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INITIAL STEPS IN THE REGENERATION OF A FLOODPLAIN MEADOW AFTER A DECADE OF DOMINANCE OF AN INVASIVE TRANSFORMER SHRUB, *AMORPHA FRUTICOSA* L.

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Abstract: The flora and vegetation of two floodplain meadow sites invaded by the nonindigenous shrub, *Amorpha fruticosa* L. were compared. One of the sites (site [A]) was previously completely invaded by the species, which had transformed the habitat into a monodominant thicket for more than ten years before it was cleared in 2000. The other site (site [B]) was more or less continuously mowed therefore *Amorpha* only reached here 50 % cover on average and large patches of the grassland community remained intact. The two sites are managed similarly, by mowing or stalk-cutting twice a year, which prevents seed set and sprouting of *Amorpha*. The flora of the sites was censused and vegetation was sampled by estimating species cover in 4×4 m quadrates, 30 sampling units in each site. Our floral investigations detected 107 species in site [A] and 115 in site [B]. The species pool of the two sites was similar, and almost all species characteristic to the target vegetation (represented by site [B]) were present in the recovering area, site [A]. The vegetation investigations revealed that species richness per quadrates was significantly lower in site [A], which was mainly due to the rareness of subordinate species. The cover of *Amorpha* did not correlate with species richness within the sites. Fifteen species had significantly higher cover in site [B] while only two species, including *Amorpha* had higher cover in site [A]. PCoA ordination of the quadrates based on species presence information markedly discriminated the two sites, while NMDS ordination based on species cover data did not segregate them to much extent. The points representing site [A] were more scattered in the ordination space. The orientation of the quadrates in the ordination scattergram was not associated with the cover of *Amorpha* when within site variability was investigated. The variation in species combinations and dominance relationships was associated mainly with the opposite behaviour of two dominants: *Alopecurus pratensis* and *Bidens tripartita*. Interspecific correlations showed that the invasive species has almost as mani positive as negative correlations in both sites at the scale of investigations. The most remarkable is the strong negative correlation between *Amorpha* and the dominant *Alopecurus pratensis* in site [A].

We concluded that although only weak evidence supports that *Amorpha* has considerable present impact on the within-site vegetation variation, the lower species richness, the absence or low cover of subordinate meadow species and the patchiness of vegetation in site [A] can be attributed to the past dominance of the invasive species. The species pool of the site [A] area is promisingly rich for future rehabilitation. The dominants of the target vegetation are already quite frequent which assures regeneration, while most of the subordinate species are rare and scattered. The vegetation seems to have low resistance to colonization which might enforce recolonization of both natural species and invasion of aliens. Only systematic management of the area assures successful regeneration.

Keywords: plant invasion, community rehabilitation, Tisza river, inundation area, Alopecurus pratensis, Bidens tripartita

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Introduction

False indigo, *Amorpha fruticosa*, a leguminous shrub of North-American origin is considered as one of the most problematic invasive plant species in the inundation area of the Tisza river. The species has effectively utilised the ecological corridor properties of the river and by this timeit is abundant all over the Tisza flood area (Bartha and Mátyás 1995). Although *Amorpha* is able to invade different seminatural riverside communities with more or less success (Zavagno and D'Auria 2001), the most endangered target communities are probably the floodplain pastures and meadows. These species rich seminatural communities evolved under the traditional human disturbance regime. As the traditional extensive management practices, grazing and mowing are abandoned (as has been happening near the Tisza in the recent decades, cf. Tóth 2001) they are reoccupied by gallery forests as the course of a natural succession. The presence of *Amorpha* significantly alters the above outlined dynamics: in the absence of grazing or mowing the invasive species is able to immediately colonise the meadow community, and with its rapid growth it transforms the habitat into a homogeneous thicket within 5-6 years (Kóra 2002). Under the closed canopy of *Amorpha* most of the meadow species cannot survive, and a very poor community of opportunistic species develops (Zavagno and D'Auria 2001, Kóra 2002). The homogeneous *Amorpha*-thicket represents a long-lasting successional state in the meadow-forest sere. The development of the gallery forest state is supposed to eventually happen (Zavagno and D'Auria 2001), but it is only supported by anecdotal information, and might only happen after 25-30 years when the *Amorpha* stand grows old and collapses probably due to self-generating processes (Tóth 2001, Kóra 2002).

The floodplain meadows have high natural conservation value, therefore it is desirable to prevent their invasion by *Amorpha fruticosa* and reverse the process if it is possible. The aim of the present study is to evaluate the first observations of a recent rehabilitation experiment, in which a cca. 10-years-old homogeneous *Amorpha*-thicket developed in an abandoned floodplain meadow was cleared one and a half years before the observations. As a control area, we used a neighbouring meadow which has been mown more or less regularly, and abundance of the invasive species has been kept at a relatively low level.

The questions of the study are the following: 1) How similar is the species pool of the two sites; are the species characteristic of the floodplain meadow present in the recovering area? 2) What are the characteristics of the dominance relations of the vegetation in the two areas; which species' abundance values are different between the two sites? 3) Are plant community characteristics different in the two sites? 4) Is the dominance of *Amorpha* related to the variation of the vegetation between and within the two sites?

Materials and methods

Study species

Amorpha fruticosa L. (Fabaceae) is a shrub of 3 to 4 m maximum height (Gencsi and Vancsura 1992). It originates from the South-eastern parts of North-America (Wilbur 1975, Zavagno and D'Auria 2001), where it is a pioneer of riverbanks and wetlands. The species was introduced into Hungary before 1907 (Priszter 1997). *Amorpha* was spread by the forestry mainly after the 1st World War all over the country (Szentesi 1999). Its spontaneous invasion has been most intensive in the floodplains of the Great Hungarian Plain (Bartha and Mátyás 1995).

Amorpha fruticosa propagates sexually by one-seeded indehiscent pods. Plants in Hungary usually blossom from June to July. Pod production of an average individual in a homogeneous stand is estimated ca. 12,000 a year (Kóra 2002). Seed loss due to seed predation is low (Szentesi 1999). Most effective germination is from shallow (> 1 cm) soil depths and at high (20/30°C) temperatures (Zasada and Martineau n.d.). Anecdotal evidence suggests that dry soil conditions prevent successful germination. Seeds have a limited viability of 3-5 years under laboratory conditions (Zasada and Martineau n.d.). The buoyant pods are spread by water, but birds and small mammals might also play some role in the seed dispersal.

Vegetative reproduction is possible by sprouting, which can be very intensive when the stems are frozen or cut (Gencsi and Vancsura 1992, Kóra 2002). After cutting or mowing *Amorpha* quickly regenerates by sprouting. Stems can also root at the nodes (Kóra 2002).

Amorpha is a week competitor in forests and is usually excluded by tree species (Magyar 1960), but due to its fast growth, shading, and probably its allelopathyc effects (Elakowich and Wooten 1995, Csiszár, unpublished data) and nitrogen-fixing ability (Wang et al. 1999) it is a superior transformer species in meadows and pastures. *Amorpha fruticosa* is unpalatable for most invertebrates except an introduced seed predator (Szentesi 1999), but ruminants readily eat its leaves and young shoots (Papachristou et al 1999, Tóth and Gadó 2000).

Study site

The study site is situated at 46º50'40" north 19º59'30" east, near the village Tiszaalpár in the Great Hungarian Plain. The site is the part of a cca. 0.5 km^2 meadow-marsh complex about 3 km from the recent riverbed of Tisza. The original riverbed (the Lakitelek-backwater), that was artificially separated in the 1870' s is about 1 km away. Although recently the study area was inundated quite frequently (in the winter of 1999/2000, and in the spring of 2000 and 2001), the period from 1970 to 1999 was flood-free. The area is bordered by *Alnus glutinosa* forests from the East and North, by a marsh (Sulymos-Lake) from the West, and by a cca. 50 m wide marshy channel from the South. The area contains three almost equal-sized meadows that are completely separated by two marshy channels (50 and 200 m wide, respectively) (Fig. 1). The three meadow patches have similar abiotic conditions, but the invasion of *Amorpha* reached different levels. The eastern patch (patch [A] Fig. 1) is not easily accessible and its mowing was stopped in the second half of the 1980's. Than, a homogeneous *Amorpha*-thicket developed there, which reached more than 3 m height by 2000 when it was cleared by stalk-cutter. Since then, the area has been managed by stalk-cutter twice a year to prevent reestablishment of *Amorpha* by sprouts and to mimic the traditional mowing regime (mowing is only possible after some years, after new *Amorpha* sprouts become week enough). In the year of the study *Amorpha* reached here 2 m height and 60-70 % cover (maximal data, i.e. before cutting). The mowing of the central patch (patch [B] Fig 1) was not stopped, but it was not regular except for the last two years, therefore *Amorpha* was able to permanently establish with 30-40 % cover and 1m height (maximal data, i.e. before mowing). Both [A] and [B] meadows are bordered by a thick and continuous line of adult *Amorpha* shrubs at the edge of the marshy channels, where management is not effective. This shrubby border is a source of a continuous and heavy propagule pressure. The western site, which is the most easily accessible was managed continuously and *Amorpha* forms only small patches. Our investigations were conducted in the eastern [A] and the central [B] meadows. In the present paper site [B] serves as the control area since it represents a reasonable target state of the vegetation that might be reached by systematic management.

The vegetation of the meadows is not homogeneous. Although the variation of the surface is less then 1 m (81.0-81.5 m above sea level), the area slightly slopes towards the east and the marshy channels. As far as it is discernible in the presence of the invader, the following vegetation types can be distinguished *a priori* on the basis of the dominant species: most of the two sites is covered with *Alopecurus pratensis* dominated grassland community. Abundance of *Amorpha* is high in this vegetation type. A considerable part of the *Alopecurus* grassland was burnt in 2001 in site [A]. This patch is abundant in opportunistic coloniser species. In the lower elevations *Carex acuta* dominated dense sedge communities prevail, which seem to be quite resistant to *Amorpha* invasion. In a single invader-free wet patch in site [A] *Scirpus lacustris* ssp. *lacustris* prevails. In the edges of the sites near the marshy channels *Amorpha* predominates with some marsh species and alluvial climbers like *Calystegia sepium, Solanum dulcamara,* and the nonindigenous *Echinocystis lobata*.

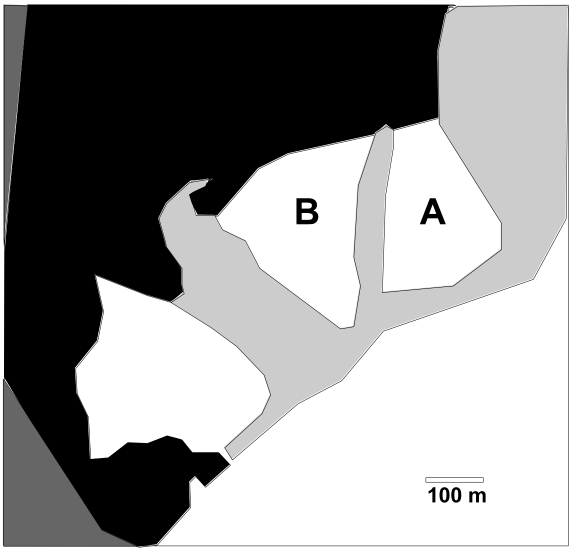

Fig. 1. The landscape location and the surrounding habitats of the two investigated sites [A] and [B]. Black: forest vegetation, dark grey: anthropogenic habitats, light grey: marsh vegetation, white: meadow vegetation.

Sampling

The flora of the two sites was investigated in 2002 from early spring to late autumn. It is more than probable that some of the rare species were not found (especially in site [A] where the dense and high *Amorpha* shrub made it more difficult to find all species), but the intensity of the field work assures reasonable representativity.

The vegetation of the sites was sampled in 30-30 quadrates of 4×4 m area each. Percent cover of each plant species was estimated in the quadrates. In the arrangement of the sampling units our aim was to representatively sample the meadow vegetation types which are affected by *Amorpha* invasion and are common in both sites. Therefore the *Carex acuta* dominated patches were not sampled in neither sites, nor the burnt areas or the *Scirpus lacustris* dominated patches in site [A]. Except for the omitted types the samples were blocked in 6 lines uniformly arranged in the site. Within the lines the 5-5 quadrates were placed randomly.

Data analysis

The species richness of the two sites was compared first on the basis of the total flora and second on the basis of the species pools of the quadrates. Species richness per quadrate was compared with the nonparametric Wilcoxon-Mann-Whitney test. The abundance of each population was also compared with the above mentioned test (because of the great number of simultaneous tests we used a significance level of $\alpha = 0.01$ in this case). We also computed the correlation between *Amorpha* cover and plant species richness, separately for the two sites ($N = 30$). The applied statistics was the non-parametric Goodman-Kruskal's gamma correlation.

For the evaluation of the variance in the vegetation we performed two kinds of ordination on the basis of the data of the 4×4 m quadrates. In the first type of ordination we ignored cover data and only the similarity of species combinations was taken into account. The similarity matrix was computed using Jaccard's index ($JAC = a/[a+b+c]$, the notation refers to the cells of the 2×2 contingency table), the ordination method was the principal coordinates analysis (PCoA). In the second type species dominance relations were also taken into account. The similarity matrix in this case was the correlation matrix based on the species' percent cover values, the ordination method was the non-metric multidimensional scaling (NMDS), because this method is quite robust to nonnormality and nonlinearity in data (Podani 1997). The ordinations were performed for the whole sample. Only those species were taken into account in the ordination that were present at least in 3 quadrates. Because the aim of the study was to assess the relation of the invasive species on the variation of the vegetation, the cover of *Amorpha* was not taken into account in computing the NMDS ordination in order to avoid circularity (the results of the PCoA are not affected, because *Amorpha* was present in all quadrates). The performance of the PCoA was evaluated on the basis of the explained percent variance of the first three axes. This value was rather low (less than 30%), but preliminary analysis showed that sequential omission of the rarest species results in gradual increase of explained variance without considerably affecting the final configuration of the quadrates in the ordination space. Therefore we consider the results of the PCoA acceptable. The performance of the NMDS analysis was evaluated on the basis of the Goodman-s stress value, which was sufficiently low (0.13) in our case. The ordination analyses were performed by the Syn-Tax 5.0 program packet (Podani 1993).

The coordinates of the quadrates on the first two axes of the ordination scattergrams were correlated with the cover of the species that were present at least in 1/5 of the sampling units (e.g. 12 quadrates). The applied statistics was Goodman-Kruskal's gamma, because this type of nonparametric correlation performs well in cases when a lot of identical rank values are present in the sample (Siegel and Castellan 1988). Because of the great number of simultaneous test we used a significance level of $\alpha = 0.005$ in this case.

Results

Altogether 131 species were found on the two sites during the year: 107 species in site [A] and 115 in site [B] (Appendix 1). The difference of the species pools results from mainly occasional species represented by one or a few individuals, with the only exception of *Cichorium intybus* and *Cynodon dactylon* that was quite common in site [B] but absent from site [A]. In the sixty 4×4 m quadrates taken in June 92 species were detected: 67 species in site [A] and 78 species in site [B]. This means an approximate 6:7 ratio. The most common species (*Amorpha fruticosa, Alopecurus pratensis, Bidens tipartita, Potentilla reptans*) are the same in both places, but many of them appear in considerably different frequencies (Table 1). The species number per quadrate was significantly ($p << 0.001$) higher in site [B] than in site [A] (medians 24 and 15, interquartile range 6 and 3, respectively). When only species with frequency of 20% or higher are considered, the species pool ratio is about 3:4 indicating that subordinate species are more common in site [A]. The most valuable species from a nature conservation view, *Leucanthemella serotina* and *Ophioglossum vulgatum*, are present in both places. The former is somewhat more abundant in site [A] and the latter is much more common in site [B] (the difference was not detectable by the 4×4 m quadrates because by the time of sampling the aboveground parts of *Ophioglossum* had mainly disappeared while *Leucanthemella* was just beginning to sprout).

The cover of *Amorpha* did not correlate significantly with the species richness of the

Table 1. The most frequent (fr > 4) species in the 4×4 m quadrates in the two sites [A] and [B]. Species are sorted by descending frequency.

A

Code	Species	Frequency
AMOFRU	*Amorpha fruticosa*	30
ALOPRA	*Alopecurus pratensis*	28
POTREP	*Potentilla reptans*	28
BIDTRI	*Bidens tripartita*	25
LYSVUL	*Lysimachia vulgaris*	21
CARPRA	*Carex praecox*	20
FRAPEN	*Fraxinus pennsylvanica (juv.)*	20
CARHIR	*Carex hirta*	19
LACSER	*Lactuca serriola*	18
GLEHED	*Glechoma hederacea*	17
VALLOC	*Valerianella locusta*	16
CARMEL	*Carex melanostachya*	15
VICANG	*Vicia angustifolia*	13
IRIPSE	*Iris pseudacorus*	11
POATRI	*Poa trivialis*	11
RANREP	*Ranunculus repens*	11
LYTVIR	*Lythrum virgatum*	10
GALAPA	*Galium aparine*	9
VICCRA	*Vicia cracca*	9
ELYREP	*Elymus repens*	8
VICHIR	*Vicia hirsuta*	8
CALSEP	*Calystegia sepium*	7
VIOPUM	*Viola pumila*	7
ACENEG	*Acer negundo (juv.)*	6
ATRPRO	*Atriplex prostrata*	6
CIRARV	*Cirsium arvense*	6
SOLDUL	*Solanum dulcamara*	6
XANITA	*Xanthium italicum*	6
LYCEXT	*Lycopus sp.*	5
SONASP	*Sonchus asper*	5
VICTET	*Vicia tetrasperma*	5

B

Code	Species	Frequency
ALOPRA	*Alopecurus pratensis*	30
AMOFRU	*Amorpha fruticosa*	30
BIDTRI	*Bidens tripartita*	30
POTREP	*Potentilla reptans*	30
CARHIR	*Carex hirta*	29
CARPRA	*Carex praecox*	29
GLEHED	*Glechoma hederacea*	25
LYSVUL	*Lysimachia vulgaris*	24
CONCAN	*Conyza canadensis*	23
POTANS	*Potentilla anserina*	23
CARMEL	*Carex melanostachya*	22
PLALAN	*Plantago lanceolata*	22
DAUCAR	*Daucus carota*	21
TRIPRA	*Trifolium pratense*	21
VICANG	*Vicia angustifolia*	21
ELYREP	*Elymus repens*	18
VICCRA	*Vicia cracca*	16
JUNCOM	*Juncus compressus*	15
TRIDUB	*Trifolium dubium*	14
CERDUB	*Cerastium dubium*	13
RANREP	*Ranunculus repens*	13
LACSER	*Lactuca serriola*	12
IRIPSE	*Iris pseudacorus*	10
LYCFLO	*Lychnis flos-cuculi*	10
LYCEXT	*Lycopus sp.*	10
SYMOFF	*Symphytum officinale*	10
VICHIR	*Vicia hirsuta*	10
AMBART	*Ambrosia artemisiifolia*	9
ASCSYR	*Asclepias syriaca*	9
CREBIE	*Crepis biennis*	9
PLAMAJ	*Plantago major*	9
SONASP	*Sonchus asper*	9
VALLOC	*Valerianella locusta*	9
CERFON	*Cerastium fontanum*	8
FRAPEN	*Fraxinus pennsylvanica (juv.)*	8
INUBRI	*Inula britannica*	8
POATRI	*Poa trivialis*	8
CENJAC	*Centaurea jacea*	7
CICINT	*Cichorium intybus*	6
CIRARV	*Cirsium arvense*	5
CIRVUL	*Cirsium vulgare*	5
GALAPA	*Galium aparine*	5
LYTVIR	*Lythrum virgatum*	5
PRUVUL	*Prunella vulgaris*	5
VERCHA	*Veronica chamaedrys*	5

quadrates in neither sites. It should be mentioned, however, that the correlation was positive (gamma = 0.277) and marginally insignificant ($p = 0.052$) in site [A] (In site [B]: gamma = -0.114, $p = 0.405$).

When comparing the cover values of the species in the quadrates the difference is significant ($p < 0.01$) in 17 cases (Table 2). Only two species have higher dominance in site [A]: *Amorpha fruticosa* itself and another alien species *Fraxinus pennsylvanica*, which is represented only by juvenile individuals. On the contrary, 15 species have significantly higher cover in site [B] (Table 2). Most of them are subordinate generalists of mesophylous meadows but some (*Carex hirta*, *C. praecox*, *C.*

melanostachya, *Potentilla reptans*, *Elymus repens*) are codominants of the community with considerable dominance in site [B]. It is also worth mentioning that there is no significant difference in the cover of opportunistic species of disturbed inundation areas, like *Xanthium italicum, Calystegia sepium, Echinocystis lobata, Bidens tripartita* (although the latter has much higher maximal cover percentages in site [B], and a wider range of values, which unfavourably affects the power of the Wilcoxon-Mann-Whitney test). The cover of the dominant grass species *Alopecurus pratensis* tends to be somewhat higher in site [B], but the difference is not significant ($p = 0.032$).

The PCoA ordination of the quadrates based on the Jaccard similarity index markedly separated the two sites along the 1st axis (Fig. 1). It is also noteworthy that the points belonging to site [A] are more scattered, which indicates that the variation of the species combinations (despite the lower species number per quadrate) is greater here than in site [B], e.g. the vegetation is less coordinated.

Table 2. The significant ($p < 0.01$) results of the Wilcoxon-Mann-Whitney test on the cover of the species in the two sites. For the abbrevations of the species see Table 1.

Species	rank sum		U	p-value
	(A)	(B)		
POTANS	576	1440	111	1.268E-07
POTREP	584	1432	119	2.299E-07
CONCAN	617	1399	152	2.364E-06
PLALAN	630	1386	165	5.607E-06
AMOFRU	1288	728	167	6.386E-06
CARPRA	632.5	1383.5	167.5	6.596E-06
DAUCAR	645	1371	180	1.462E-05
TRIPRA	645	1371	180	1.462E-05
CARHIR	666	1350	201	5.221E-05
JUNCOM	702	1314	237	0.0003849
TRIDUB	731	1285	266	0.0016258
VICANG	743.5	1272.5	278.5	0.0028895
CARMEL	747.5	1268.5	282.5	0.0034532
CERDUB	765	1251	300	0.0072872
VICCRA	768	1248	303	0.0082382
FRAPEN	1149.5	866.5	305.5	0.009114
ELYREP	771.5	1244.5	306.5	0.0094869

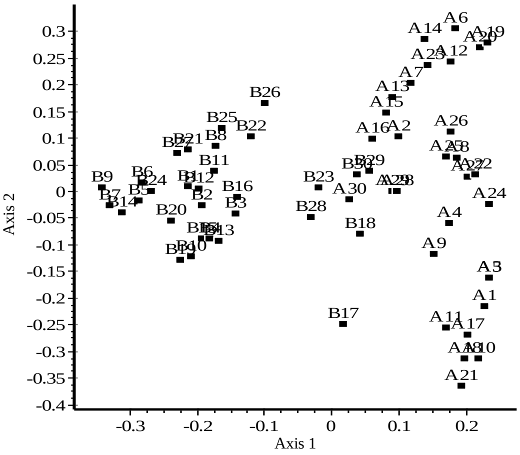

Fig. 2. The scattergram of the PCoA ordination of the 4×4 m quadrats based on Jaccard's similarity index.

Table 3. Goodman-Kruskal's gamma correlations ($p < 0.005$) between the species cover values and the PCoA axes (see Fig. 2). For the abbrevations of the species see Table 1.

PCoA axis coordinates and species	gamma	p-value
axis1 & AMOFRU	0.469	0.00000
axis1 & FRAPEN	0.503	0.00000
axis1 & ACENEG	0.505	0.00290
axis1 & POTANS	-0.785	0.00000
axis1 & TRIPRA	-0.832	0.00000
axis1 & DAUCAR	-0.764	0.00000
axis1 & PLALAN	-0.696	0.00000
axis1 & CERDUB	-0.801	0.00000
axis1 & JUNCOM	-0.666	0.00000
axis1 & POTREP	-0.472	0.00000
axis1 & CONCAN	-0.514	0.00000
axis1 & TRIDUB	-0.581	0.00000
axis1 & CARPRA	-0.409	0.00001
axis1 & SYMOFF	-0.508	0.00017
axis1 & CARMEL	-0.342	0.00028
axis1 & ELYREP	-0.362	0.00066
axis1 & LYCEXT	-0.392	0.00175
axis1 & CARHIR	-0.254	0.00485
axis2 & POATRI	0.624	0.00000
axis2 & BIDTRI	0.471	0.00000
axis2 & GALAPA	0.624	0.00000
axis2 & GLEHED	0.381	0.00007
axis2 & VALLOC	0.407	0.00014
axis2 & LACSER	0.393	0.00017
axis2 & CARMEL	0.283	0.00269
axis2 & ALOPRA	-0.516	0.00000
axis2 & PLALAN	-0.396	0.00060

The results of correlation analysis between the PCoA coordinates and the species' cover (Table 3) are qualitatively the same in the case of the 1st axis as that of the Wilcoxon-Mann-Whitney test on the species cover values (c.f. Table 2). This means that the discrimination of the quadrates of the two sites is mainly based on the numerous species common in site [B] but rare or absent in site [A]. The only species correlating with the 1st axis that are common in both places are *Amorpha fruticosa, Potentilla reptans, Carex hirta* and *C. melanostachya*. The species correlating with the 2nd axis (Table 3) represent the variability within the sites. Of these the two most common and dominant ones, *Alopecurus pratensis* and *Bidens tripartita* together with *Carex melanostachya* show correlation in opposite directions (Table 3). As the variation of cover of both *Alopecurus* and *Bidens* is less is site [B] than in site [A] this result is consistent with the fact that the quadrates of site [B] are less scattered among the 2nd axis of the PCoA scattergram (cf. Fig. 2).

The NMDS ordination of the quadrates (Fig. 3) based on the correlation matrix did not as markedly separate the quadrates of the two sites as the PCoA analysis (Fig. 2). Points belonging to site [B] are mainly concentrated along the diagonal in the NMDS scattergram (Fig. 3). Those belonging to site [A] are more scattered, with a more compact subset in the bottom left quarter.

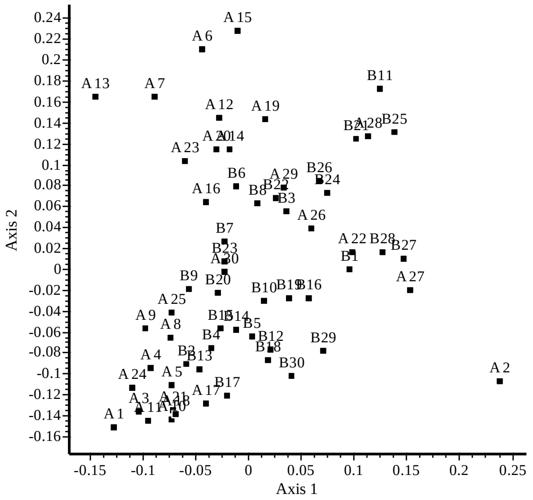

Fig. 3. The scattergram of the NMDS ordination of the 4×4 m quadrates based on the correlation matrix.

Table 4. Goodman-Kruskal's gamma correlations ($p < 0.005$) between the species cover values and the NMDS axes (see Fig. 3.). For the abbreviations of the species see Table 1.

NMDS axis coordinates and species	gamma	p-value
axis1 & POTREP	0.465	0.00000
axis1 & PLALAN	0.429	0.00020
axis1 & DAUCAR	0.405	0.00086
axis1 & POATRI	-0.375	0.00105
axis1 & LYSVUL	-0.282	0.00175
axis2 & BIDTRI	0.513	0.00000
axis2 & POATRI	0.527	0.00000
axis2 & LYSVUL	0.372	0.00004
axis2 & GALAPA	0.427	0.00085
axis2 & GLEHED	0.313	0.00101
axis2 & CARMEL	0.304	0.00124
axis2 & ALOPRA	-0.636	0.00000
axis2 & FRAPEN	-0.325	0.00151

The correlation analysis with the NMDS axes (Table 4) has different results for the 1st axis than in the case of the PCoA, but the results for the 2nd axis are similar (c.f. Table 3). Three of the species correlating with the 1st axis probably represent between-site variability (*Potentilla reptans, Plantago lanceolata, Daucus carota*) but the other two (*Lysimachia vulgaris, Poa trivialis*) do not. The coordinates of the quadrats along the 2nd axis are associated with the opposite behaviour of some dominant species: *Alopecurus pratensis* represents one direction while *Bidens tripartita* and some others, like *Lysimachia vulgaris* and *Carex melanostachya* the other (Table 4), like in the case of the PCoA (c.f. Table 3). The cover of *Amorpha fruticosa* does not correlate significantly with any of the axes (note that the cover of this species was not used in the calculation of the NMDS).

Table 5. Goodman-Kruskal's gamma correlations ($p < 0.05$) of Amorpha fruticosa with the other species in the two sites. For the abbreviations of the species see Table 1.

	gamma	p-value
site (A)		
AMOFRU & LACSER	0.5404531	0.0003993
AMOFRU & GALAPA	0.65	0.0005640
AMOFRU & POTREP	0.4670185	0.0007149
AMOFRU & VALLOC	0.3648649	0.0198986
AMOFRU & VICHIR	0.4385965	0.0342645
AMOFRU & ALOPRA	-0.480315	0.0004754
AMOFRU & VIOPUM	-0.6219512	0.0027716
AMOFRU & CIRARV	-0.6231884	0.0062587
AMOFRU & CALSEP	-0.4819277	0.0203251
AMOFRU & ACENEG	-0.4893617	0.0298758
AMOFRU & CIRVUL	-0.6410257	0.0331997
site (B)		
AMOFRU & VALLOC	0.5532995	0.0039416
AMOFRU & LYTVIR	0.5593221	0.0240022
AMOFRU & GALAPA	0.5254237	0.0339808
AMOFRU & SONASP	0.4010152	0.0344457
AMOFRU & CENJAC	-0.6923077	0.0007993
AMOFRU & TRIPRA	-0.4715909	0.0009681
AMOFRU & PRUVUL	-0.7	0.0040703
AMOFRU & PLAMAJ	-0.4653465	0.0137923
AMOFRU & LYSVUL	-0.3090909	0.0242866

Amorpha fruticosa has approximately as many positive as negative correlations with other species (Table 5). There are only two species (*Galium aparine* and *Valerianella locusta*) that correlate with the invasive species in the same way (positively) in both sites. The dominants are not involved in the correlations except the strong negative association with *Alopecurus pratensis* in site [A] (Table 5).

Discussion

Species pool of the two sites

The species pool of the two sites can be considered essentially identical. The difference is partly due to the fact that in a small fraction of site

[A] the abiotic conditions are different: in a wet patch species like *Scirpus lacustris* ssp. *lacustris, Bolboschoenus maritimus, Glyceria maxima* prevail, and in the burnt area some early coloniser species like *Myagrum perfoliatum, Chenopodium strictum, Echinochloa crus-galli* or *Fumaria vaillanti* appear. On the other hand, some generalist meadow species, like *Cichorium intybus, Leontodon autumnalis, Achillea millefolium, Trifolium repens or Cynodon dactylon* were not found in site [A]. In addition some opportunistic species of drier grasslands, like *Arenaria serpyllifolia, Holosteum umbellatum, Thlaspi arvense* or *Bromus tectorum* were detected only in site [B]. Probably some of the above species might have been found with a more thorough survey, but still their absence in site [A] is indicative. It is reasonable to attribute it to the preceding monodominance of *Amorpha fruticosa*. Nevertheless, the species richness of site [A] almost equals that of the control area, and most species characteristic to the potential (target) vegetation are already present, including those of high conservation value. The cause of the relative richness of site [A] is not clear: some species might survive under the closed canopy of the invader (e.g. *Ophyoglossum vulgatum*, which develops in the soil for years must have been present before *Amorpha* was cleared from the area). The propagules of other species might have been transported by the recent years' frequent floods, but other dispersal mechanisms might have also been important (e.g. *Cirsium brachycephalum*, an anemochorous species, which was represented by one flowering specimen in both areas has large stands southwards some hundreds of metres away, and was probably transported by wind). It is not clear which was the dominant mechanism. Previous studies by Kóra reported only a few opportunistic species living under complete *Amorpha* cover (e.g.: *Galium aparine, Urtica dioica, Calystegia sepium, Humulus lupulus*) (Kóra 2002). However, gaps of a few square metres where the canopy of the invader was not closed could serve as refuges for many species. Similarly, the coenotone zones between the *Alopecurus* grassland and the invasion-resistant *Carex acuta* sedge meadow could also preserve some species (e.g. *Leucanthemella serotina* was found mainly in such situations in site [A]).

Vegetation of the two sites

The vegetation of the two sites is rather different, when only compositional data are assumed (PCoA results, Fig. 2), but they are much more similar when species dominance data are taken into account (NMDS results, Fig. 3). Apart from the invasive species, the characteristics of the *Alopecurus pratensis*-meadow typical of floodplains can be identified in both sites, although the vegetation of site [A] is more patchy and inhomogeneous (see Figs 2 and 3) and species-poor on the local (quadrate) scale. The *Alopecurus pratensis* dominated meadow community shows transition either towards the more humid sedge meadows or towards the drier grassland types, forming a zonation complex, as detailed by Bodrogközy (1962, 1982, 1990). In our case, distinct appearance of zones was not detected: in site [A] the vegetation is still not well developed, while in site [B] species of humid (e.g. *Carex melanostachya, Eleocharis palustris*) or dry (e.g. *Carex praecox, Convolvulus arvensis*) habitats coexist from the scales of a few centimeters to several meters (Szigetvári, unpublished data). In our case another transition seems to be more important in the variation of the vegetation, which most characteristically manifests in the opposite behaviour of three dominant species: *Alopecurus pratensis, Bidens tripartita* and *Carex melanostachya*. The variation of cover of these species can be related to the variation of the species combinations (see the PCoA results: Fig. 2 and Table 3) and to the species dominance relations (see the NMDS results: Fig. 3 and Table 4). Their role is probably different: *Alopecurus* and *Carex melanostachya* are the dominant competitor species of the community, while *Bidens* is a colonizer of open surfaces with good competitive abilities. In earlier long-term studies Bodrogközy (1979) has shown that there is a peculiar relationship between these species: after years of permanent floods the cover of *Carex melanostachya* increases to the expense of *Alopecurus*. In flood-free years *Alopecurus* regenerates, but in the transitional period opportunistic species the propagules of which was previously spread by the flood increase their dominance (Bodrogközy 1979). This scenario is probably applicable to our case, with some remarks (see below).

Probable impact of the invader on the vegetation

The impact of the invader can be evaluated in two aspects: first, the relationships of the invader on the within-site variation can be investigated. Formally, we can draw conclusions from a vegetation “snapshot”, but such result gained from simple observations are usually doubtful (Lepš 1990). Satisfactory conclusions can only be drawn from long-term studies (Blossey 1999) or planned experiments (Morrison 1997). Second, the relationships of the invader with the between-site variation can be used. The costs of the latter approach are that we should a priori hypothesise that (1) the characteristics of the two sites are essentially identical, and their difference is (2) due to the impact of *Amorpha fruticosa* in site [A] in the preceding period. The first hypothesis can be supported by the similar species pools of the sites. The second hypothesis cannot be directly supported by the present study, we should rely on anecdotal information and literature data concerning the properties of the species.

The present study provides only week support to the hypothesis that *Amorpha* has any impact on the within site vegetation variation. The cover of the species does not correlate with the species richness per quadrate in either sites (or the “nearly significant” correlation is positive, like in site [A]). Also in the ordination analyses, the cover of *Amorpha* does not show any relationships with the variation of the species combinations or the dominance relationships within the sites. Some conclusions can be drawn from the analysis of interspecific correlations, which show that some species are positively, some are negatively associated with the invader. Only one of them, the negative correlation in site [A] between *Amorpha* and *Alopecurus pratensis* (the dominant of the target vegetation) suggests that the invasive species has adverse effects on the vegetation.

If we compare the two sites, the differences: lower species richness, absence or low abundance of many subordinate meadow species, greater patchiness (as manifested in the more scattered points in the ordination scattergram), can be interpreted as the after-effect of the permanent dominance of *Amorpha fruticosa*. Aware of the relative competitive abilities and allelopathyc capacity of the invader it is reasonable to hypothesise that these assumptions are correct. Two years since the *Amorpha* thicket was cleared and the systematic management has started most of the species have not been able to regenerate and spread, and there are still open surfaces to colonise in site [A]. Perhaps this state is similar in some aspect to that after the permanent floods. The lasting inundation weakens the meadow vegetation, and before the regeneration of *Alopecurus pratensis* is completed opportunistic coloniser species, like *Bidens tripartita* increase their cover (Bodrogközy 1979). It is also indicative, that the abundance of *Fraxinus pennsylvanica* seedlings is significantly higher in site [A] than in site [B] which — aware of the fact that there are a lot of ash trees near both sites, therefore propagule limitation perhaps does not play any role — is probably due to the many gaps ready to colonisation. The success of *Fraxinus pennsylvanica* in site [A] refers to reduced invasion resistance, which can also be interpreted as the after-effect of *Amorpha* invasion.

Prospects of regeneration

As the present investigations revealed, the species pool for the regeneration is already present in site [A]. Although the cover of *Amorpha* is still very high, it can be reduced to a reasonable level by systematic cutting (Papanastasis *et a.l* 1998). At the present management regime the invasive species seems not directly hinder regeneration except for the negative correlation with *Alopecurus pratensis*. Despite this fact, *Alopecurus* seems to quickly regenerate, and the most important codominant species are also abundant. It is mainly the subordinate species that are much rarer and have a more patchy distribution than in the control site. Their regeneration and dispersion in the whole site probably takes more time. At the present state the recovering habitat seems to be more susceptible to invasions after floods either by the buoyant seeds of *Amorpha* (or another alien species) or natural colonisers. This susceptibility might promote the regeneration through the colonisation of indigenous species only if alien species are managed by proper and systematic control methods. Therefore it is essential to continue mowing twice a year or pursue continuous grazing to prevent *Amorpha’s* seed set and regeneration from sprouts.

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Appendix 1. Species list for the two sites [A] and [B]. Species presence is marked by "+"sign.

Species	(A)	(B)
Acer negundo	+	+
Achillea millefolium		+
Agrostis stolonifera	+	+
Alisma plantago-aquatica	+	
Alopecurus pratensis	+	+
Althaea officinalis	+	+
Ambrosia artemisiifolia	+	+
Amorpha fruticosa	+	+
Anthemis arvensis		+
Apera spica-venti	+	+
Arabidopsis thaliana	+	+
Arenaria serpyllifolia		+
Aristolochia clematitis	+	+
Asclepias syriaca	+	+
Asparagus officinalis	+	+
Atriplex prostrata	+	+
Bidens tripartita	+	+
Bolboshoenus maritimus	+	+
Bromus sterilis		+
Bromus tectorum	+	+
Calystegia sepium	+	+
Capsella bursa-pastoris		+
Carduus nutans	+	
Carex acuta	+	+
Carex hirta	+	+
Carex melanostachya	+	+
Carex praecox	+	+
Carex riparia	+	+
Centaurea jacea	+	+
Cerastium dubium		+
Cerastium fontanum	+	+
Chenopodium album	+	+
Chenopodium strictum	+	
Cichorium intybus		+
Cirsium arvense	+	+
Cirsium brachycephalum	+	+
Cirsium vulgare	+	+
Convolvulus arvensis		+
Conyza canadensis	+	+
Crepis biennis	+	+
Crepis tectorum	+	
Cynodon dactylon		+
Daucus carota	+	+
Descuriania sophia	+	+
Digitaria sanguinalis	+	+
Echinochloa crus-galli	+	
Echynocystis lobata	+	+
Eleocharis palustris	+	+
Elymus repens	+	+
Epilobium tetragonum		+

Appendix 1. (continued)

Species	(A)	(B)
Equisetum palustre	+	+
Erophila verna ssp. majuscula	+	+
Euphorbia lucida	+	
Fraxinus pennsylvanica	+	+
Fumaria vaillanti	+	
Galium aparine	+	+
Galium palustre	+	+
Glechoma hederacea	+	+
Glyceria maxima	+	
Glycyrrhiza echinata	+	+
Gratiola officinalis	+	+
Holosteum umbellatum		+
Inula britannica	+	+
Iris pseudacorus	+	+
Juncus compressus	+	+
Lactuca saligna		+
Lactuca serriola	+	+
Lamium purpureum	+	+
Lathyrus tuberosus	+	+
Leontodon autumnalis		+
Leucanthemella serotina	+	+
Lotus glaber	+	+
Lychnis flos-cuculi	+	+
Lycopus sp.	+	+
Lysimachia nummularia		+
Lysimachia vulgaris	+	+
Lythrum salicaria	+	+
Lythrum virgatum	+	+
Medicago lupulina	+	+
Mentha aquatica	+	+
Mentha arvensis x (male sterile)	+	+
Myagrum perfoliatum	+	
Myosotis ramosissima	+	+
Myosotis stricta	+	+
Ophioglossum vulgatum	+	+
Picris hieracioides	+	
Plantago lanceolata	+	+
Plantago major	+	+
Poa pratensis	+	+
Poa tivialis	+	+
Potentilla anserina	+	+

Species	(A)	(B)
Potentilla reptans	+	+
Prunella vulgaris	+	+
Pulicaria dysenterica	+	+
Quercus robur	+	+
Ranunculus repens	+	+
Rhinanthus angustifolius		+
Rorippa amphibia	+	
Rorippa astylis		+
Rorippa palustris	+	+
Rumex crispus	+	+
Scirpus lacustris ssp. lacustris	+	
Scutellaria galericulata		+
Scutellaria hastifolia	+	+
Senecio erucifolius		+
Senecio vernalis		+
Setaria pumila	+	+
Sisymbrium orientale		+
Sium latifolium	+	+
Solanum dulcamara	+	+
Sonchus asper	+	+
Stachys palustris	+	+
Stellaria media	+	+
Stenactis annua	+	+
Symphytum officinale	+	+
Taraxacum officinale	+	+
Thalictrum flavum	+	+
Thalictrum lucidum	+	+
Thlaspi arvense		+
Tragopogon dubius	+	+
Trifolium dubium	+	+
Trifolium pratense	+	+
Trifolium repens		+
Valerianella locusta	+	+
Veronica chamaedrys		+
Vicia angustifolia	+	+
Vicia cracca	+	+
Vicia hirsuta	+	+
Vicia tetrasperma	+	
Viola pumila	+	+
Xanthium italicum	+	+