and expansion, and on the other hand, an adaptive response for damage (Jenik 1994). This is why it is so difficult to clear black locust out.

Native communities on sand also contain a lot of clonal species. Clonality is frequent among herbs, grasses, shrubs and trees as well. Growth forms of the clones play very important roles in the structural development of vegetation. Growth dynamics of the

species determine the pattern of ramets in space and the changes of this pattern in time (Oborny and Bartha 1998).

Those ramets that belong to the same genet and are connected by horizontal structures (such as rhizomes or stolons) are often capable of transporting nutrients, water and photoassimilates to each other. This is how mother ramets can subsidise their offspring until they become established, and thus, help to occupy new microhabitats and compete with neighbours. The clonal growth habit provides various opportunities for special resource exploitation strategies, which promote persistence in the sites that have been occupied. Thus, clonality can strongly influence the spatial pattern of plant communities, and their successional processes (Klimes and Klimesova 1994, Oborny and Bartha 1995).

The objective of our study on clonal trees

We hypothesise that clonality may be an important factor in the invasion of sandy habitats.

Therefore, we compare the success of a native and of an adventive, invasive species in the same site. The adventive species that we observe is *Robinia pseudo-acacia* L. The comparable native species is *Populus alba* L. which is an edicator species of the *Junipero-Populetum albae* community (Simon 1979, Szodfridt 1969).

White poplar also shows predominance of clonal reproduction in its life history. Because of its economic use, this species has also gone through artificial selection, and several cultivated varieties exist.

The questions addressed:

1. What kind of spatial and temporal dynamics of clonal growth can be described/recognised in the case of *Robinia pseudo-acacia* and *Populus alba*?
2. What is the difference between the dynamics of clonal spreading in *Robinia pseudo-acacia* and *Populus alba*?
3. Could these traits be responsible for the difference in the success of the native and adventive species?

Material and methods

Study site

The investigations were carried out in the Kiskunság National Park, Great Hungarian Plain, near to villages Bugac and Fülöpháza.

This area is one of the typical sandy habitats with dry grasslands, *Festucion vaginatae* (Soó 1929, 1964-1980), and forest communities, *Junipero-Populetum albae* (Simon 1979, Szodfridt 1969, Körmöczi 1983, Fekete 1992). These communities form patchy vegetation, and provide *Robinia pseudo-acacia* suitable habitat. Their distribution is related to the sandy soil. The Bugac region is rather plain with slight undulation of the surface. In the Fülöpháza region, the elevation of sand-hills is more pronounced. The communities of the area have been formed due to the soil and climatic conditions, and have many centuries of history.

Their high biodiversity represents a great value for nature conservation. Grazing have been reported to control the expansion of white poplar and black locust patches (Kelemen *et al.* 1995). At the first sight, *Robinia* and *Populus* are rather similar in their ability to spread and attain local dominance. In Fülöpháza, for example, the numbers of *Populus* and *Robinia* patches are nearly equal. On the other hand, after a forest fire which happened at Bócsa in 1993, *Robinia* proved to be more aggressive and successful in the occupation of the newly opened sites by vigorous establishment of brush-wood.

The established locust stand then prevents the emergence of other woody species (Gobbi *et al.* 1995). Though neither kind of invasion plays a positive role in the vegetation diversity, but *Populus* is less detrimental in this region than *Robinia* because it is native and, as it can coexist with other characteristic, often valuable species of the sand flora.

The model plants

Individual genets were chosen for investigating the mechanism of clonal spread in sandy soil. We chose solitary mother trees with sprouts around them.

We measured the distance between the mother and the offspring ramets. We estimated the age of the mother and the new saplings from the diameter of the trunks at 1.3 m height. According to the literature, there is an allometric relationship between age and diameter (Sopp 1974). These relationships are frequently used in the practice of forestry. We used a linear model for estimating the age (determination coefficient >0.95 ; the standard error ranged from 0.16 to 2.43 years). The relationship depends on the quality of the environment, especially of the soil. Based on these differences, six quality classes are used in forestry. The origin of the tree is also important: sprouts differ from saplings that have derived from seeds.

The identification of these soil-based quality-classes is difficult, therefore we calculated the

average of the six classes, and we used the data for the sprout-originated trees.

Because of the variety of factors that influence the age-diameter relationship, our estimation can be considered as a rough approximation.

We selected 13 white poplar and 14 black locust solitary genets at Bugac and Fülöpháza (about 12 km² each). We found and measured about 400 sprouts. After damage of the seminal shoot of the young trees (e.g. due to grazing), regeneration takes place with intensive branching, and both *Robinia* and *Populus* can take a bushy growth form. We considered those shoots that originate from one trunk as parts of one ramet, and they ramify above the ground. We infer to the spatial and temporal dynamics from the proliferation of the sprouts around the genet. We measured the distances of the offsprings from the mother tree, and calculated the age of them (from the diameter of the trunk). The age differences between the mother and their offsprings can be converted to time-delay by computing the years which passing till the appearance of a new offspring (relative time).

Results

The growth pattern in space and time

We used the spatial pattern of sprouts around each mother tree to reconstruct the temporal dynamics of clonal growth. We calculated the regression of the mother tree—sprout's distance in relation to their emergence time (the emergence time=mother age minus the age of the offsprings). We found a positive linear relationship between these variables. The correlation coefficient for black locust was $r=0.52$, and for white poplar somewhat weaker, $r=0.428$. The determination coefficient, however, was 0.27 for black locust, and 0.183 for poplar (Fig. 1). Although the correlations that we found were rather weak, the points on the space-time diagram clearly show a non-random pattern.

What is the difference between *Robinia pseudo-acacia* and *Populus alba* in the dynamics of clonal spreading? Clear differences can be seen between the two clonal species in the distance and time of ramet emergence, calculated for all offspring ramets in the population (Figs 2 and 3). Poplar sprouts emerge later in time and further from the mother tree than black locust sprouts.

The distance of offsprings of *Populus* ranges from 1-2m to 10-20m from the mother. The area occupied by the clones of *Robinia* is smaller. It covers mostly less than 10m radius circle, and

generally the closest sprouts grow a few cm from the mother plant.

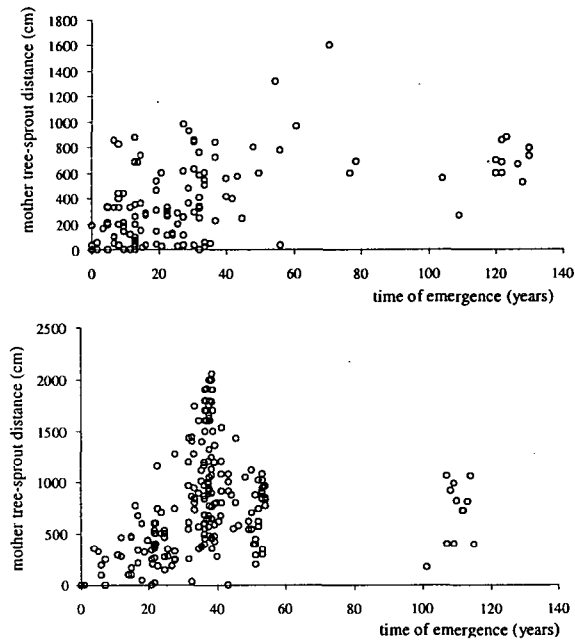


Fig. 1. Distribution of the distance of the ramets in relation to relative time of clone emergence. Upper: black locust (correlation 0.52, determination coefficient 0.27), lower: white poplar (correlation 0.43, determination coefficient 0.18).

The difference in the temporal pattern of clonal spreading is also remarkable. The reconstructed time course of sprouting shows that emergence of *Robinia* sprouts have shorter delay compared to the establishment of the mother tree. In general sprouting becomes less frequent with time. A sharp decrease is detected after 40 years in the frequency of emergence, in contrast *Populus* shows an increase in the frequency after 40 to 60 years.

Differences in space and time

Could the differences in the dynamics of expansion be responsible for the success of the adventive species relative to the native species?

The first twenty years proved to be decisive in the fate of the populations. *Robinia* has a definite advantage in the occupation of opened space: almost 50% of the sprouts of *Robinia* emerge in the first twenty years, but *Populus* develops only 4-5% of its ramets in this period.

Robinia has no such big difference in the intensity of sprouting in time. It produces similar proportion in the first and in the second twenty years.

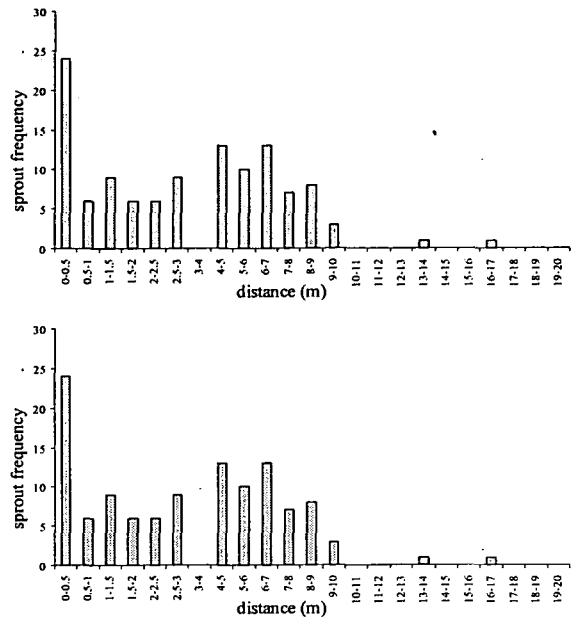


Fig. 2. Frequency distribution of the distance between mother and offspring (upper) and of the time of emergence (lower) in black locust.

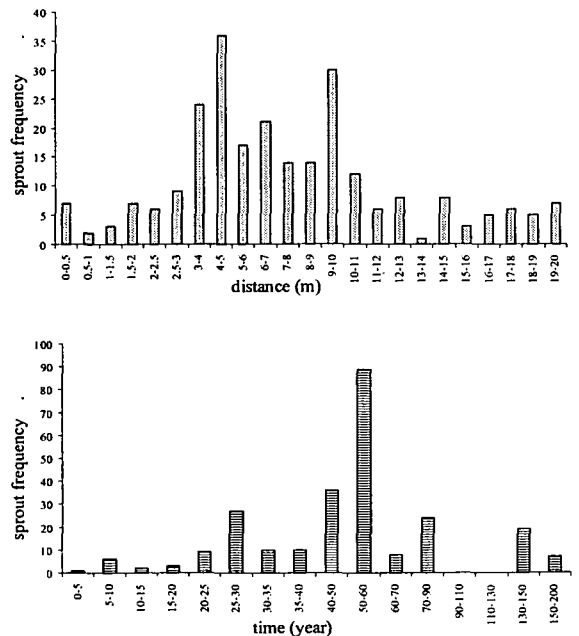


Fig. 3. Frequency distribution of the distance between mother and offspring (upper) and of the time of emergence (lower) in white poplar.

Populus shows an increase in the intensity of sprouting. In the first twenty years 4-5% of the sprouts emerged, and the rest was added in the second twenty years. No sprouting occurred from 60 to 100 years, and the frequency of later emergence was very low (Figs 2 and 3).

Growth dynamics of the individuals shows a different trend in the case of the two species. In the first twenty years, black locust shows quicker thickening than white poplar. But later, the diameter of poplar clones exceeds that of locust clones of the same age (Fig. 4).

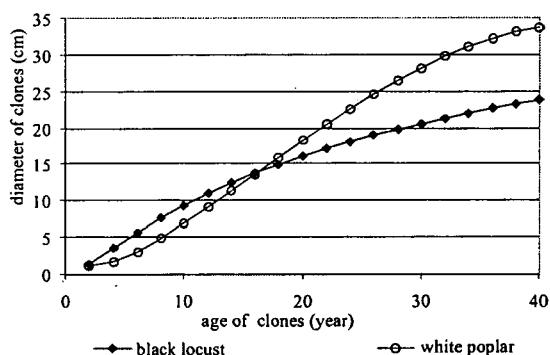


Fig. 4 Comparison of the growth dynamics of the two species (based on estimation from stand quality classes).

We used a linear model for age-estimation, but at a given age there are opposite deviations in the trunk's diameter of the two species, and the estimation of the ages may be false because of different growth dynamics. Therefore we checked the results by another age-calculation. We do not calculate the absolute ages, only the diameters of the trunks were compared. The diameter of the mother trunk was considered as 100%, and the percentage diameter of the sprouts was calculated compared to this. The difference of percentage diameter can be used as a relative time-delay. If the time-delay was estimated only from the thickness differences of the trunks, the same separation can be recognised between the black locust and the poplar sprout emergence.

Discussion

The dispersal pattern

The availability of propagules is very important in the occupation of gaps. An alternative way of spreading is clonal growth. An advantage of vegetative reproduction is that the mother plant can subsidise its offspring by nutrients, water and photo-assimilates. Thus, the vegetative offspring usually

has much better chances for survival than the generative progeny (van Groenendaet *et al.* 1996). Vegetative spreading to new sites provides special opportunities for microhabitat selection (Herben *et al.* 1994, Oborny and Bartha 1995). Accordingly, clonal species play an important role in the succession of vegetation (Stöckling and Baumler 1998).

We reconstructed the dynamics of clonal growth on the basis of the spatial pattern and estimated age of sprouts around mother trees. Capacity for dispersal is very important in the exploitation of new openings in the habitat, therefore we investigated separately the spatial and the temporal pattern of spreading to draw the frequency distribution of sprout distances and of emergence time. The question is whether any deterministic rule can be recognised in the dynamics of clonal spread of *Robinia pseudo-acacia* or *Populus alba*. The first step is to recognise the process in space and in time, and find non-random patterns in the emergence of clonal offspring. As shown in Figs 2 and 3, several peaks can be found in the emergence frequency in space and time. The distribution of these peaks are different in the case of *Robinia* and *Populus*. *Robinia* sprouts emerge earlier and closer to the mother tree, while *Populus* have its offsprings further in space and later in time.

From the growth patterns detected in the present study, we can conclude that *Robinia* resembles more to the phalanx growth strategy, and *Populus* to the guerrilla strategy (Sutherland 1990).

We have presented some observable tendencies in the clonal growth habit of these species, but several additional factors may influence the growth pattern of a species in any particular habitat. For example, low availability of water and nutrients can significantly change the growth form, as well as herbivores or other injury in the root or shoot system (de Kroon *et al.* 1994). An interesting, community-level outlook from the description of growth strategies may be to study the „spatial combining” ability of different species (Herben 1995).

Conclusions

Robinia pseudo-acacia shows rather quick and aggressive lateral spreading compared to the native species, *Populus alba*. *Robinia* can vigorously invade the native communities on sand, and attains stabile persistence in the habitat as a dominant species. Why is *Populus* less successful in the invasion to new gaps and exclusion of other species?

One of the key factors may be that its clonal spreading is slower, and its stand of shoots is less tightly packed (more guerrilla-like).

Our study calls for further research on the role of clonality in sandy habitats, and on the dynamics of competition between native, stress-tolerant species and invasive clones.

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