

SMALL-SCALE SPATIOTEMPORAL DYNAMICS OF PLANT COVER DURING THE INITIAL PHASE OF PRIMARY SUCCESSION IN AN ABANDONED ORE-WASHERY SEDIMENTATION BASIN

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Abstract

Permanent plots and repeated mapping of the initial primary succession in the abandoned sedimentation basin in Chvaletice (E Bohemia, Czech Republic) demonstrated plant cover dynamics of colonizing species living in an extreme environment. The analysis used autocorrelation and cross-correlation (Moran's I) over lags in space and time (13 years long period). Short-lived and long-lived (clonal) plants exhibit complementary small-scale dynamics characterized by clumping in space. Variation among plants is increased by pioneer woody species with different features in their bionomy and a different tolerance towards stress and disturbance. After more than one decade of complicated development of the vegetation, the following stand components alternate their dominant position, depending on the actual year's conditions: *Vicia tetrasperma* (annual), *Calamagrostis epigejos* and *Phragmites australis* (clonal grasses), *Betula pendula* and *Populus tremula* (trees, clonal – the second one).

Keywords

Primary succession, ore-washery sedimentation basin, fine-scale monitoring, colonization dynamics, tree seedlings, clonal plants, annuals, herbs, spatial/temporal autocorrelations, spatial/temporal cross-correlations.

Introduction

Colonization of unfavourable substrata, such as human-made deposits, largely depends on the ability of plant individuals to establish locally; these colonized

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patches further serve both as sources of diaspores and centres for clonal growth to unoccupied sites. Field observations suggest that any microscale environmental fluctuation near the deposit surface from year to year could slow down or divert the successional process.

In the youngest successional line, there are species of different growth forms coexisting together. There are plants of both unitary individuals (*Vicia tetrasperma*, *Betula pendula* and occasionally *Populus tremula* seedlings) and parts of individuals (ramets) and/or polycormones (*Calamagrostis epigejos*, *Phragmites australis*, occasionally *P. tremula*). Apparently, the plant assemblage is composed of species differing in life strategy and ecology; this is partly due to a sequence of different environmental episodes: abandoned bottom of the former sedimentation pond is the source of *Ph. australis* and *Salix* sp. div. (Kovář 1979), surrounding ruderal stands on the pyrite surface are the source of *C. epigejos*, *B. pendula* and *P. tremula* (Dostál 1997). Surface fire and dispersal by ants contribute to the spread of *V. tetrasperma* (Štefánek 2004; Jarešová, Kovář 2004). Spatial growth dynamics of each of these ecologically dissimilar species is likely to differ, with important consequences for the colonization dynamics and succession rate of the community.

Examining the plant cover dynamics of colonizing species living in extreme environment helps to identify space-encroachment strategies that plants use to cope with temporal and spatial changes at the site (Urbanska 1997; Willems, Bobbink 1990). Permanent plots with a small-scale monitoring system were used to study the initial primary succession in the abandoned sedimentation basin in Chvaletice (E Bohemia, Czech Republic; see Kovář 1999). In the present study, we used repeated mapping of the same area and subsequent spatial statistics to identify how important are fine-scale colonization dynamics, and how individual species differ in the spatial patterns of their growth.

Methods

In 1986, nine 1 × 1 m permanent plots were established in the unreclaimed plateau of the abandoned sedimentation basin in Chvaletice, to follow plant cover dynamics in the youngest successional line. The stand was structurally very simple, dominated by the clonal grass *Calamagrostis epigejos* with the presence of sparse tree seedlings (*Betula pendula*, *Populus tremula*, *Salix* sp. div.), a stress-tolerant littoral macrophyte *Phragmites australis* and an annual legume *Vicia tetrasperma*. The substrate surface was overgrown with cryptogams and herbs (tree seedlings appeared but disappeared later). The plots were recorded annually (end of June) from 1986 to 1998 (13 years). The presence of all plants were recorded in 5 × 5 cm squares into which the 1 × 1 m plots were subdivided.

Data analysis

Spatial autocorrelation was calculated using Moran's I (Upton, Fingleton 1985). For single-species data, both spatial autocorrelations (up to the lag of 2 cells) and temporal correlations (up to the lag of 9 years) were calculated. Approximate significance of the spatial correlation was determined by full randomisation of the grid data (200 randomisations); a significance threshold of 0.05 was used. Small-scale cross-correlations (at the level of individual 5×5 cm squares) were also measured by means of Moran's I; their approximate significance was assessed by means of the rotational/reflexion/positional shift of one grid (Palmer, van der Maarel 1995); individual grids were kept separate in these randomisations.

Results and discussion

Spatial relationships

Spatial correlation of the main species with *Calamagrostis epigejos* in the abandoned sedimentation ore-washery material (calculated over the whole data-set of 13 years) indicate generally negative, albeit weak, relationships of *Calamagrostis* with herbs (*Phragmites australis*, *Vicia tetrasperma*) and with *Populus tremula*. These plants tend not to occur in the tussocks of *Calamagrostis*. In contrast, the other woody species (in particular, *Salix* sp. div., to a lesser degree *Betula pendula*) show a positive correlation with *Calamagrostis* (Fig. 1), indicating perhaps a sheltering effect of the grass on their seedlings. Succession on the deposited raw material starts from perennial grasses (*C. epigejos*, *Ph. australis*); small seedlings of all the plants including annuals rarely survive episodes of surface overheating (Hroudová, Zákavský 2004) and may benefit from sheltering by established plants of *Calamagrostis*. Also, seedlings of woody species (*B. pendula*, *P. tremula*, *Salix* sp. div., occasionally *Populus alba*, *P. nigra* or *Pinus sylvestris*) may even die under the stress. The semi-open stand with dominant grasses resists colonization by shrubs and trees for a longer time, especially in this type of nutrient-poor soil (Rebele 1992). In respect to discussions about the character of succession on anthropogenic substrates (primary vs. secondary, e.g., Miles 1979; Pfadenhauer *et al.* 1986), the facts mentioned above show that the process of primary succession is important in this case.

The spatial pattern of individual species results from their ways of dispersal, growth forms and strategies of space occupation (e.g., Malkinson 2003). Spatial autocorrelations (Fig. 2) show differences when the nearest (lag = 1) and the next nearest (lag = 2) cells are calculated (Herben *et al.* 1995). In the current data, *V. tetrasperma* (an herb) and *B. pendula* (a tree) are plants with very low spatial autocorrelation even over small lags; this is due to their largely generative

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type of reproduction with no clonal growth. In contrast, the grasses *C. epigejos* and *Ph. australis*, with higher values of autocorrelation, form more compact aboveground structures. Clonal woody species *Populus tremula* and *Salix* sp. div are somewhere in the middle; they tend to be slightly more aggregated in space than *Betula* and *Vicia*, but with much lower intensity than the clonal grasses.

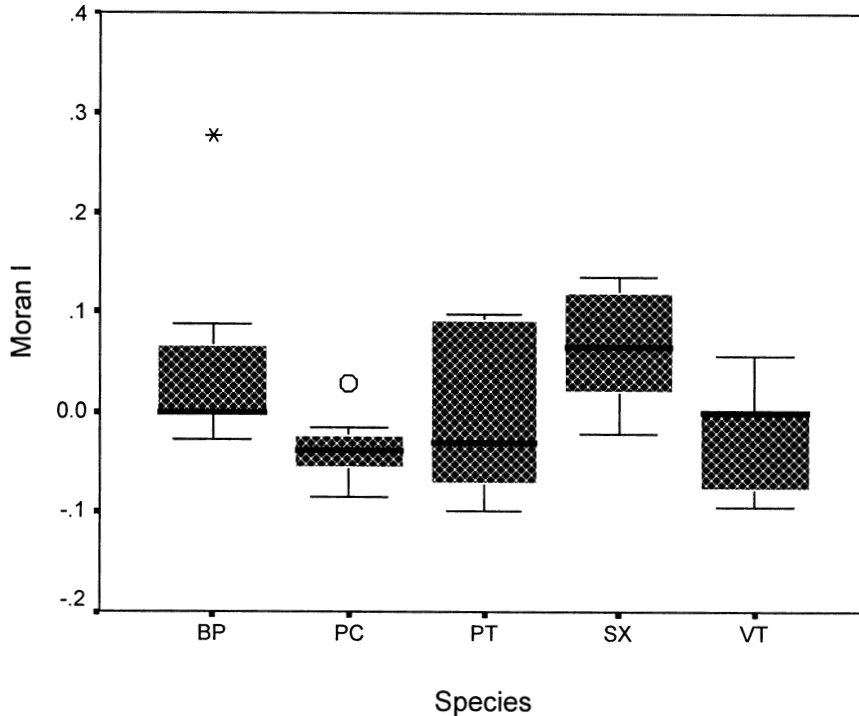


Fig. 1: Correlation of the other species with *Calamagrostis epigejos* using data of cells 5×5 cm (BP – *Betula pendula*, PT – *Populus tremula*, SX – *Salix* sp. div., PC – *Phragmites australis*, VT – *Vicia tetrasperma*).

Temporal relationships

Seedling recruitment of *Calamagrostis epigejos* is generally infrequent in industrial substrates (Lehman 1997). This is dependent on the optimal course of the spring meteorological regime and because of its prevailing form of its propagation, consisting of creation of a number of ramets (Bryndová, Kovář 2004). The species is capable of reproduction on sites polluted by heavy metals or by sulphur, where most other plants are eliminated (Rebele 1996). A common way of spread is multiplication of shoots: the stronger the stress (e.g., salinity, overheating of the soil surface or shortage of water), the higher the density of ramets and the slower the growth rate, as seen in the ore-washery deposit compared

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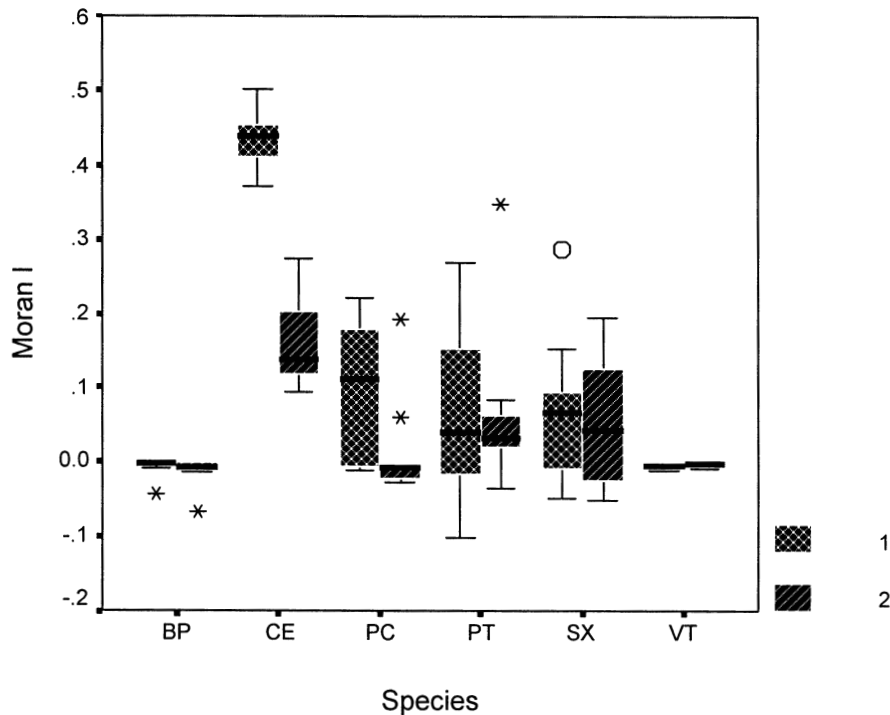


Fig. 2: Spatial autocorrelations of the all species present (lag = 1 and lag = 2) using data of cells 5×5 cm (BP – *Betula pendula*, CE – *Calamagrostis epigejos*, PT – *Populus tremula*, SX – *Salix* sp. div., PC – *Phragmites australis*, VT – *Vicia tetrasperma*).

with the ash-deposit (Kovář 1999). Patterns of temporal autocorrelations widely differ between the species, indicating very different patterns in occupation of space (Fig. 3). Most species, (e.g., *Phragmites australis*, *Salix* sp. div. and *Betula pendula*) tend to occupy a site for a few years (temporal autocorrelation is positive over 3 years for *Phragmites* and *Salix* and over 4 years for *Betula*) and then disappear. In these species, the autocorrelation is never negative, indicating that once-occupied sites are not avoided by newly establishing individuals. This contrasts with *Populus tremula* and *C. epigejos*. These species differ in their spatial persistence (it is very high in *Populus* where the autocorrelation is positive up to a lag = 10, and weaker in *Calamagrostis*), but turn negative at large temporal lags, indicating that once-occupied sites are less likely to be colonized by newly establishing individuals than sites that have never been occupied. A moderate increase in the overall trend may be seen after the fire in 1994 (Štefánek 2004) when most of the tree species (in the form of growing seedlings) were destroyed and the released nutrients supported plant growth. The occurrence of the annual plant *Vicia tetrasperma* was random both in time and space (absent before the 1994 fire). Also, the presence of the clonal common reed

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(*Ph. australis*) was sporadic and random in spite of the early starting point where a clump of ramets was present before dying later. A good example of different ecological behaviour is provided by comparing two woody plants, the clonal tree *P. tremula* and the non-clonal one *B. pendula*. The decreasing temporal autocorrelation of *P. tremula* can be explained as a result of thinning of young seedlings, which was slightly compensated for later by rejuvenation from underground tillers of the surviving individuals. By this way, a relatively dense and homogeneous aspen stand, of shoot height about 0.5–1 m, was formed prior to the mid-1990s. This could be (together with similar conditions in the herb layer, dominated by the grass *C. epigejos*) a supporting factor for the easy rise of the midsummer fire in 1994, due to accumulation of flammable plant biomass and extreme temperatures at the soil surface (Štefánek 2004).

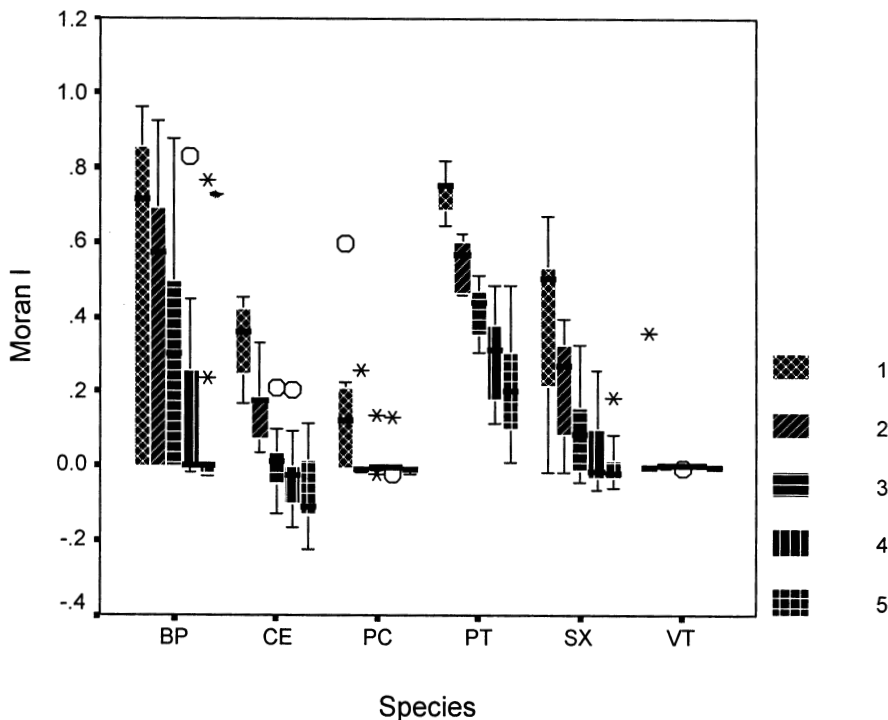


Fig. 3: Temporal autocorrelations of the all species present (lag = 1 ... lag = 5) using data of cells 5 × 5 cm (BP – *Betula pendula*, CE – *Calamagrostis epigejos*, PT – *Populus tremula*, SX – *Salix* sp. div., PC – *Phragmites australis*, VT – *Vicia tetrasperma*).

The distribution of *B. pendula* was similar at the beginning of the monitored succession, however its ability to substitute aboveground biomass after exclusion of part of the individuals is strongly limited due to its non-clonal nature. This was probably one of the reasons why the proportion of young trunks after the

fire in 1994 rapidly shifted towards aspen (*P. tremula*), in addition to the effective use of released nutrients by its developing network system of subsurface tillers. The behaviour of willows (*Salix* sp. div.) may be interpreted as a combination of both previous species. Their ability to spread clonally is limited in this habitat by water stress, however, their seedling bank is restocked every year with many new individuals from a heavy seed rain. The seeds are then exposed to massive selection.

In general, our results are in agreement with those from other types of communities. In particular, growth form (woody, annual, clonal) is the most important factor determining the spatiotemporal patterns of species (Herben *et al.* 1995): short-lived and perennial (clonal) plants exhibit complementary small-scale dynamics characterized by different clumping in space. Further variation among plant species is due to the existence of pioneer woody species with different growth forms and also different tolerances to stress and disturbance. In general, the clonal growth strategy (Fig. 3) seems to be more important for the spatiotemporal dynamics of species than their lifespan or whether they are woody or not (for example, *Calamagrostis epigejos* and *Populus tremula*). After more than one decade of complicated development of this stand, both species are the main components of the present plant cover of the abandoned sedimentation basin.

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References

- BRYNDOVÁ I., KOVÁŘ P. (2004): Dynamics of the demographic parameters of the clonal plant *Calamagrostis epigejos* (L.) Roth in two kinds of industrial deposits (Abandoned sedimentation basins in Bukovina and Chvaletice). – This volume, pp. 267–276.
- DOSTÁL P. (1997): Succession on abandoned ore deposit of the sedimentation pond in Chvaletice (SE Labe River Basin, Czech Republic). – Ms. [Dipl. Thesis, depon. in Library of the Department of Botany, Charles University, Benátská 2, Praha 2]. [in Czech]
- HERBEN T., DURING H. J. and KRAHULEC F. (1995): Spatiotemporal dynamics in mountain grasslands: species autocorrelations in space and time. – *Folia Geobot. Phytotax.*, 30: 185–196.
- HROUDOVÁ Z., ZÁKRAVSKÝ P. (2004): The influence of the moss layer on soil surface microclimate in an abandoned ore-washery sedimentation basin. – This volume, pp. 235–247.

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- JAREŠOVÁ I., KOVÁŘ P. (2004): Interactions between ants and plants during vegetation succession in the abandoned ore-washery sedimentation basin in Chvaletice. – This volume, pp. 300–310.
- KOVÁŘ P. (1979): Geobotanical aspects of the sedimentation pond reclamation after pyrite processing near surface mining at Chvaletice. – *Práce a Studie-Přír.*, 11: 63–78. [in Czech]
- KOVÁŘ P. (1999): Biotic interactions and restoration ecology of abandoned sedimentation ponds of toxic materials. – In: Kovář P. (ed.): *Nature and Culture in Landscape Ecology (Experiences for the 3rd Millennium)*, The Karolinum Press, pp. 290–302.
- LEHMANN C. (1997): Clonal diversity of populations of *Calamagrostis epigejos* in relation to environment stress and habitat heterogeneity. – *Ecography*, 20: 483–490.
- MALKINSON D., KADMON R. and COHEN D. (2003): Pattern analysis in successional communities. – As approach for studying shofts in ecological interactions. – *JVS*, 14: 213–222.
- MILES J. (1979): *Vegetation dynamics*. – Chapman and Hall, London.
- PALMER, M. W., van der MAAREL, E. (1995): Variance in species richness, species association and niche limitation. – *Oikos*, 73: 203–213.
- PFADENHAUER J., POSCHLOD P. and BUCHWALD R. (1986): Überlegungen zu einem Konzept geobotanischer Dauerbeobachtungsflächen für Bayern. Teil I. Methodik zur Anlage und Aufnahme. – *Ber. ANL*, 10: 41–60.
- REBELE F. (1992): Colonization and early succession on anthropogenic soils. – *JVS*, 5: 201–208.
- REBELE F. (1996): *Calamagrostis epigejos* (L.) Roth auf anthropogenen Standorten – ein Überblick. – *Verh. Ges. Ökol.*, 26: 753–763.
- ŠTEFÁNEK M. (2004): Secondary succession after fire on an abandoned ore-washery sedimentation basin – different trajectories (A comparison with primary succession). – This volume, pp. 248–266.
- UPTON G. J. G., FINGLETON F. (1985) *Spatial data analysis by example. Vol. I. Point pattern and quantitative data*. – Wiley and Sons, Chichester.
- URBANSKA K. M. (1997): Safe sites – interface of plant population ecology and restoration ecology. – In: URBANSKA K. M., WEBB N. R. and EDWARDS P. J. (eds): *Restoration ecology and sustainable development*, Cambridge Univ. Press, pp. 81–110.
- WILLEMS J. H., BOBBINK R. (1990): Spatial processes in the succession of chalk grassland on old fields in The netherlands. – In: KRAHULEC F., AGNEW A. D. Q., AGNEW S. and WILLEMS J. H. (eds): *Spatial processes in plant communities*, Prague, pp. 237–249.