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DISTRIBUTION AND PHYTOSOCIOLOGICAL RELATIONS OF TWO INTRODUCED PLANT SPECIES IN AN OPEN SAND GRASSLAND AREA IN THE GREAT HUNGARIAN PLAIN

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Two introduced plant species, *Cenchrus incertus* and *Ambrosia artemisiifolia* were studied in a 0.5 km^2 open sand area in the Kiskunság National Park. The site is covered by valuable semi-natural grassland and is bordered by dirt roads. The aim of the study was to assess the extent and pattern of the area occupied by the two species and to describe the composition of the vegetation invaded with more or less success. Populations of the two species were mapped. In each stand of *Cenchrus*, in fifty-three 4 m^2 quadrats aboveground plant cover, slope and exposition were documented.

Both species concentrated on the roads. They – especially *Ambrosia* – were rare inside the intact part of the site, and were absent on abandoned roads. *Cenchrus* was found also in small patches not related to roads, in sites grazed with sheep. No colonization was detected from the road populations into adjacent intact natural vegetation. The analysis of the quadrats showed that *Cenchrus* cover was low where perennial or annual open sand grassland specialists dominated, and cryptogam cover was high. *Cenchrus* dominated quadrats on road or non-road sites were not discriminated from each other by cluster analysis. In non-road quadrats *Cenchrus* cover positively correlated with slope. *Ambrosia* was only present in quadrats taken on or near the roads.

Aware of the life history traits of the species and of the vegetation dynamics of the target community it can be concluded that propagule transport, soil perturbation and disturbance of the native vegetation together enhance colonization and persistence of both species.

Key words: *Ambrosia artemisiifolia*, *Cenchrus incertus*, disturbance, invasion, propagule transport, roads, soil perturbation

INTRODUCTION

Human-driven plant invasions pose a global threat to nature reserves causing radical changes in the endangered native communities (Macdonald *et al.* 1989, Cronk and Fuller 1995). However, only a small fraction of introduced species becomes a "pest" for any respect (Williamson 1996, Williamson and Fitter 1996), and probably an even narrower proportion has impacts on natural communities. However, once become a successful invader, the damage caused

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in nature reserves as well as the costs of eradication and control is enormous (Pimentel *et al.* 2000). Assessment of potential impact of naturalized species is therefore an urgent need in order to distinguish species with minor impact from those with large effect, so as to prioritize management efforts (Hiebert 1997, Parker *et al.* 1999).

The aim of the present paper is to examine the potential role of two invasive plant species *Cenchrus incertus* and *Ambrosia artemisiifolia* in the open sand grassland communities endemic to the Carpathian Basin. The two focal species of the study are regarded noxious by conservationists in Hungary (Török 1997), however no detailed study has examined their behaviour in natural communities. On the other hand, the invaded habitat and its communities have been in the centre of interest of nature conservation and vegetation science, because of its uniqueness and richness in endemic species, and because it is one of the natural habitats that have persisted in a fairly great extent and diversity in Hungary. This paper presents the results of a descriptive study applying classical methods: mapping and coenological sampling carried out in one of the representative open sand grassland areas.

MATERIAL AND METHODS

Study species

Field sandbur or Coast sandspur, *Cenchrus incertus* M. A. Curtis (syn. *Cenchrus pauciflorus* Benth.), Poaceae, is native to America from the southern part of the United States through Central America to coastal Southern America (DeLisle 1963, Reed 1970, Parker 1972). The species has also naturalized as an introduced alien in South Africa, Australia, in the Mediterranean Basin and Europe (Priszter 1965, 1997, Holm *et al.* 1979, Dafni and Heller 1990, Fox 1990, Parsons and Cuthberson 1992, Bromilow 1995). As a casual alien it has also appeared in Finland (Kurtto and Lahti 1987). *Cenchrus incertus* is a summer annual or a short-lived perennial bunchgrass with erect or prostrate stems, which might root at the lower nodes. It often forms mats and ascends. Its height varies between 10 and 60 cm and has a shallow root system. The seeds are enclosed in spiny hairy 5–8 mm long burs (1–3 seeds in each), which cling to skin and fur of animals, shoes and clothing and might painfully injure skin (Sárospataki 1957, Priszter 1960, DeLisle 1963, Parker 1972, Ujvárosi 1973).

Recent taxonomic investigations (Mosyakin 1995, Guzik and Pacyna 1999) suggest that the central and eastern European sandbur populations should belong to another, closely related species, *Cenchrus longispinus* (Hack.) Fern, Longspine sandbur. The two species are very similar in appearance and ecology, and their identification is often confused (DeLisle 1963, Twentyman 1972). As no systematical taxonomic revision has been made in the Hungarian populations I refer to the species as *Cenchrus incertus* in the sequel.

The biology of *Cenchrus incertus* is poorly documented, but is probably similar to that of *Cenchrus longispinus*, of which detailed information is available (Twentyman 1974, Boydston 1989, 1990). Each bur of the latter species contains two types of seed that differ in dormancy pattern: seeds from upper spikelets typically germinate within one year, while seed from lower spikelets germinate more slowly and can remain dormant for longer periods. Light appears to inhibit germination and induce dormancy of seeds. Burs on the soil surface can have a prolonged germination of more than 3 years, but seedlings seldom establish. Optimal seedling emergence is from 1–3 cm soil depth; however in sandy soils, seedlings can emerge from depths to 25 cm. Most seed of buried burs germinates within 2 years (Twentyman 1974, Boydston 1989, 1990). In Hungary Sárospataki (1957) conducted germination experiments with *Cenchrus incertus* in Petri dishes. He found that ability to germinate was better in seeds that had overwintered in the laboratory rather than in the field, and germination success showed a decreasing trend with seed age in the three year sequence examined (Sárospataky 1957). Germination in Hungary starts when the soil temperature is at least about 20 °C (Ujvárosi 1973). Young plants are very sensible to late frost (Sárospataky 1957). Seed production is highest in plants emerging early in the season: in *Cenchrus incertus* the maximum number of burs is above 1000 (Parker 1972), in *Cenchrus longispinus* this number might exceed 3000 (Boydston 1990).

In its native and novel range *Cenchrus incertus* is a common pioneer weed in dry sandy soils in cultivated fields, roadsides, lawns, pastures and waste places (DeLisle 1963, Reed 1970, Parker 1972, Dafni and Heller 1990, McKinney and Fowler 1991, Parsons and Cuthberson 1992, Bromilow 1995). Sandbur, since its first detection in Hungary in 1922 has rapidly spread over the dry basic sand soils of the "Duna–Tisza köze" (Danube–Tisza interfluve) region mainly after the Second World War (Priszter 1960, 1965). According to regional distribution data *Cenchrus* reached the site before 1939 (Priszter 1960). The species in the early literature is erroneously referred to as *Cenchrus tribuloides* L. in Europe and Hungary due to misidentification (Priszter 1965, cf. Sárospataky 1957, Priszter 1960). In Hungary the species is annual, and preferres warm, dry, loose basic sandy soils that are poor in nutrients and organic matters (Soó 1964–1980: V, Ujvárosi 1973).

Common ragweed, *Ambrosia artemisiifolia* L. (syn. *Ambrosia elatior* L.), Asteraceae, is native to North America (Basset and Crompton 1975) and it has been introduced all over the world (Béres and Hunyadi 1980). *Ambrosia artemisiifolia* is an erect summer annual herb 5–70 (–200) cm high with a taproot. Stems usually bushy branched. Flower heads contain either male or female flowers. Male heads are 10–100-flowered, female heads are 1-flowered (Ujvárosi 1973, Basset and Crompton 1975, Béres and Hunyadi 1980). The fruit possesses no obvious dispersal mechanism, it is usually the one-seeded flower heads or rarely the achenes or the seeds that are dispersed (Béres and Hunyadi 1980). The main dispersal agents are water, birds and man (Basset and Crompton 1975). Soó (1970) classifies the species as exozoochorous. Seed production varies between some hundreds to tens of thousands, the observed maximum is 62,000 (Dickerson and Sweet 1971).

As seeds of *Ambrosia artemisiifolia* mature they are innately dormant (primary dormancy) and they require moist chilling (stratification) – which occurs naturally during winter – to be able to germinate (Payne and Kleinschmidt 1961). However in darkness, at temperatures above 20 °C seeds enter secondary dormancy and again they need stratification for coming out of dormancy (Bazzaz 1970, Baskin and Baskin 1980). Seed longevity experiments by Duvel (1905) and Beal (1884) detected successful germination after 39 (Toole and Brown 1946) and 40 years (Darlington 1922, Baskin and Baskin 1977) in *Ambrosia artemisiifolia* seeds, but there was no germination after longer periods of time (Kivilaan and Bandurski 1973). These properties enable the species to maintain sufficiently large seed banks. Seeds germinate at or near the soil surface (Bazzaz 1970).

Ambrosia artemisiifolia in its native and novel range is a common weed in cultivated fields, on roadsides, vacant lots, abandoned croplands and in other kinds of disturbed habitats (Ujvárosi 1973, Basset and Crompton 1975). In abandoned fields it is one of the earliest colonizers and sometimes the most abundant plant in the first years but subsequently disappears as other species become dominant (Bazzaz 1968, Raynal and Bazzaz 1975, Tilman 1988, Kosola and Gross 1999). Common ragweed was first presented from Hungary in the beginning of the 20th century (Jávorka 1910, Lengyel 1923, Boros 1924). After a rapid spread especially after the Second World War the species has become one of the most abundant weeds all over the country (Priszter 1960, Ujvárosi 1973, Béres and Hunyadi 1980, Béres 1982, Ilovai 1995). The region where the study site is found was invaded between 1966 and 1977 (Béres and Hunyadi 1980). *Ambrosia artemisiifolia* has no special soil requirements in Hungary, nevertheless it tends to prefer loose sandy or silt soils (Soó 1970, Ujvárosi 1973).

Research area

The examinations were carried out in August 1999, in a sand dune area of territory IV of the Kiskunság National Park near Fülöpháza (20 km west of the city of Kecskemét) in the "Duna–Tisza köze" region in Hungary. The two species were mapped and relevés were taken in a *ca* 0.5 km^2 seminatural open sand grassland area with high sand hills up to 30–35 m relative elevation. This area is bordered by a dirt road separating a *Pinus nigra* plantation from the northwest, by an old (abandoned) dirt road separating a more wooded sand grassland from the northeast, by a dirt road and a loose line of trees separating a more disturbed and flattened sand grassland from the southeast and by a line of small woods and invasive *Ailanthus altissima* stands separating a more disturbed grassland from the southwest (Fig. 1).

The climate of the area is of moderate continental type. The mean annual temperature is 10–11 °C with –1.5–2 °C in January and 21–22 °C in July. The mean annual precipitation is about 550 mm with a maximum in June and November. The number of sunny hours is about 2,050, the water balance is negative (Iványosi Szabó 1979, Borhidi 1993). The sand dunes of the area consist of basic wind-blown sand of Danubian origin. The soil of the sand hills is a very poor basic skeleton soil, without expressed soil profile differentiation. The clay and colloid fraction is extremely low, the humus content is less than 1%. The calcium-carbonate content is considerable, the pH measured in distilled water is around or above eight. The concentration of nutrients is very low. The soils of the depressions have slightly higher humus fraction and lower reaction (Szabolcs 1979, Várallyai 1993, Bagi 1997).

Most of the area is covered by open perennial grassland dominated by xerophilous grasses like *Festuca vaginata*, *Stipa borysthenica*, *Koeleria glauca*, and

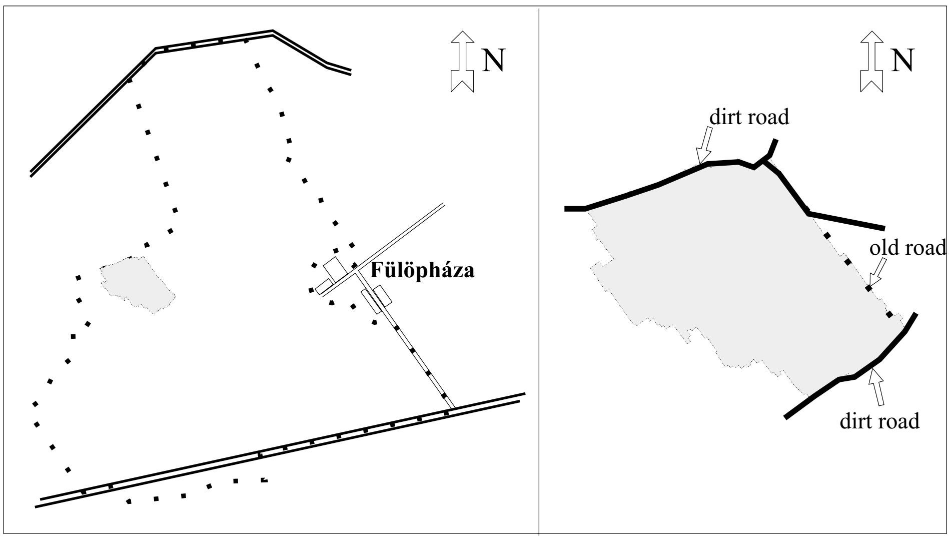

Fig. 1. The position of the research site (shaded area) within the territory IV of the Kiskunság National Park. The dotted line represents the border of the protected area

on the poorest soils by the dwarf shrub *Fumana procumbens*. In deeper depressions a meadow-like community is found with more dense vegetation of *Scirpoides holoschoenus*, *Poa angustifolia* and *Calamagrostis epigeios*, with shrubs of *Salix repens* subsp. *rosmariniifolia*. Patches of the open annual grassland dominated by annual grasses like *Secale sylvestre* and *Bromus tectorum* and weedy species develops where disturbance – mainly grazing, trampling, ploughing, drying – destroyed or degraded the original vegetation and nutrients accumulated in the soil. The sand vegetation types are described in detail in Magyar (1933), Hargitai (1940), Soó (1957), Biró and Molnár (1998), Borhidi and Sánta (1999). A considerable proportion of the area – mainly the sites adjacent to dirt roads and those formerly occupied by open perennial grassland – has been invaded by the grass *Cleistogenes serotina* for the recent two decades (Bagi 1997, 2000, Molnár 2000). The area has been strictly protected since 1974. Before that date it was heavily grazed, and for the recent decades there has been a tendency for the grasslands to become more closed. Moderate grazing by goat was applied as site management from the middle of the 1980s until 1994. For the recent few years the area has been grazed with sheep again. Grazing occurs in early spring and late autumn, though its extent and duration is rather uncontrolled (Pál-Szabó, personal communication). Other kinds of disturbance are burrowing and grazing by wild animals and recently, sparsely but strikingly, motocrossing.

Mapping and vegetation sampling

The whole research area was walked all over and systematically surveyed twice during the flowering time of the species of interest in August 1999, and all stands as well as isolated solitary individuals found were indicated on a 1 : 3,500 arial photograph made in 1988. Inside the area in each stand of *Cenchrus* absolute percent cover of all plant species was estimated in randomly placed 2 m × 2 m quadrats, 45 altogether, and five 4 m × 1 m quadrats were taken on the middle strip of the dirt road bordering the area from the southeast. Additional three 2 m × 2 m quadrats were taken in a site near, but outside of the mapped area adjacent to the dirt road mentioned above in a SE-facing slope. Only the latter eight quadrats include *Ambrosia* as stands of this species – except some solitary individuals – were only found on the dirt roads. Besides the living – summer green – species I also estimated the cover of the dead plants of the vernal aspect on the basis of the dry stalks. Although the cover estimate from dead parts is probably more biased than that of the living plants I did not exclude the species of the vernal aspect from the subsequent analyses because of their considerable mass and phytosociologically indicative character.

Data analysis

The fifty-three 4 m^2 quadrats were classified on the basis of the absolute percent cover of the phanerogamic species using Euclidean distances for the distance matrix and Ward's method as the fusion algorithm. This latter algorithm, which attempts to minimize the sum of squares of any two possible clusters that can be formed in each step is widely used in vegetation classification because it tends to create distinct clusters that are easy to interpret (Podani 1997). For the subsequent analyses I cut the dendrogram at a linkage distance, which separated a manageable number of distinct clusters. These clusters were than considered as vegetation type units with internal hierarchy neglected and for the statistical analyses I regarded them as treatments in a statistical sense.

Each phanerogamic species was *a priori* classified based on their phytosociological character, which indicates the preference of each species to plant associations (vegetation types). For the classification I rely on the categories of Soó (1964–1980). The groups are the following: PE – perennial open sand grassland specialists, AN – annual open sand grassland specialists, SA – sand grassland specialists (species characteristic to either type of open sand grassland), DR – dry grassland specialists (species occurring in any type of dry grasslands), WE – weed species characteristic of secondary vegetation on nutrient rich soils. These categories correspond to the following phytosociological classification: PE – Festucion vaginatae, AN – Bromion tectorum, SA – Festucetalia vaginatae, DR – Festuco-Brometea, WE – different weed associations, mainly Tribulo-Eragrostion (Soó 1964–1980). Although this kind of classification is rather subjective and controversial for single species it can be effectively used for vegetation-concerned studies. The sum of the percent cover of species belonging to each group was summed for each quadrat for the subsequent analyses. Because the sampling design focused on *Cenchrus*, moreover the classification of this species in the phytosociological system – perhaps partly because it is a neophyte – is rather ambiguous (Soó 1973, see also Borhidi 1995) I did not add the cover of this species to any of the groups. However, in the case of *Ambrosia* it does not mean circularity to add the species to the respective weed group (WE), which is also a consistent classification in the literature (Soó 1970, Borhidi 1995). Therefore I performed the subsequent analyses with both *Ambrosia* included in and omitted from the WE group.

Because the precision of cover estimation for species with low and high cover is probably different I classified the summed cover values for the different species groups into ordered categories in order to avoid artefacts that can arise in rank statistics because of minimal apparent differences. The midpoints of the categories below 15% are the integers, between 15% and 30% the midpoints are 17.5, 20, 22.5, 25, 27.5%, above 30% the midpoints are fives and tens. The vegetation types discriminated by the cluster analysis were analysed by Kruskal-Wallis test (Zar 1984) to decide whether they differ in the sum of percent cover of species belonging to each of the above phytosociological groups (PE, AN, SA, DR, WE, WE+*Ambrosia*), in the percent cover of *Cenchrus* , and in the sum of the percent cover of the cryptogamic species (CR). Altogether eight tests were performed. In order to avoid increase of Type I error I applied Bonferroni-correction: the P-values were multiplied by 8. Subsequent pairwise comparisons were calculated using Dunn's method (Zar 1984).

As the cover of the species belonging to the different phytosociological groups is not independent from each other the result of the analysis is rather informative than precise. I also measured the correlation between *Cenchrus* cover and slope. In the analysis I omitted the five 4 m × 1 m quadrats taken at the dirt road. I calculated the measure of the correlation using Goodman and Kruskal's gamma (Siegel and Castellan 1988), because this test is appropriate when data contain many tied observations (in this case many quadrats have 0° slope). For the calculation of the Kruskal-Wallis test and the correlation as well as for the cluster analysis I used Statistica for Windows program package (Statsoft Inc. 1995).

RESULTS

Ambrosia is found almost exclusively on and near the dirt roads bordering the area from the northwest and from the southeast. There are only small groups of 1 to 5 individuals inside the area (Fig. 2). *Cenchrus*, however, has several small stands apparently not related to the roads (Fig. 3). The latter populations are found on either horizontal surface or – presumably the densest stands – on south-facing, relatively steep (30–50°) slopes. Most recent survey of the area in March 2001 revealed that sheep trampling was very intense in the *Cenchrus* stands within the area, because these patches lie on the regular routes of the flock, where traces go in one direction in a 10–15 m stripe. In addition, in stand "j" (cf. Fig. 3) most individuals were found in a wheeltrack in 1999. Neither of the species was found on the abandoned road and no colonization can be detected in sites adjacent to road populations on the scale of the map (Figs 2–3).

The quadrats contain 45 phanerogamic species of which seven belong to the vernal aspect. Twelve species occur in less than 5% of the quadrats (Table 1). The average cover of the living phanerogamic plants is quite low (median: 47%, quartiles: 31 and 50%). On the basis of the cluster analysis it seems reasonable to discriminate three groups (Fig. 4). Clusters B and C are somewhat

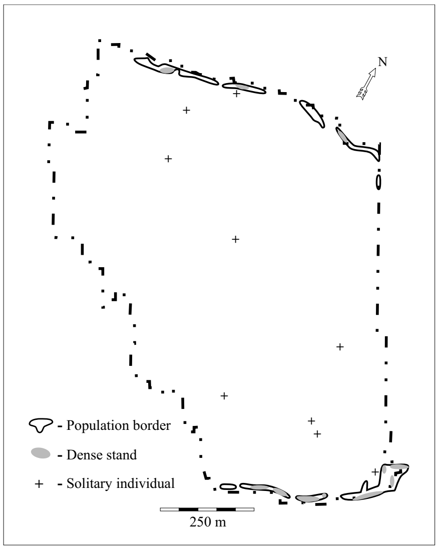

Fig. 2. The distribution of *Ambrosia artemisiifolia* in the study area. Dense stands refer to patches where the species has at least appr. 10% aboveground cover

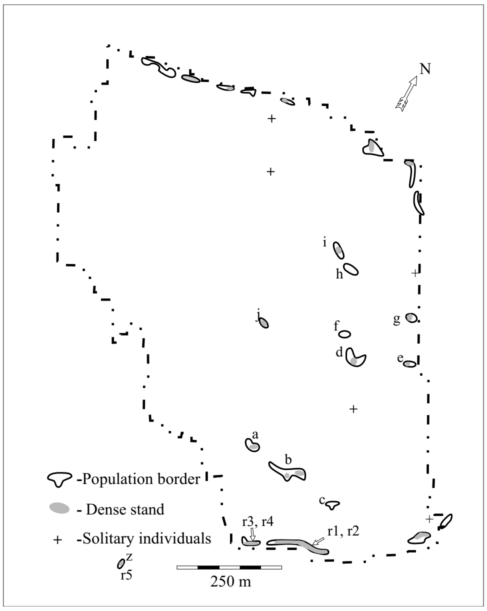

Fig. 3. The distribution of *Cenchrus incertus* in the study area. Distinct populations apparently not related to roads are denoted by lower case letters ("a–i"), sampled populations on the dust roads are denoted by letter "r", population near the road by letter "z". Dense stands refer to patches where the species has at least appr. 10% aboveground cover

Table 1
The list of species occurring in the quadrats, their classification in the species groups (PE: perennial open sand grassland specialists, AN: annual open sand grassland specialists, SA: sand grassland specialists, DR: dry grassland specialists, WE: weeds, CR cryptogams), and their frequency and average cover in the different clusters (cf. Fig. 4). Average cover was computed only for quadrats where the given species was present

Species	Group	Frequency			Average cover		
		Clusters (NA=16, NB=14, NC=23)					
		A	B	C	A	B	C
Cenchrus incertus M. A. Curtis	(SA)	16	14	23	4.9	22.3	2.9
Ambrosia artemisiifolia L.	(WE)	0	7	0	0	4.9	0
Alkanna tinctoria (L.) Tausch	PE	3	4	4	2.0	0.9	0.7
Alyssum tortuosum W. et K.	PE	6	11	11	1.1	1.8	4.1
Artemisia campestris L.	PE	0	5	1	0	2.5	2.5
Centaurea arenaria M. B. ex Willd.	PE	7	3	8	1.0	0.4	1.1
Dianthus serotinus W. et K.	PE	0	1	0	0	4.0	0
Erysimum canum (Pill.) Mitterp.	PE	7	4	9	1.9	0.7	1.3
Euphorbia segueriana Necker	PE	9	9	19	3.6	2.3	5.5
Festuca vaginata W. et K.	PE	5	10	12	1.3	5.9	3.1
Fumana procumbens (Dun.) Gren. et Godr.	PE	1	6	15	0.1	1.7	5.6
Koeleria glauca (Schkuhr) DC.	PE	5	3	8	1.2	0.7	1.9
Minuartia verna (L.) Hiern.	PE	10	6	2	0.8	4.4	0.1
Stipa borysthenica Klokov	PE	14	9	18	2.5	2.7	8.7
Tragopogon floccosus W. et K.	PE	1	1	0	1.0	0.1	0
Bassia laniflora (S. G. Gmel.) A. J. Scott	AN	6	5	9	2.3	0.6	0.4
(*Bromus squarrosus*) L.	AN	2	5	5	3.0	1.4	0.9
(*Bromus tectorum*) L.	AN	0	1	1	0	1.0	4.0
Salsola kali L.	AN	3	1	1	2.3	0.1	1.0
(*Secale sylvestre*) Host	AN	16	13	20	21.1	3.0	3.1
(*Silene conica*) L.	AN	1	0	0	0.5	0	0
Asclepias syriaca L.	WE	0	0	2	0	0	0.1
Conyza canadensis (L.) Cronq.	WE	14	9	6	5.2	2.2	1.6
Crepis rhoaedifolia M. B.	WE	8	7	6	2.0	1.1	1.2
Eryngium campestre L.	WE	1	0	0	0.1	0	0
(*Medicago minima*) (L.) Grufbg.	W	3	0	1	1.3	0	0.1
Setaria viridis (L.) P. B.	WE	0	3	1	0	1.0	1.0
Tragus racemosus (L.) All.	WE	7	1	3	0.9	0.5	1.5
(*Arenaria serpyllifolia*) L.	SA	2	1	0	0.1	0.1	0
Carex liparicarpos Gaud.	SA	1	1	0	20.0	4.0	0
Corispermum nitidum Kit.	SA	12	14	18	6.4	2.0	1.1
Equisetum ramosissimum Desf.	SA	11	4	3	2.1	0.9	0.9

Table 1 (continued)

Species	Group	Frequency			Average cover		
		Clusters (NA=16, NB=14, NC=23)					
		A	B	C	A	B	C
Linaria genistifolia (L.) Mill.	SA	0	0	1	0	0	0.5
Polygonum arenarium W. et K.	SA	15	14	19	3.9	3.5	2.2
Silene otites (L.) Wib.	SA	5	10	19	5.6	1.8	3.1
Asparagus officinalis L.	DR	0	1	0	0	0.5	0
Bothriochloa ischaemum (L.) Keng	DR	10	3	6	6.8	3.0	1.5
(*Camelina microcarpa*) Andrz.	DR	0	1	2	0	1.0	0.6
Cynodon dactilon (L.) Pers.	DR	8	1	7	6.7	0.5	2.6
Euphorbia cyparissias L.	DR	1	0	0	4.0	0	0
(*Poa bulbosa*) L.	DR	0	0	2	0	0	0.1
Potentilla arenaria Borkh.	DR	1	0	0	0.5	0	0.0
Scabiosa ochroleuca L.	DR	1	3	2	4.0	3.7	1.6
Stipa capillata L.	DR	1	0	2	0.1	0.0	1.3
Thymus odoratissimus Mill. subsp. *glabrescens*	DR	4	1	1	10.0	0.5	4.0
Populus sp.		2	2	5	0.1	0.8	1.9
Tortula ruralis (Hedw.) Gaertn. et al.	CR	15	2	8	40.3	0.3	15.1
Nostoc sp.	CR	6	2	3	13.8	7.8	2.5
Cladonia furcata (Huds.) Schrad.	CR	3	0	0	0.5	0	0
Parmelia pokornyi (Koerb.) Szat.	CR	3	0	0	5.1	0	0
Cladonia convoluta (Lam.) P. Cout.	CR	2	1	1	0.3	0.1	0.5

Table 2

Groups of quadrats discriminated by the cluster analysis (A, B, C, cf. Fig. 4.) ranked by their average ranks in decreasing order, and results of the Kruskal-Wallis test on the cover of *Cenchrus incertus*, the phytosociological groups (PE: perennial open sand grassland specialists, AN: annual open sand grassland specialists, SA: sand grassland specialists, DR: dry grassland specialists, WE: weeds, WE+*Ambrosia*: weeds including *Ambrosia artemisiifolia*) and CR: cryptogams. Bonferroni-corrected significance values for the Kruskal-Wallis test are the following: **: $p \times 8 < 0.01$, ***: $p \times 8 < 0.001$, ns: $p \times 8 > 0.05$. Average ranks not significantly different from each other at = 0.05 by Dunn's test are underlined. See also Fig. 5

Group tested	Ranked average rank	Kruskal-Wallis H (2, 53)
Cenchrus	B A C	29.648***
PE	C B A	15.074**
AN	A C B	29.206***
SA	(A B C)	9.118 ns
DR	A C B	14.510**
WE	A B C	16.545**
CR	A C B	26.816***
WE+Ambrosia	B A C	24.169***

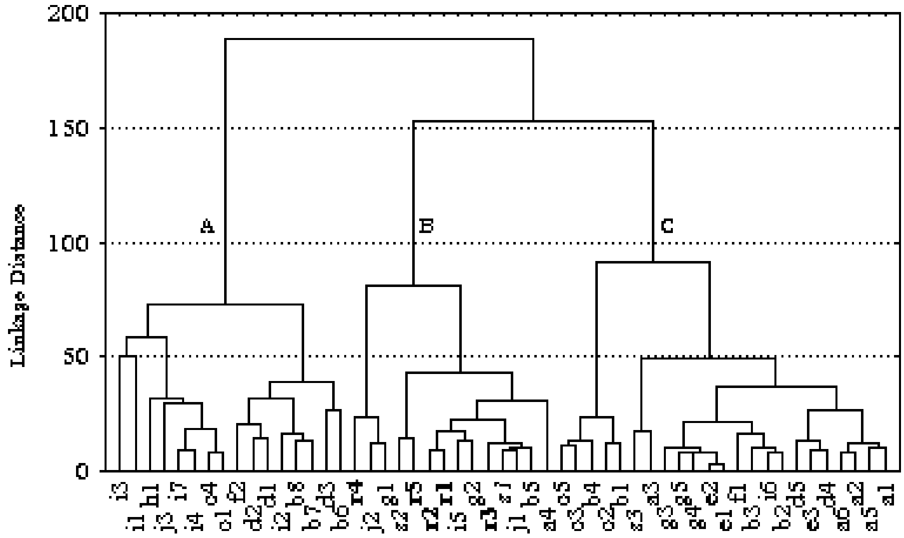

Fig. 4. Cluster analysis of fifty-three 4 m^2 quadrats on the basis of the phanerogamic plant cover. Individual quadrats are identified by lower case letters referring to the populations where they were taken from (cf. Fig. 3). Quadrats taken on the road are in bold type, quadrats near the road are in italics. Capital letters A, B and C represent the clusters that are regarded as coherent groups in the statistical analyses

more similar to each other than to cluster A. Most of the stands is represented in at least two of the clusters (cf. Fig. 3). The quadrats taken at the dirt road, however, are only found in cluster B, although they do not form a distinct group within it. *Ambrosia* is only found in cluster B in the quadrats taken at and right next to the dirt road (quadrats r1-r5 and z1-z2, Figs 3–4). The main species of all vegetation types of the site can be found in the quadrats except those of the meadow-like vegetation characteristic of the depressions, as well as the invasive dominant *Cleistogenes serotina*.

The percent cover of each phytosociological group (except SA) altogether with that of *Cenchrus* and the cryptogam layer was detected to be significantly different between the clusters by the Kruskal-Wallis test, although the results of the pairwise comparisons are somewhat ambiguous (Fig. 5, Table 2). Cluster B has the highest cover of *Cenchrus*, while clusters A and C have the character of the annual and the perennial open sand grassland, respectively. Cluster B and C are common in the extremely low cover of cryptogams, annual sand grassland specialists (it is mainly the absence of the species of the vernal aspect that contribute to this) and the low cover of dry grassland specialist (this latter trend is rather due to the dominance of *Bothriochloa ischaemum* or *Cynodon dactylon* in some of the quadrats in cluster A, cf. Table 1). The cover of perennial sand grassland specialist, weeds, and sand grassland specialist is intermediate in the *Cenchrus* dominated cluster B, although when *Ambrosia* is included in the weed group, the cover of the WE species is not significantly different from that of cluster A (Fig. 5, Table 2).

The correlation between slope and *Cenchrus* cover is highly significant when quadrats from the road are omitted (gamma = 0.401, N = 48, $p < 0.001$). Only 26 of these 48 quadrats had slope >0°, and 25 of these 26 quadrats had SW, S or SE exposition, the remaining one faced east.

DISCUSSION

The 1999 snapshot on the distribution of the two species suggests that *Cenchrus* and *Ambrosia* are associated to dirt roads currently in frequent use, and are relatively rare inside the area (even adjacent to the road stands) and on the abandoned road. In addition, *Cenchrus* is also found in places where sheep trampling is intense. I propose three different mechanisms that can explain this pattern: (1) propagules are better dispersed along the roads, remote areas inside the territory have much less intense propagule supply; (2) the two species for their growth or germination require the kind of disturbance (e.g. stirring up the soil surface) that is characteristic of the roads; (3) negative biotic interactions are less intense on roads and trampled sites than in intact areas because of continuous disturbance.

The first approach (1) refers to the seed limitation hypothesis, an important factor in plant invasions (Turnbull *et al.* 2000 and references therein). In our case this (1) is a plausible explanation, because both *Cenchrus* and *Ambrosia* are adapted to external transport by animals or man. The wider distribution of *Cenchrus* can be attributed to the fact that its spiny burs are apparently more adapted to this kind of transport, but it should also be mentioned that *Ambrosia* was first documented in the region a few decades later than *Cenchrus* (Priszter 1960, Béres and Hunyadi 1980), thus it had a shorter period of time to reach all available sites. On the other hand, seed transportation alone could result a much wider distribution, as the extent of the grazed area pretty much exceeds the area occupied by either of the species. However, grazing occurs only in late autumn and early spring (Pál-Szabó, pers. comm.), which is not the optimal seed dispersion time for these two late summer species. This hypothesis alone also does not explain the absence of the two species on the abandoned road, though we have no information about whether the invasives had been present in the area before the road was abandoned.

(2) also seems to be a possible explanation. Although the two species has opposite requirements for germination – burs of *Cenchrus* should be buried to successfully germinate while seeds of *Ambrosia* tend to germinate on the surface – trampling by man or sheep or perturbation of the soil surface by car readily satisfy both. The low success of *Cenchrus* in the quadrats where cover of cryptogams is high might also be an argument for (2), because the lack of bare soil and thick moss layer in such sites probably prevents seed burying.

(3) is consistent with hypotheses that couple invasion success with disturbance (e.g. Hobbs 1989, Hobbs and Huenneke 1992, Burke and Grime 1996) and that predict decreasing invader success in advancing successional seres (Rejmánek 1989). This approach can also be applied since *Ambrosia* is documented as a pioneer that quickly disappears after a few years of disturbance and *Cenchrus* is also described as a pioneer of disturbed areas. The correlation of *Cenchrus* cover with slope is consistent with this idea, because steep surfaces often preserve loosely organized vegetation (Horváth 1997, Margóczi 1995) and early successional phases (Zólyomi 1958, Fekete 1992), which are thus

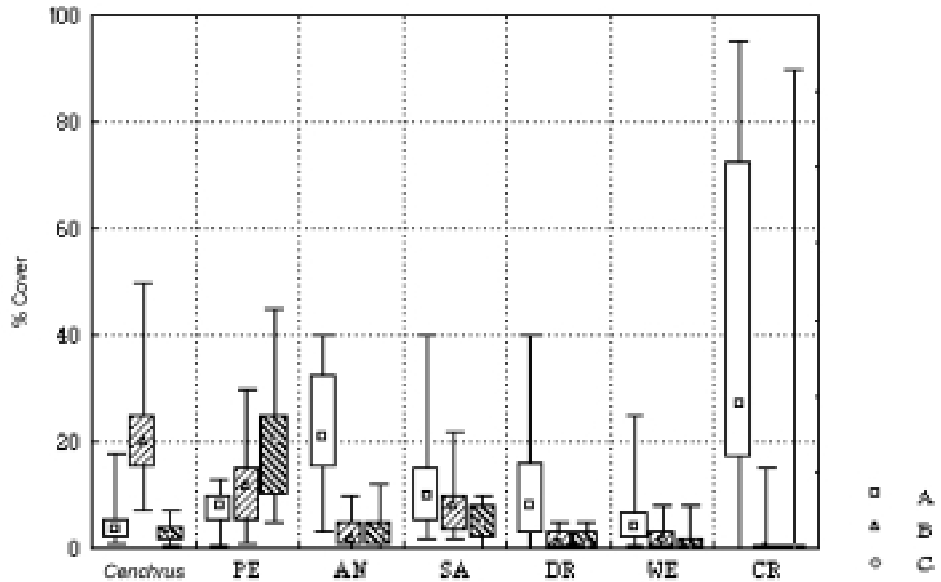

Fig. 5. The percent cover of the *Cenchrus incertus* and the summed cover of the species belonging to the phytosociological groups (PE = perennial open sand grassland specialists, AN = annual open sand grassland specialists, SA = sand grassland specialists, DR = dry grassland specialists, WE = weeds) and cryptogams (CR) in the groups of quadrats distinguished by the cluster analysis (A, B, C, cf. Fig. 4). Box center: median, box: quartiles, whiskers: range. See also Table 2

probably less resistant to invasion. Absence of the two invasives on the abandoned road also supports this hypothesis. Low aboveground cover and relative dominance of either annuals or perennials is unanimously described as pioneer characteristics by the different assumed or described successional pathways in sand grassland dynamics (Magyar 1933, Hargitai 1940, Zsolt 1943, Bagi 1990, Fekete 1992, Margóczi 1993, Biró and Molnár 1998, Bartha 2000). It is problematic, however, to discriminate the fine degrees of "pioneerness" in this habitat because in our site, the Fülöpháza sand dunes, the composition and the structure of the grasslands show marked pioneer characteristics in a wide range of scales as compared to other sand grassland regions in Hungary (Kovács-Láng *et al.* 2000, Gosz *et al.* 2000).

Evaluation of the quadrats in our sample showed low aboveground cover and species composition – whether PE or AN species dominated – that might be characteristic of an early pioneer phase. It is noteworthy that vegetation composition in sites dominated by *Cenchrus* is similar on the road quadrats (where frequent disturbance is evident) and non-road quadrats, which indicates similar response of the vegetation. The only significant difference between the *Cenchrus* dominated and the perennial open sand grassland type quadrats (clusters B and C in Fig. 4) is – besides the dominance of the invasive species – cover of PE species (Fig. 5, Table 2). The low cover of the PE group might entail reduced concurrence, because the members of this species group can be considered as potential competitors as they are medium to large sized plants that share the summer aspect (Kárpáti and Kárpáti 1954) with *Cenchrus*. The comparison with the annual open sand grassland type (cluster A in Fig. 4) indicates differences in three species groups (Fig. 5, Table 2). Of these, AN species are unlikely to be potential competitors as they are mainly small sized vernal species that die back by summer (Kárpáti and Kárpáti 1954, cf. Table 1). On the other hand, medium and large sized DR species like the perennial *Bothriochloa ischaemum* and *Cynodon dactylon*, might concur with *Cenchrus*, though they are present only in part of the quadrats in that cluster (cf. Table 1). The third different group, the cryptogams I do not consider as potential competitors, although thick moss layer might prevent recruitment as discussed above.

As a summary it can be concluded that the above mechanisms separately do not sufficiently explain the distribution pattern of this two species. Nevertheless, when they are put together they describe the present distribution quite well and make testable predictions for further research. It is rational to connect the above hypotheses, as they are not independent in a sense, that different traits (e.g. seed transportation, germination, growth, competitive abilities) of plant species with weedy characteristics are adapted to circumstances that often correlate in disturbed habitats (Baker 1974). A great number of studies that detect association between roads and degree of plant invasion (e.g. Tyser and Worley 1992, Cowie and Werner 1993, Lonsdale and Lane 1994, Wasilowska 1999, Bagi 1997, Molnár 2000, Parendes and Jones 2000) all emphasize two main factors: the role of propagule transport and disturbance of natural vegetation along roads. Neither dispersal nor disturbance is road-specific however, and the same mechanisms can act, though less obviously, in areas not adjacent to roads. It is also noteworthy that the invasive species, *Cleistogenes serotina*, of which spread was found to be associated to roads (Bagi 1997, Molnár 2000), does not seem to be associated to either species of the present study.

The results suggest that the stands of *Ambrosia* and *Cenchrus* are maintained and dispersed by trampling either by tourists, sheep or cars. Trampling is mainly concentrated on the roads, which hold the largest populations, which are thus the main propagule sources but it has similar effects in the more intact area. Without this kind of disturbance they probably pose a minor threat and are likely to disappear from the vegetation at the same time as regeneration, although large seed production and seed longevity allows for maintaining considerable seed bank, and disturbance by wild animals, such as rabbits also favours recruitment of weedy species (Altbäcker 1998). Further dispersal in the intact areas might be prevented by reducing or appropriate timing of grazing, though large stands on the roads together with the seed bank remain continuous threat as sources for population outbursts. It should be mentioned, however, that data of the present study are limited, especially in the case of *Ambrosia*, so the above conclusions should be treated with care. Genetic adaptation to the new environment might also occur, which has been demonstrated in the case of *Cenchrus* (McKinney and Fowler 1991). Long-term examinations in a wider range of sand steppe habitats should be conducted to better understand the role and future impact of these two species.

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