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Research article

Role of substrate and landscape context in early succession: An experimental approach

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ABSTRACT

Both local site conditions and landscape context influence the course of succession, but there is a lack of experimental studies on the relative importance of these two factors. It is hypothesised that convergence vs. divergence in succession is determined by the interplay of site factors, such as type of substrate and the nature of the surrounding landscape. In order to evaluate the role of substrate and surrounding landscape in the initial development of vegetation, experimental plots with tertiary clay, sand, peat, sterilised local soil and undisturbed local soil as a control were established in two contrasting regions, and the cover of all the species present was recorded annually for 10 years. In early succession, vegetation was affected by both the substrate and surrounding landscape, but their effects resulted in different trends. The importance of the substrate gradually decreased, while that of the landscape context increased. In the course of succession the vegetation between the two regions diverged and converged within each region. We concluded with regard to the divergence vs. convergence dichotomy in succession: if contrasting habitats occur in the same or similar landscapes, convergence is expected, whereas if similar or the same habitats are located in contrasting landscapes, divergence is expected. For the remaining combinations, i.e. contrasting habitats in contrasting landscapes or the same habitats in the same or a similar landscape, successions may exhibit no or only slight divergence or convergence.

Introduction

The successional development of vegetation is determined by the available pool of species, substrate quality, biotic interactions, disturbance regime and climatic conditions (Walker and del Moral, 2003). Species that are available and establish at a given site (community species pool) are determined by the local species pool, which largely depends on regional climate and the history of landscape management in the region (Settele et al., 1996). These external factors constitute the 'landscape context' in which succession proceeds at a particular locality. Biotic interactions in the initial stages of succession are usually of much lesser importance than in the later stages, especially in primary successions starting on bare ground (Callaway and Walker, 1997). In this study, there were no additional disturbances at the plots under concern. Thus, only two basic groups of environmental factors, i.e. substratum quality and landscape context, were considered.

The important influence of substrate quality on the course of succession was appreciated even in the first studies on succession (Clements, 1916; see Walker and del Moral, 2003 for other references). Many studies have investigated the influence of various soil factors especially nutrient content (Tilman, 1988; van der Putten et al., 2013), soil moisture (Morecroft et al., 2004), pH (Prach et al., 2007a) and soil texture (Ejrnæs et al., 2003) on the course of succession. Some studies experimentally manipulated these soil factors (Mitchley et al., 1996).

The role of landscape, especially the surrounding vegetation being a source of propagules, is also well studied, and the importance of adjacent vegetation and land cover in the wider surroundings on the course of succession documented (Rydin and Borgegård, 1991; Roche et al., 1998; del Moral et al., 2005; Dovčiak et al., 2005; Benjamin et al., 2005; Novák and Konvička, 2006; Řehounková and Prach, 2008). In some cases the surrounding landscape has a more important role than local site conditions in the course of succession (Salonen and Setälä, 1992) or even than

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successional age (Řehounková and Prach, 2006). The surrounding vegetation determines ecological succession via the local species pool (Zobel et al., 1998) and especially the early stages of primary succession are often “donor controlled”, with species composition closely depending on the pool of species available in the close surroundings (Wood and del Moral, 1987).

Macroclimate is another important landscape factor driving succession (Otto et al., 2006; Prach et al., 2007a) as it can directly affect species establishment and have an indirect effect as it determines the regional species pool (Settele et al., 1996). Dispersal and establishment are the main factors that restrict the colonisation of recently exposed habitats (Jones and del Moral, 2009). Dispersal is associated with the local species pool, while whether a species becomes established or not is related to abiotic site conditions, such as the character of the substrate and microclimate, and competition/facilitation.

Quantification of the role of particular factors driving succession has both theoretical and practical implications. The former may improve the understanding of succession, the latter in helping restore vegetation at disturbed sites and indicate the ways in which certain factors may be manipulated in order to direct the succession in a desired direction (Walker et al., 2007).

How is the nature of the substrate and landscape related to convergence or divergence during succession? Answering this question may substantially help predict the course of succession in various environments (del Moral, 2007; Walker et al., 2010). Early studies simply expected convergence towards a single climax community (Clements, 1916), but this was soon contradicted and more diverse successions and endpoints suggested (see Walker and del Moral, 2003 for references). It seems that the resulting trends in succession, i.e. divergence or convergence, are largely determined by the initial (dis)similarity in local site conditions and how they change over time, and by the space-temporal scale of a study (Lepš and Rejmánek, 1991; del Moral, 2007). Divergence or convergence in succession is usually quantified by means of similarity indices or multivariate methods based on species composition (Philippi et al., 1998).

In contrast to the many experimental studies on the influence of substrate quality on the course of succession, there are only a few sites experimentally created in order to determine the role of landscape in driving succession. They include reciprocally transplanting peat between two adjacent peatlands differing in substrate quality (Salonen, 1990; Salonen and Setälä, 1992) or exposing small boxes of the same sort of soil at two adjacent sites, which differ in surrounding vegetation, and observing the course of succession in relation to the composition of the nearby vegetation (Lanta and Lepš, 2009). To obtain a broader perspective of the role of substrate quality and landscape context, we conducted an experiment using five contrasting types of substrate exposed for 10 years at two contrasting localities, one in a relatively dry and warm region and the other in a cold and wet region. This made it possible to ask the following questions: (i) To what extent is the course of succession influenced by substrate quality and landscape context; (ii) How does the importance of these driving factors change in the course of succession; and (iii) Is succession divergent or convergent on the different substrates and between the two localities?

Methods

Site description, experimental design and data recording

The experiment was established in spring 2002 at two climatically different localities (hereafter called Locality), in the Czech Republic, central Europe:

1. A just abandoned part of an arable field (total size ca 0.3 km^2) near the village of Vroutek, located in a rather warm and dry lowland area (hereafter referred as Lowland); altitude 355 m a.s.l.; latitude 50°11′44″ N; longitude 13°21′24″ E; average annual temperature 8.6 °C; average annual precipitation 461 mm (long-term data from nearby meteorological stations at Blšany and Kryry; www.chmi.cz). This site is surrounded mostly by ruderal and weedy vegetation on and along arable fields, by strips of mesic grassland dominated by *Arrhenatherum elatius*, scrubland along paths, and semi-natural oak-hornbeam woodland about 30 m distant from the study plots.
2. A part of an arable field (ca 0.15 km^2) abandoned shortly before the start of the experiment, located near the village of Benešov, located in a relatively cold and wet upland area (hereafter referred as Upland); altitude 665 m a.s.l.; latitude 49°19′51″ N; longitude 15°00′13″ E; average annual temperature 6.7 °C; average annual precipitation 759 mm (long-term data from a nearby meteorological station at Černovice; www.chmi.cz). This site is surrounded by regularly mown meadow dominated by *Phleum pratense*, *Festuca pratensis* and *Festuca rubra*, and by arable land with common weeds in the distance up to 30 m; the distance to the nearest forest (a Norway spruce plantation) is ~100 m.

The following substrates (hereafter called Substrate) were used to establish experimental plots at each locality: (i) tertiary clay from the overburden of brown-coal (hereafter referred as clay); (ii) sand from an active sand pit (sand); and (iii) peat from peat diggings (peat). In addition, (iv) local soil was excavated, placed in an oven at 110 °C to kill plant propagules and then returned to the site (Topsoil), and (v) untouched local soil used as a control (Control). The sterilisation treatment was not needed in the case of allochtonous substrates (clay, sand, peat) because they were excavated from the depth below the surface (clay ~100 m, sand several metres, peat ~2 m). The three substrates represented different seres, which are described in detail elsewhere, i.e. spoil heaps resulting from brown-coal mining (Prach, 1987; Hodačová and Prach, 2003), sand pits (Řehounková and Prach, 2006, 2008, 2010) and peat diggings (Konvalinková and Prach, 2010). The plots with local soil represent the abandoned fields described by Prach et al. (2007b) and Jírová et al. (2012).

All substrates were put in beds, 1.5 × 1.5 m in area and 0.3 m deep, dug into the local soil. Five replicates were arranged in a Latin-square design, resulting in 25 plots at each site. The beds containing the various substrates, except the controls, were isolated from the surrounding soil by plastic foil perforated at the bottom to prevent vegetative expansion of clonal species in underground. The controls were left without plastic foil because they were identical with the surroundings. Strips 0.5 m in width around each plot, except controls, were sprayed annually in May with Glyphosate to preclude vegetative colonisation of the experimental plots by species from the surrounding vegetation especially by surface stolones. Substrate chemistry, summarised in Table 1, was assessed at the start and the end of the experiment using standard methods (Sparks et al., 1996). A mixed sample was taken from each substrate just before transportation to the localities. In the established experimental plots, a mixed sample consisting of five replicates was taken from each of the plots from the 5 cm layer below a thin surface layer that was removed before the sampling.

The central 1 m^2 of each plot was sampled annually in July or August 2002–2011, at the time of maximum development of the vegetation. All vascular plants were identified and their percentage cover visually estimated (Kent and Coker, 1992). Nomenclature follows Flora Europaea (http://rbg-web2.rbge.org.uk/FE/fe.html).