

Immobilization of soil nitrogen as a possible method for the restoration of sandy grassland

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Abstract. Experiments were designed to test the applicability of nitrogen immobilization as a means of accelerating the recovery of an endemic open sandy grassland (Festucetum vaginatae danubiale) on old fields in the Great Hungarian Plain. Effects of various carbon sources (sucrose, starch, cellulose and sawdust) and their combinations in different quantities were studied in laboratory microcosms. Carbon addition decreased nitrogen availability in all cases, the intensity and timing of change being dependent on the type of carbon source applied. The combination of 2 g each of sucrose and polysaccharides (starch, cellulose, sawdust) per kg soil was found to be the most effective, as sucrose decreased available nitrogen content of soil intensively and the polysaccharides maintained the immobilized nitrogen for a longer period. In a follow-up experiment, sucrose and sawdust were selected for field application to test their effectiveness in immobilizing N and accelerating restoration. The field experiment was established to test the importance of abiotic site differences in the immobilization of soil nitrogen. Selected sites were located along an elevation, moisture and productivity gradient. Soil organic matter, microbial biomass-C and decomposition rate varied between sites depending on the elevation gradient. At two sites with lower soil moisture and organic matter levels carbon addition increased microbial activity and nitrogen immobilization significantly.

Keywords: Carbon source; *Festucetum vaginatae*; Hungary; Nitrogen availability; Secondary succession.

Nomenclature: Horváth et al. (1995).

Introduction

Secondary succession on abandoned fields is often slow, and can remain at an intermediate state dominated by weeds for a long period. Weedy abandoned fields are very common in habitats that would otherwise be suitable for endemic, open, sandy grassland (*Festucetum vaginatae danubiale*) on the Great Hungarian Plain. As a consequence of possible admission to the European

Union cessation of agricultural activity in areas of such low productivity will be even more extensive. The regional nature conservation authority (Kiskunság National Park) aims to raise the ecological value of its territories by promoting the restoration of semi-natural communities on abandoned fields.

Numerous factors have the potential to influence the rate of recovery of disturbed lands. Many of them can be readily manipulated in order to hasten or redirect natural succession on disturbed sites. By understanding the mechanisms involved in secondary succession, it may be possible to restore these unique sand grassland habitats.

Changes in soil nutrient status have been shown to influence plant community structure and successional processes (Pigott & Taylor 1964; Tilman 1986, 1987). Plants belonging to different seral stages differ in their responses to resource availability and resource supply ratios (Tilman 1987). Nitrogen availability was found to be a primary mechanism controlling the rate of succession (Carson & Barrett 1988; Klein et al. 1996; McLendon & Redente 1991, 1992a, b; Paschke et al. 1996; Tilman 1984, 1986; Zink & Allen 1998).

Available N is inversely related to the abundance of late-seral dominants in a number of ecosystems. Increased N-availability affects the seral process in semi-arid ecosystems, slowing the replacement of annuals by herbaceous perennials (McLendon & Redente 1991, 1992a, b; Paschke et al. 1996; Trent et al. 1992). Conversely, decreased N-availability is correlated with the replacement of early-seral species by mid-seral species (McLendon & Redente 1991; Paschke et al. 1996; Tilman & Wedin 1991; Wedin & Tilman 1990) and the rate of seral replacement in semi-arid plant communities can be increased by increasing N-limitation (McLendon & Redente 1992a, b; Paschke et al. 1996).

Nitrogen is the only nutrient for which ecosystem cycling is almost exclusively regulated by biological processes (Bobbink et al. 1996). Major chemical transformation of N takes place in the soil and is mainly controlled by the activity of the soil microbial community

(Bolton et al. 1993; Santruckova 1992; Zak et al. 1990). Thus, manipulations of N-availability have to focus on the soil biological system.

Addition of a carbon source to soils leads to increases in microbial biomass and enzyme activity and thus results in rapid N-immobilization under laboratory conditions (Antal et al. 1988; Gulyás & Füleky 1994). Changes in the below-ground microbial community related to successional status and N-availability have also been observed in field studies (Klein et al. 1995, 1996).

Several carbon sources have been found to have positive effects on the rate of succession by stimulating soil microbial activity. The addition of bark and straw was beneficial for the restoration of native shrubs on disturbed lands in California (Zink & Allen 1998). In semi-arid areas of the Western United States sucrose applications resulted in an increased rate of succession (McLendon & Redente 1992a; Paschke et al. 1996)

Experiments were designed to test the applicability of N-immobilization as a means for accelerating recovery of degraded vegetation in a semi-arid grassland in Hungary. An experimental site was chosen which was similar to ones that have been investigated in the western US (McLendon & Redente 1992a, b; Klein et al. 1996).

The objectives of this study were:

- To identify the most effective carbon source addition for immobilizing soil nitrogen in semi-arid sandy grassland in the Great Hungarian Plain.
- 2. To test the importance of abiotic site differences in the effectiveness of N-manipulations.

Site description

The study site is situated in the Kiskunság National Park, Hungary. The Danube-Tisza Mid-Region lies in the warm temperate zone with an annual mean temperature between 10.2 °C and 10.8 °C and annual precipitation of 513 mm with maxima in May and November. The water table in the region has decreased by 2 - 4 m during the last 20 yr, which has resulted in important changes in vegetation composition (Körmöczi 1991).

The Danube-Tisza Region represents an important

source of biodiversity in Hungary because of its unique native plant communities on sand dunes. The sand dunes provide a patchy environment that is reflected by the hierarchical mosaic pattern of the vegetation at different scales (Kovács-Láng et al. 1997, 1998; Kertész & Bartha 1997). This study focused on the community scale, where spatial heterogeneity appears in the scattered pattern of stands of the same association with different species composition. The main types of our study community (Festucetum vaginatae) are determined partly by soil moisture availability (Körmöczi & Balogh 1990) and other environmental constraints (Szujkó-Lacza & Kováts 1993). There is a lot of overlap in the coenological character of these types and stochastic events have an important role in the dynamics of the transitions (Fekete 1992).

Three sites were selected for a field experiment within an abandoned farm at the edge of a strictly protected sand dune area (46°52'88" N; 19°24'55" E). The farm is surrounded by a mosaic of sandy grasslands, Juniperus-Populus forests, black locust plantations and arable fields. Two vegetation references were also selected in the surrounding sandy grassland. Cultivation of the field stopped in 1991 at one part of the farm and in 1995 at the other part. The sites were established along an elevation gradient: the site at the lowest altitude was probably a meadow community (Meadow = M), the second is located in a depression (Depression = D) and the third site was on top of a dune (Hummock = H). Abiotic conditions of the field sites are summarized in Table 1. A moisture and productivity gradient was evident from the driest and low productive (H) through an intermediate (D) to the least dry and more productive (M) area. Measured vegetative cover supports this trend of abiotic conditions with the mean total cover of vascular plants of 28, 42 and 39% for H-, D- and M-sites, respectively. The highest soil surface temperature (site H) is evidently the result of topography, low organic matter content and sparse vegetation.

The vegetation of the study sites and the reference grassland were characterized by life strategy variables (annual/perennial ratio and naturalness) and ecological indicator values of species (Table 2). There were important differences between the vegetation of the

Table 1. Abiotic variables of the study sites measured during the growing season of 1998.

Site Meadow (M)	Elevation (m a.s.l.)	Age of old- field (yr)	Mean coarse sand in 0 - 30 cm (%)	Depth to finer layer (cm)	Soil organic- C (%)	Soil moisture content (%) in June (0 - 10 cm)	Soil temp. in Oct. (°C)	
	105	8	56.0	140	0.44	3.3	21	
Depression (D)	106	4	46.3	70	0.26	7.3	20	
Hummock (H)	107	4	55.3	> 200	0.12	4.2	23	
Grassland	108		44.7	180	> 0.5	5.0	20	

Table 2. Relative abundance of species of the dominant categories in the vegetation of study sites and an adjacent reference grasslands. W = soil moisture requirement (12-category scale of Borhidi in Horváth et al. 1995): 1 = extremely dry habitats; 2 = xero-indicators; 3 = xero-tolerants; 5 = semi-humid habitats. N = mineral nitrogen requirement (a 9-category scale): 1 = extremely poor; 2 = very poor; 4 = sub-mesotrophic; 5 = mesotrophic; 7 = N-rich habitat indicators. The relative abundance of the dominant nature conservation types of Simon (in Horváth et al. 1995) reflects the 'naturalness' of the vegetation: disturbance tolerant species (DT), weeds (We), natural pioneers (NP), natural community constituents (NC) and protected species (P).

Sites Meadow (M)	Ann./ perenn. ratio	Dominant W-category	Dominant N-category	Dominant nat. conserv. type		
	0.79	5 (32.6 %) 2 (24.5 %)	5 (34.9 %) 7 (21.0 %)	We (53.4 %)		
Depression (D)	6.35	2 (46.5 %)	1 (34.8 %) 4 (23.4 %)	NP (46.3 %) We (41.0 %)		
Hummock (H)	0.29	3 (79.6 %)	5 (61.5 %)	DT (61.5 %)		
Grassland (G)	0.06	2 (65.7 %) 1 (20.0 %)	2 (49.9 %) 1 (35.0 %)	NC (36.2 %) P (26.7 %)		

reference grassland and the study sites, and also among the study sites. Community constituents and many endemic and protected species characterize the grassland. Annuals dominate the Depression site and perennials dominate the native Grassland but the eight year old Meadow had vegetative cover with a balanced ratio of annuals and perennials. These findings support the general observation that old-fields are dominated by nitrophilous annual weeds and the natural community by perennials. The vegetation of the Hummock does not fit this rule; it has a relatively dense perennial cover due to the dominance of Cynodon dactylon (60%), a C4 type clonal grass, which had a dominant influence on the data. The moisture requirement categories (W) show the effect of the soil moisture gradient (Table 2). Investigations of the surrounding area show that the native vegetation of the experimental locations would be a particular type of sandy grassland community assigned to the Festucetum vaginatae. These are: M = subassociation salicetum rosmarinifoliae, D = subass. stipetosum or typicum and H = subass. fumanetosum (Borhidi 1956; Soó 1957).

Methods

The experiments were designed to represent the heterogeneity of the region at the community scale and to find an applicable low input restoration methodology, which could be applied widely in nature conservation. Three experiments were conducted, the concept of the experimental design is indicated below.

1	2	3		
Dosage Lab	Efficiency Lab	Field		
Experiment	Experiment	Experiment		
Variables studied:	Variables studied:	Variables studied:		
C-sources and	selected C-source	site heterogeneity		
doses	selected doses	C-addition - control		
N-saturated	N-limited			

Dosage lab experiment

The experiment was designed to test N-immobilization efficiency of different carbon sources in laboratory microcosms. Carbon sources (sucrose, starch, cellulose and sawdust) and their combinations were applied at 1, 2, 3 and 4 g/kg soil. Soil samples were incubated at a moisture level of 8 vol. % at 22 °C. The available N of the soil samples was originally low (3 - 8 mg/kg soil), mineral N (as KNO₃) was added to the samples (50 mg N/kg soil) to achieve more pronounced differences in the effects of various carbon sources. Nitrate-N and ammonium-N content of the soil was measured during a 3-month period. Soil moisture was checked and adjusted every other day to keep it constant.

Efficiency lab experiment

The most effective carbon source combination was sucrose plus sawdust (2 g C/kg soil each) and this was used in the second experiment to simulate field conditions. Soil moisture level and temperature were the same as in the first experiment. Nitrate-N and ammonium-N content of the soil was measured during a 3-month period. Samples taken from the upper 10 cm of soil at the sites selected for the field experiment were used for both laboratory experiments (500 g soil/treatment with three replications).

Field experiments

Sucrose and sawdust were selected for the field experiment, as the most easily accessible of the tested carbon sources. The field experiment commenced in 1998. Six treatment and six control plots (10 m × 10 m each) were placed randomly at each site (M, D and H). Based on the laboratory studies, 700 kg carbon·ha⁻¹· yr⁻¹ was spread by hand on treatment plots as sucrose (1300 kg·ha⁻¹·yr⁻¹) and sawdust (300 kg·ha⁻¹·yr⁻¹). Sucrose was applied four times during the growing season while sawdust was spread only at the first treatment.

1998	16 April	29 April	27 May	23 June	29 June	15 July	1 Sept.	29 Sept.	14 Oct.
Treatment	Sucrose (300 kg/ha)	Sucrose (300 kg/ha)	73	Sucrose (300 kg/ha)	ži.		E.		ħ)
	Sawdust (300 kg/ha)		8		•	(-)		Sucrose (400 kg/ha)	56
Soil sampling	Moisture Available N	Moisture Available -N	Moisture available-N	20	Moisture Available-N	30	5		20
	Cmic		Cmic	E.	Cmic	95U ₃₀	5	2	53
Decomposition test	1st exp	82	2 nd exp	2	1.0	3rd exp	2	12	48
	(41 days)	32	(49 days)	12	1.2	(56 days)	2	12	
Surface temperature	=0	ie.	=		(*)	G=	*	19	X
Vegetation sampling	T.	25	Species cover estimation	i _e	15:	55	Species cover estimation	ê	30

Soil samples were taken from 14 randomly selected points at each plot from the upper 10 cm of the soil. For the determination of basic soil characteristics, core samples were taken from different depths (0 - 2 m) in 20 cm steps. Treatments and sampling are summarized in Table 3. Soil organic C was measured by wet digestion (Walkley & Black 1934). Moisture content was determined gravimetrically after drying at 105 °C. Soil-available N (ammonium and nitrate) was analysed using the steam distillation method (Bremner 1965), Microbial-biomass C was determined using the chloroform fumigation extraction method (Vance et al. 1987). To test decomposition rates, cellulose mesh bags (mesh size = 1 mm) containing 2.5 g cellulose each were placed in the soil at a depth of 5 - 8 cm and were replaced periodically. They were exposed for 41 to 56 days (Table 3). Surface temperature was measured by a Teletemp Corp. AG 42 type thermometer on 14 October. Statistical analyses were performed by one-way ANOVA.

Vegetation was sampled in three permanent quadrats

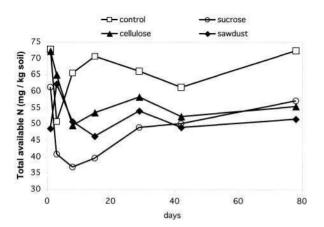


Fig. 1. Dosage Lab Experiment. The effect of C-addition on available N during incubation with 50 mg/kg nitrate-N (KNO₃). The amount of C-sources was 2g/kg soil. Significant difference between control and treatments at P < 0.05 are indicated.

(2 m×2 m) in each plot. In case of the reference (natural) site, 18 permanent quadrats were established at each location. The cover of vascular species was determined twice in 1998. Ecological indicator values of species were established according to Horváth et al. (1995).

Results

Laboratory experiments

Carbon addition (C) in the Dosage Lab Experiment resulted in a significant decrease of available N for all treatments (Fig. 1). The intensity and duration of changes were dependent on the C-source type. Available N decreased rapidly in the first 10 days, but increased afterwards. Sucrose produced the most intensive effect during the first three days, whereas sawdust kept the nitrogen immobilized for the longest period, probably due to its slow decomposition. The microcellular-structured cel-

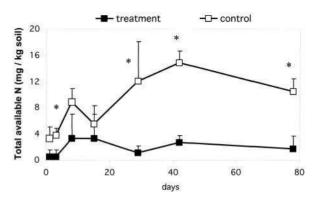


Fig. 2. Efficiency Lab Experiment. Changes of available N during incubation without mineral-N addition. Treatment was addition of sucrose plus sawdust (2 g/kg soil each). Confidence intervals at 95% probability and significance at P < 0.05 are indicated.

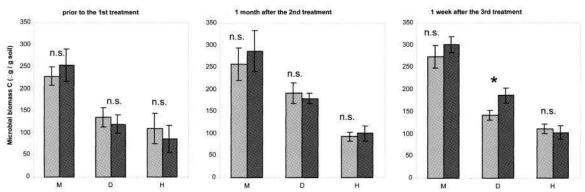


Fig. 3. Changes in mean microbial biomass-C in the field experiment for the three sampled periods. Light-grey bars indicate average values measured in control plots, dark-grey bars represent treated plots. M = Meadow; D = Depression; H = Hummock. Confidence intervals at 95% probability and significance at P < 0.05 are indicated.

lulose-bead was slightly less effective than sawdust due to lower surface contact with soil particles. The dose of added C had a limited influence on the N-immobilization rate, as the effects of carbon addition were significant even at the lowest dose (1 g C/kg soil). The combination of sucrose and sawdust at an intermediate dose (2 g/kg soil of each C-source) was selected for the Efficiency Lab Experiment.

The results of the Efficiency Lab Experiment supported the efficacy of C-addition in N-immobilization under field conditions (3 - 8 mg N/kg soil) (Fig. 2). After ca. 15 days of incubation N-mineralization caused a significant increase (P < 0.05) in total available N up to 15 mg/kg soil in the control samples, while the C-addition treatments resulted in continuous low N-availability throughout the experiment. Sawdust was chosen for the follow-up field application, because it was the most easily available in practice.

Field experiment

Microbial biomass-C (Cmic) showed significant (P < 0.05) differences between sites (Table 4), with the highest values at M and the lowest at H (means of 269 and 108 µg/g soil, respectively). These results follow the pattern of the abiotic conditions (Table 1). Elevation, soil moisture and organic matter gradient from M to H is

the likely cause of the observed decrease in Cmic along this gradient. No significant effect of C-addition was found on Cmic (179 and 184 μ g/g soil for control and treatment plots), except for the third sampling at D (Fig. 3).

Decomposition rates of cellulose (Fig. 4) reflected the differences in the Cmic between the sites (the lower the biomass, the less decomposition of cellulose): with mean values of 36.7, 25 and 10.6 mg/g cellulose per day for M, D and H, respectively. The effect of treatment was indicated by a higher residue of cellulose in most cases, except for H, as a consequence of the presence of a more easily available carbon source that decreased the N-availability.

Sites also differed in N-availability (Fig. 5 and Table 4), M and D had similar values of total available N (6.1 and 6.0 mg N/kg soil respectively), but the proportion of ammonium-N to nitrate-N was 3.7:2.4 at M and 4.1:1.8 at D. Nitrogen availability was significantly lower at H (4.6 mg N/kg soil), and the ratio of ammonium-N to nitrate-N (3.5:1.1) was similar to that at D.

Available N was relatively high in the spring before the treatments (6.2 mg/kg soil), and probably resulted from over-winter decomposition and mineralization. Ammonium-N was responsible for detected changes in available N-content of soil, except for the sampling at the end of June when both forms of inorganic N increased. Carbon addition resulted in a significant de-

Table 4. Mean values of selected variables and the significance of their relationships. Means followed by the same letter are not statistically significant (P < 0.05).

Variables	Date					Site	Treatment		
	April 16	April 29	May 27	June 29	Meadow	Depression	Hummock	Control	TREATED
No. of observations	36	36	36	36	48	48	48	72	72
Soil moisture (w%)	5.4a	3.9b	5.6a	4.2b	5.6a	5.2a	3.4b	4.7a	4.8a
Cmic(mg/g soil)	175a	- 2	183a	187a	269a	167b	108c	179a	184a
NH ₄ -N mg/kg soil	5.1a	2.9b	3.1b	4.0c	3.7a	4.1a	3.5a	3.8a	3.8a
NO3-N mg/kg soil	1.1a	1.2a	1.4a	3.4b	2.4a	1.8a	1.1b	2.3a	1.2b
NH ₄ +NO ₃ -N mg/kg soil	6.2a	4.2a	4.5a	7.3b	6.1a	6.0a	4.6b	6.1a	5.0b

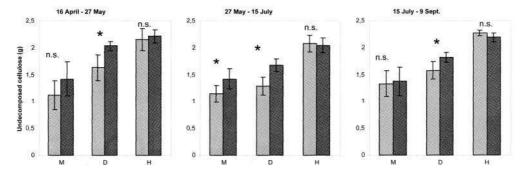


Fig. 4. Cellulose residues in the decomposition test in the field experiment for the three sampled periods. Stipulated bars indicate average values measured in control plots, cross-hatched bars represent treated plots. M = Meadow; D = Depression; H = Hummock. Confidence intervals at 95% probability and significance at P < 0.05 are indicated.

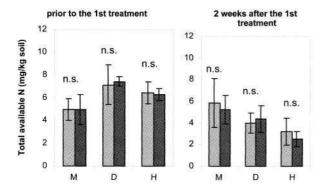
crease in N-availability due to the changes in nitrate-N for the entire study (Table 4). The influence of treatment was more pronounced at the D and H sites (Fig. 5) which had lower organic C (Table 1). At the M site, the highest Cmic (Fig. 3), organic C and moisture resulted in high rates of decomposition of cellulose and greater amount of available N both in control and treatment plots.

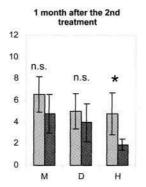
Discussion

Several studies have shown that the addition of carbon to soil increases microbial activity and, as a result, nitrogen becomes immobilized (Klein et al. 1996; Paschke et al. 1996; Zink & Allen 1998; Mary et al. 1996). This manipulation with microbes is important in restoration activities (Biro et al. 1993; Haselwandter 1996) when slow release of available N provides competitive advantage for native perennials over annuals with a rapid N-uptake (McLendon & Redente 1992a, b;

Whitford et al. 1988).

The present study made the first steps towards the determination of a restoration methodology to be used in the sandy region of Hungary, which can be adapted to the different environmental constrains occurring in the area. The laboratory experiments were conducted to identify the most effective and cost-effective carbon source to reduce nitrogen availability in the soil. The selection made was supported during the field trials. The results demonstrated that carbon addition is applicable under the local circumstances for nitrogen immobilization although it should be noted that abiotic and biotic conditions can influence the efficacy of the method. A significant decrease in N-availability was found after successive treatments, while an increase in microbial biomass was only observed in a few cases (Fig. 3). Decomposition rate decreased in treated plots at site D, this could be explained by lower microbial activity in N-limited conditions (Fig. 4). As a result of C-addition, there was a significant decrease in soil nitrate-N content this variable





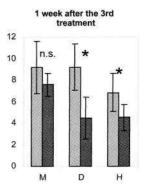


Fig. 5. Changes of available N in the soil of the control and treated plots in the field experiment. Stipulated bars indicate average values measured in control plots, cross-hatched bars represent treated plots. M = Meadow; D = Depression; H = Hummock. Confidence intervals at 95% probability and significance at P < 0.05 are indicated.

appears to be the most sensitive to carbon addition.

The influence of C-addition was more pronounced where the organic matter content and soil moisture were lowest. It is assumed that organic matter functions as a main source of nitrogen. These features caused rapid mineralization and immobilization activity in a short time alternating with longer microbiologically inactive periods. Mary et al. (1996) found a correlation between the quantity of carbon addition and the nitrogen immobilization rate in laboratory experiments. The maximum net nitrogen immobilized was between 61 mg N/g C (sucrose) and 27 mg N/g C (maize, straw). In our laboratory experiments sucrose and sawdust addition (2 g/kg soil each) resulted in 34.5 and 14 mg N/g C maximum net nitrogen immobilized. According to these results, a larger dose of carbon source would be needed to significantly effect N-availability in soils with a higher organic matter content.

Temporal dynamics of N-cycling seemed to correspond with vegetation development. Ephemeral spring annuals and perennials influence N-dynamics by early, intensive N-uptake which stops by late May when they senesce and allow available N to rise (Lhotsky 1998). Species with high growth rates in spring were detected at each site: *Poa bulbosa, Bromus tectorum* and *Secale sylvestre* (sum of relative abundances 13.8%) at M, *B. tectorum* and *S. sylvestre* (14.2%) at D and H (16%).

The next step in the determination of a suitable restoration methodology will be to evaluate the response of vegetation to carbon addition over several years. A growth response of perennial native plants was observed after three years of treatment in a coastal sage scrub habitat (Zink & Allen 1998). Similarly, compositional differences between control and carbon addition plots were detectable after three years on short grass steppe in Colorado, USA (Paschke et al. 1996).

The age of old-fields has an important influence on restoration results because a short time since abandonment reduces the chance of establishment of perennial (mainly clonal) weeds which can block the succession process (Oborny & Bartha 1995).

It is concluded that soil organic matter and moisture content must be considered when carbon addition is to be used as a restoration tool. Monitoring of the available N in the soil is an appropriate method to follow the efficiency of the treatments under field conditions.

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References

- Antal, M., Anton, A., Németh, T. & Gulyás, F. 1988. Effect of C-sources and urea on the available N content and urease activity of a calcareous sandy soil. *Zentralbl. Microbiol*. 143: 317-321.
- Biro, B., Vörös, I., Köves-Péchy, K. & Szegi, J. 1993. Symbiont effect of *Rhizobium* bacteria and vesicular arbuscular mycorrhizal fungi on Pisum sativum in recultivated mine spoils. *Geomicrobiol. J.* 11: 275-284.
- Bobbink, R., Hornung, M. & Roelofs, J.G.M. 1995. Empirical nitrogen critical loads for natural and semi-natural ecosystems. In: Convention on transboundary air pollution, Manual on methodologies mapping critical loads. 12th Task Force Meeting, Budapest. 22 March 1996.
- Bolton, H., Smith, J.L. & Link, S.O. 1993. Soil microbial biomass and activity of a disturbed and undisturbed shrubsteppe ecosystem. Soil Biol. Biochem. 25: 545-552.
- Borhidi, A. 1956. Die Steppen und Wiesen im Sandgebiet der Kleinen Ungarischen Tiefebene. Acta Bot. Hung. 2: 241-274.
- Bremner, J.M. 1965. Inorganic forms of nitrogen. In: Black, C.A. et al. (eds.) Methods of soil analysis, Part 2. Agronomy 9: 1179-1237. American Society of Agronomy, Madison, WI
- Carson, W.P. & Barrett, G.W. 1988. Succession in old-field plant communities: effects of contrasting types of nutrient enrichment. *Ecology* 69: 984-994.
- Fekete, G. 1992. The holistic view of succession reconsidered. Coenoses 7: 21-30.
- Gulyás, F. & Füleky, Gy. 1994. C- and N-transformation dynamics in the soil. *Bodenkultur* 45: 313-318.
- Haselwandter, K. 1996. Mycorrhiza, soil microorganisms and restoration ecology. In: First International Conference on Restoration Ecology and Sustainable Management, Zurich.
- Horváth, F., Dobolyi, Z.K., Morschhauser, T., Lőkös, L., Karas, L. & Szerdahelyi, T. 1995. *Flora database*. Vácrátót.
- Kertész, M. & Bartha, S. 1997. Spatial organization of open sand grasslands in Hungary. In: Annual Meeting of the Ecological Society of America, Abstracts, p. 268. Albuequerque, NM.
- Klein, D.A., McLendon, T., Paschke, M.W. & Redente, E.F. 1995. Saprophytic fungal-bacterial biomass variations in successional communities of a semi-arid steppe ecosystem. *Biol. Fert. Soils* 19: 253-256.
- Klein, D.A., McLendon, T., Paschke, M.W. & Redente, E.F. 1996. Nitrogen availability and fungal-bacterial responses in successional semi-arid steppe soils. *Arid Soil Res. Rehabil*. 10: 321-332.
- Kovács-Láng, E., Fekete, G. & Molnár, Zs. 1998. Pattern, process and scale: long-term ecological research in the Kiskunság. In: Fekete, G. (ed.) Advances in community ecology, pp. 209-224. Scientia, Budapest. (In Hungarian.)
- Kovács-Láng, E., Kröel-Dulay, Gy., Kertész, M., Mika, J., Rédei, T., Rajkai, K., Hahn, I. & Bartha, S. 1997. Changes in the species composition and structure of sand grasslands along a semiaridity gradient. Annual Meeting of the Ecological Society of America, Abstracts, p. 271. Albuequerque, NM.
- Körmöczi, L. 1991. Drought-induced changes in a sandy grass-

- land complex in the Great Hungarian Plain. *Acta Biol. Szeged* 37: 63-74.
- Körmöczi, L. & Balogh, A. 1990. The analyis of pattern change in a Hungarian sandy grassland. In: Krahulec, F., Agnew, A.D.Q., Agnew, S. & Willems, J.A. (eds.) Spatial processes in plant communities, pp. 49-58. Academia, Prague.
- Lhotsky, B. 1998. Spatial and temporal dynamics of the biomass of some sand grassland species in Hungary. Ph.D. Thesis, L. Eötvös University, Budapest. (In Hungarian.)
- Mary, B., Recous, S., Darwis, D. & Robin, D. 1996. Interactions between decomposition of plant residues and nitrogen cycling in soils. *Plant Soil* 181: 71-82.
- McLendon, T. & Redente, E.F. 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. *Ecology* 72: 2016-2024.
- McLendon, T. & Redente, E.F. 1992a. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. *Oecologia* (*Berl.*) 91: 312-317.
- McLendon, T. & Redente, E.F. 1992b. Role of nitrogen availability in the transition from annual-dominated to perennial-dominated seral communities. In: S.B. Monson & S.G. Kitchen (eds.) Proceedings of the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands. U.S. Forest Service, Intermountain Research Station. Gen. Tech. Rep. INT-GTR-313, pp. 352-362. Ogden, UT.
- Norman, J. M., Garcia, R. & Verma, S. B. 1992. Soil surface CO₂ fluxes and the carbon budget of a grassland. *J. Geophys. Bot.* 97: 18845-18853.
- Oborny, B. & Bartha, S. 1995. Clonality in plant communities: an overview. In: Oborny B. & Podani J. (eds.) Clonality in plant communities. Abstr. Bot. 19: 115-127.
- Paschke, M.W., McLendon, T., Klein, D.A. & Redente, E.F. 1996. Effects of nitrogen availability on plant and soil communities during secondary succession on a shortgrass steppe. *Bull. Ecol. Soc. Am.* 77: 342.
- Piggott, C.D. & Taylor, K. 1964. The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil. J. Ecol. Suppl. 52: 175-185.
- Santruckova, H. 1992. Microbial biomass, activity and respira-

- tion in relation to secondary succession. *Pedobiologia* 36: 341-350.
- Soó, R. 1957. Conspectus des groupements végétaux dans les Bassins Carpathiques. Acta Bot. Acad. Sci. Hung. 3: 43-64.
- Szujkó-Lacza, J. & Kováts, D. (eds.) 1993. The flora of the Kiskunság National Park I: The flowering plants. Magyar Természettudományi Múzeum, Budapest.
- Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. *Ecology* 65: 1445-1453.
- Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. *Ecology* 67: 555-563.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.* 57: 189-214.
- Tilman, D. & Wedin, D.A. 1991. Dynamics of nitrogen competition between successional grasses. *Ecology* 72: 685-700.
- Trent, J.D., Young, J.A. & Blank, R.R. 1992. Potential role of soil microorganisms in medusahead invasion. In: Monson, S.B. & Kitchen, S.G. (eds.) Proc. Symp. Ecology, Management, and Restoration of Intermountain Annual Rangelands. U.S. Forest Service, Intermountain Research Station. Gen. Tech. Rep. INT-GTR-31, pp.140-142. Ogden, UT.
- Vance, E.D., Brookes, P.C. & Jenkinson, D.S. 1987. An extraction method for measuring soil microbial biomass-C. Soil Biol. Biochem. 19: 703-707.
- Walkley, A. & Black, I.A. 1934. An examination of the Degtjareff method for determining soil organic matter and a proprosed modification of the chromic acid titration method. Soil Sci. 37: 29-38.
- Wedin, D.A. & Tilman, D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia (Berl.)* 84: 433-441.
- Whitford, W.G., Aldon, E.F., Freckman, D.W., Steinberger, Y. & Parker, L.W. 1988. Effects of organic amendments on soil biota on a degraded rangeland. J. Range Manage. 42: 56-60.
- Zak, D.R., Grigal, D.F., Gleeson, S. & Tilman, D. 1990. Carbon and nitrogen cycling during old-field succession: Constraints on plant and microbial biomass. *Biogeochem*. 11: 111-129.
- Zink, T.A. & Allen, M.F. 1998. The effects of organic amendments on the restoration of a disturbed coastal sage scrub habitat. *Restor. Ecol.* 6: 52-58.

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