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How small can steppe habitats be? Results from a landscape of porphyry outcrops in the central valley of the River Saale, northwest of Halle

Abstract

The fragmented porphyry landscape to the northwest of Halle (arid zone of Central Germany: mean annual temperature of 9.2 °C, mean annual precipitation of 473 mm) is characterised by ca. 200 porphyry outcrops, all of which are situated within an area of intensive agriculture. The vegetation mosaic on the outcrops is composed of strongly contrasting plant communities that are generally characterised by a high species diversity and the presence of numerous rare and endangered plants. The vegetation is geobotanically characterized by an overlapping of continental, subatlantic and widespread Central-European species and forms atlantic-subatlantic dwarf-shrub heaths (*Euphorbio-Callunetum*) as well as (sub)mediterranean (*Thymo-Festucetum*) and (sub)continental dry and semi-dry grassland communities (*Filipendulo-Helictotrichetum*, *Festuco-Brachypodietum, Festuco-Stipetum* etc.). The composition of the vegetation mosaic depends on the size and age of the porphyry outcrops. With increasing size and age, the proportion of rare and valuable plant species and communities increases in line with decreasing edge effects. On the small porphyry outcrops (< 500 m²), vegetation analyses were repeated after eight years in order to analyse succession processes. The undisturbed development started with different ruderal plant communities and ended with species-poor stands of *Festuca glaucina, F. rupicola* and *F. valesiaca*, which can act as initial stages of (sub) mediterranean or (sub)continental dry and semi-dry grassland communities. For the development of species-rich communities, a transfer of seeds from the surrounding larger and older porphyry outcrops, which support higher levels of biodiversity, must take place. In a pot-experiment, the chances of establishment of dicotyledonous species in grass stands with different densities of *Festuca rupicola* were investigated. The results indicated no significant difference in germination, but the analysis showed that the survival likelihood of the chosen species (*Dianthus carthusianorum, Scabiosa ochroleuca*) was different and decreased with increasing grass density. However, the surviving individuals remained at the seedling stage in the presence of grass, even after 330 days, while both species reached the reproductive stage in the pots without *F. rupicola*. Intact steppes can develop on the small outcrops, but only after a long time. Preconditions include that the grass turf is not too dense and establishment gaps exist with seed transfer being facilitated by the traditional land-use of grazing.

Wie klein dürfen Steppen sein? – Untersuchungsergebnisse aus der Porphyrkuppenlandschaft des Mittleren Saaletals nordwestlich von Halle

Zusammenfassung

Die fragmentierte Porphyrkuppenlandschaft nordwestlich von Halle (Mitteldeutsches Trockengebiet: 9,2 °C Jahresmitteltemperatur und 473 mm jährlicher Niederschlag) wird von ca. 200 Porphyrkuppen geprägt, die in eine stark landwirtschaftlich genutzte Fläche eingebettet sind. Das Vegetationsmosaik der Kuppen wird von stark kontrastierenden Pflanzengesellschaften bestimmt, die sich durch eine hohe Biodiversität und das Auftreten vieler gefährdeter und geschützter Pflanzenarten auszeichnen. Es kommt zu einer Überlagerung von kontinentalen, subatlantischen und weitverbreiteten zentraleuropäischen Geoelementen, die sowohl atlantisch-subatlantische Zwergstrauchheiden (*Euphorbio-Callunetum*) als auch (sub)mediterrane (*Thymo-Festucetum*) und (sub)kontinentale Trocken- und Halbtrockenrasen (*Filipendulo-Helictotrichetum, Festuco-Brachypodietum, Festuco-Stipetum*) aufbauen. Die Zusammensetzung des Vegetationsmosaiks auf den Porphyrkuppen ist u. a. stark abhängig von der Größe und Genese der Kuppen. Mit zunehmender Größe und höherem Alter nimmt der Anteil an seltenen und wertvollen Pflanzenarten bzw. -gesellschaften infolge von verminderten Randeffekten zu. Typische, artenreiche Gesellschaften wurden auf alten und sehr alten Kuppen ab einer Größe von ca. 1.500 m² gefunden.
Auf den sehr kleinen Kuppen (bis 500 m²) wurde nach acht Jahren eine Wiederholungskartierung vorgenommen, um Sukzessionsprozesse zu analysieren. Die ungestörte Entwicklung verläuft zunächst über verschiedene Ruderalgesellschaften bis hin zu artenarmen Beständen von *Festuca glaucina, F. rupicola* und *F. valesiaca*, die als Initialen von (sub)mediterranen bzw. (sub)kontinentalen Trocken- und Halbtrockenrasen gelten können. Damit sich artenreiche Steppenrasen entwickeln, muss jedoch ein Diasporeneintrag von den angrenzenden großen und alten Kuppen erfolgen, die über eine hohe Biodiversität verfügen.

In einem experimentellen Ansatz wurden die Etablierungschancen von zwei charakteristischen dikotylen Trocken- und Halbtrockenrasenarten (*Dianthus carthusianorum, Scabiosa ochroleuca*) in unterschiedlich dichten Beständen von *Festuca rupicola* untersucht. Beide Arten waren nicht dormant und keimten gleich gut. Die Survivalanalyse zeigte jedoch, dass die Überlebenswahrscheinlichkeit artspezifisch unterschiedlich war. Die Mortalität von *S. ochroleuca* nahm signifikant mit zunehmender Grasdichte zu, wohingegen *D. carthusianorum* nur geringe Unterschiede zeigte. In den dichten Gras-Beständen verharrten die Individuen auch nach 330 Tagen im Keimpflanzenstadium, während ohne Gras die Entwicklung bis hin zu blühenden und fruchtenden Individuen verlief.
Intakte Steppenrasen können sich deshalb auf den kleineren Kuppen erst in sehr langen Zeiträumen entwickeln. Voraussetzung ist, dass die Grasnarbe nicht zu dicht wird und Störstellen vorhanden sind. Dies könnte, neben einem Diasporentransfer, durch traditionelle Landnutzung in Form von Beweidung unterstützt werden.

1 Introduction

The porphyry outcrops northwest of Halle were named “pontische Hügel” by Meusel (1940) due to the steppe-like ecosystem with interesting extrazonal, dry and semi-dry grassland communities, which are mainly described by Mahn (1965). The vegetation is geobotanically marked by an overlap of continental, subatlantic and widespread Central-European species, and it forms atlantic-subatlantic dwarf-shrub heaths as well as (sub)mediterranean and (sub)continental, dry and semi-dry grassland communities. In general, they are characterized by their high species diversity and the presence of numerous rare and endangered plants (Partzsch & Krumbiegel 1996). The landscape of porphyry outcrops forms a near-natural fragmented landscape with outcrops of different sizes and periods of development, which allowed for the investigation of the composition of the vegetation mosaic based on size and age of outcrops.
The outcrops are bounded within intensively farmed agrarian fields, resulting in frequent disturbance of the outcrops, with the magnitude of disturbance being dependent on the size of the outcrops. As such, the smaller outcrops offer the possibility to investigate succession processes in dry locations with repeated relevés after a given time.

Fig. 1:
Study area of the landscape of porphyry outcrops in central Germany near Halle (Saale).

The establishment of typical grassland species is an important step for new development or restoration of species-rich dry and semi-dry grassland communities over time. The establishment phase is the most sensitive stage in the life-cycle of plant species (Jongejans et al. 2006, Jorritsma-Wienk et al. 2006), which includes germination and seedling survival (Gross 1984, Tessier et al. 2000). Establishment can be affected by positive and negative interactions with neighbouring plants. Franco & Nobel (1988) described the so-called ‘nurse plant syndrome’ in which adult plants of one species facilitate the establishment of another species due to improved the environmental conditions, e.g. enhanced air humidity, prevention of extreme temperature fluctuations, improved soil properties (accumulation of nutrients and organic matter) and reduced probability of mechanical or herbivorous damage (Holmgren et al. 1997). Establishment success depends on plant traits such as seed

size and mass, dormancy, germination percentage and dispersal (Fenner & Thompson 2005, Harper 1977), and the importance of such traits to the fitness of the species is widely accepted (Grubb 1977, Higgins & Richardson 1999). Several authors found that large-seeded species had higher survival through early seedling establishment than small-seeded species (Moles & Westoby 2002, Silvertown 1981, Jakobsson & Eriksson 2000) and that large seeds enable quick initial growth, which is an important characteristic for establishment in closed turf (Baker 1972, Grime & Jeffrey 1965, Gross 1984). Using an experimental approach, the establishment of two dicotyledonous species with different seed sizes in grass-stands with different densities was investigated in order to evaluate the chance of new development or restoration of species-rich grassland communities.

2 Methods

2.1 Study area

The fragmented porphyry landscape is part of the dry region of central Germany (51°31'–51°35' N) and is characterized by a mean annual temperature of 9.2 °C and a mean precipitation of 473 mm. The geomorphology is defined by former glacial and periglacial activities as well as erosion impacts. The bedrock is acidic porphyry, which is widely covered by alkaline loess deposits. Erosion, which has been accelerated by agriculture in the last 160 years, formed the porphyry outcrops at various periods. In total, 204 porphyry outcrops, characterised by their size (between 30 m² to 33,200 m²) and time of development are distributed throughout an area of intensive agricultural (Fig. 1) and were classified in four size and four age categories (Table 1, 2; according to Partzsch & Mahn 1998). The age was determined with reference to historical maps for the area.

2.2 Vegetation analysis

A total of 104 porphyry outcrops were visited between 1992 and 1996, and all visually discernible vegetation types were sampled. A total of 595 relevés were sampled with plot sizes measuring roughly 16 m². Plant cover was estimated using the nine level cover-abundance scale of Braun-Blanquet, modified by Reichelt & Wilmanns (1973). After eight years, surveys on the smaller porphyry outcrops (< 500 m²) were repeated and compared in order to analyse succession processes.
Tabular rearrangement of survey results yielded a total of 50 plant communities (Partzsch & Krumbiegel 1996), of which 14 can be regarded as being typical of dry and semi-dry grasslands and heaths. The remaining communities included several types of woody scrub and heavily disturbed stands dominated by annuals.

Table 1:
Size categories of the porphyry outcrops (according to Partzsch & Mahn 1998).

	Size category	Area	Investigated outcrops
1	Very small outcrops	< 500 m²	46
2	Small outcrops	501–1,000 m²	13
3	Medium-sized outcrops	1,001–5,000 m²	33
4	Large outcrops	> 5,001 m²	12

Table 2:
Age categories of the porphyry outcrops (according to Partzsch & Mahn 1998).

	Age category	Historical maps	Time of developing	Investigated outcrops
1	Very young outcrops	1985/1990	ca. 10 years ago	3
2	Young outcrops	1940/1950	ca. 50-60 years ago	20
3	Old outcrops	1902/1904	ca. 100 yaers ago	40
4	Very old outcrops	1851	More than 150 years ago	41

2.3 Experiment of establishment and study species

Establishment of dicotyledonous species in grass stands of *Festuca rupicola* (F) with different densities were investigated in a pot-experiment. In February 2010, pots were placed outdoors at the Halle Botanical Garden with four different treatments: 1) Without grass individuals (F0); 2) With one grass individual (F1); 3) With two grass individuals (F2), and 4) With three grass individuals (F3). Before the start of the experiment, the grass individuals were grown into well developed tussocks (diameter: 17-21 cm). In August 2010, 20 seeds of the dicots were separately sown into the pots with different grass densities (6 replications per treatment and species; altogether 48 pots). Emerging seedlings were separately marked in order to follow their plant performance in terms of growth height, number of leaves and flowers or flower heads over one to two week intervals. Pots were located randomly and their positions were changed every two weeks. The last measurement in 2010 was made at the beginning of winter (end of October) and the first measurements in 2011 started at the beginning of spring (start of April). The experiment was finished in July 2011 when all aboveground biomass of the dicots was harvested.

The two dicotyledonous species were chosen because they are not dormant and have similar germination characteristics, but they differ in seed size and mass. *Dianthus carthusianorum* L. (Caryophyllaceae) is a perennial, 15-45 cm high hemicryptophyte. The capsules produce black seeds with an estimated mean weight of 0.4 ± 0.1 g and size of 1.84 ± 0.11 mm² (small-sized seeds). *Scabiosa ochroleuca* L. (Dipsacaceae) is a perennial, 25-60 cm high hemicryptophyte. The achenes have a mean weight of 1.2 ± 0.4 g and size of 5.85 ± 0.47 mm^2 (large-sized seeds; mean pers. calculated). Both rare species mainly occur in dry and semi-dry grasslands like *Festuca rupicola* Heuff. (Poaceae), a perennial, 15-80 cm high tussock grass (Jäger 2011). In the dry region of central Germany, *F. rupicola* is common, it has spread extensively over the last few decades and it currently often dominates corresponding grassland communities as a result of traditional land-use change (Partzsch 2000). Survival likelihood analysis was used as a statistical approach.

3 Results

3.1 Effect of area size and age of the outcrops on the vegetation mosaic

The vegetation mosaic on the outcrops included 50 plant communities and 374 plant species (Partzsch & Krumbiegel 1996, Partzsch 2000). It is composed of strongly contrasting plant communities that are generally characterized by high species diversity and the presence of numerous rare, endangered and protected vascular plants (52 species) (Partzsch 2007). The most endangered communities are *Euphorbio-Callunetum* R. Schubert 1960, *Thymo-Festucetum cinereae* Mahn 1959, *Filipendulo vulgaris-Helictotrichetum pratensis* Mahn 1965, *Festuco valesiacae-Stipetum capillatae* Mahn 1959 and *Festuco rupicolae-Brachypodietum pinnati* Mahn 1959 (Schubert 2004). Some communities developed from former species-rich to species-poor stands of *Festuca rupicola* and *Poa angustifolia* as a result of traditional land use change since 1990 (Partzsch 2000). On more nutrient-rich and disturbed locations, ruderal stands of *Arrhenatheretum elatioris* A. Fischer 1985 and *Falcario-Agropyretum repentis* Th. Müll. et Görs 1969 as well as *Convolvulo-Agropyretum repentis* Felföldy 1943 nom. invers. propos. occur, whereas on heavily disturbed locations, the annual ruderal *Sisymbrio-Atriplicetum oblongifoliae* Oberd. 1957 prevail.

The composition of the vegetation mosaic depends on the size and age of the porphyry outcrops (Partzsch 2001). There are strong positive correlations between the total number of communities and the valuable dry and semi-dry grassland communities with the size of the outcrops, whereas communities with increasing hemeroby showed low or negative correlations (Fig. 2). The correlation between the distribution of communities and the age of the outcrops shows weaker but similar relations. Only *Festuco-Stipetum* was relatively rare and did not show any correlation with size or age of the outcrops, which is a result of their habitat requirements. This community prefers south facing slopes with a very deep loess layer, which are rare on the isolated outcrops.

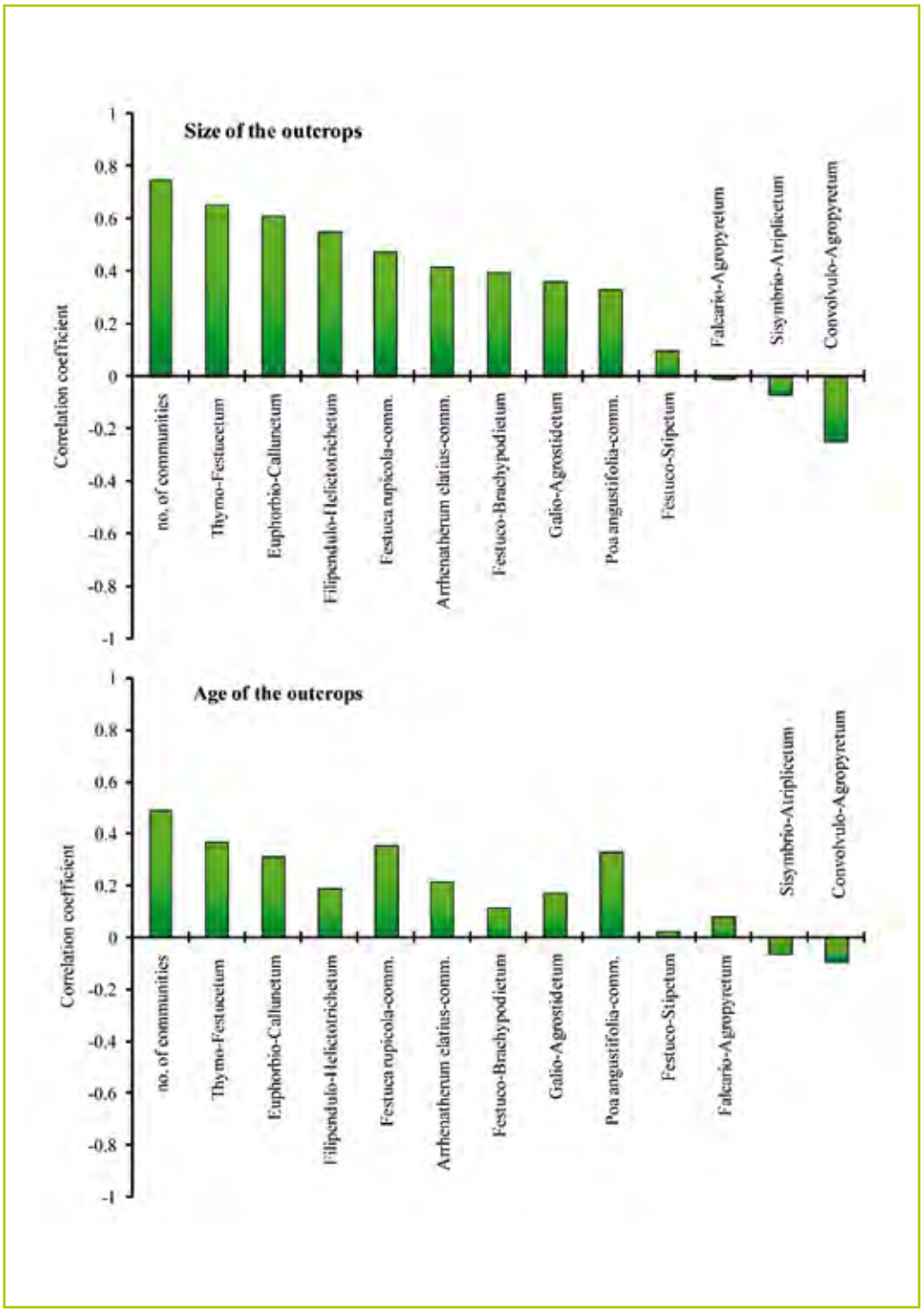

Fig. 2:
Correlation between the occurrence of the plant communities and the area size (above) and age (below) of the porphyry outcrops (from Partzsch 2001).

Size and age of the outcrops correlate in such a way that the smaller outcrops have mostly developed in recent time while the larger outcrops have developed over a longer time; however, there are also small but old outcrops and vice versa. On the younger and smaller outcrops, communities with a higher degree of hemeroby and lower naturalness such as *Falcario-* or *Convolvulo-Agropyretum* and *Poa angustifolia-* and *Arrhenatherum elatius*-stands can be found (Fig. 3). With increasing age and size of the outcrops, the above-mentioned communities mostly occur on the border of outcrops and form a buffer-zone to the adjacent agricultural land. On the less disturbed centre of the outcrops, the valuable dry and semi-dry communities occur, which corresponds with the edaphic and microclimate conditions. Well developed, species-rich communities of the *Thymo-Festucetum*, the *Filipendulo-Helictotrichetum* and the *Festuco-Brachypodietum* as well as the *Euphorbio-Callunetum* are only found on old and very old outcrops with a size over 1,500 m².

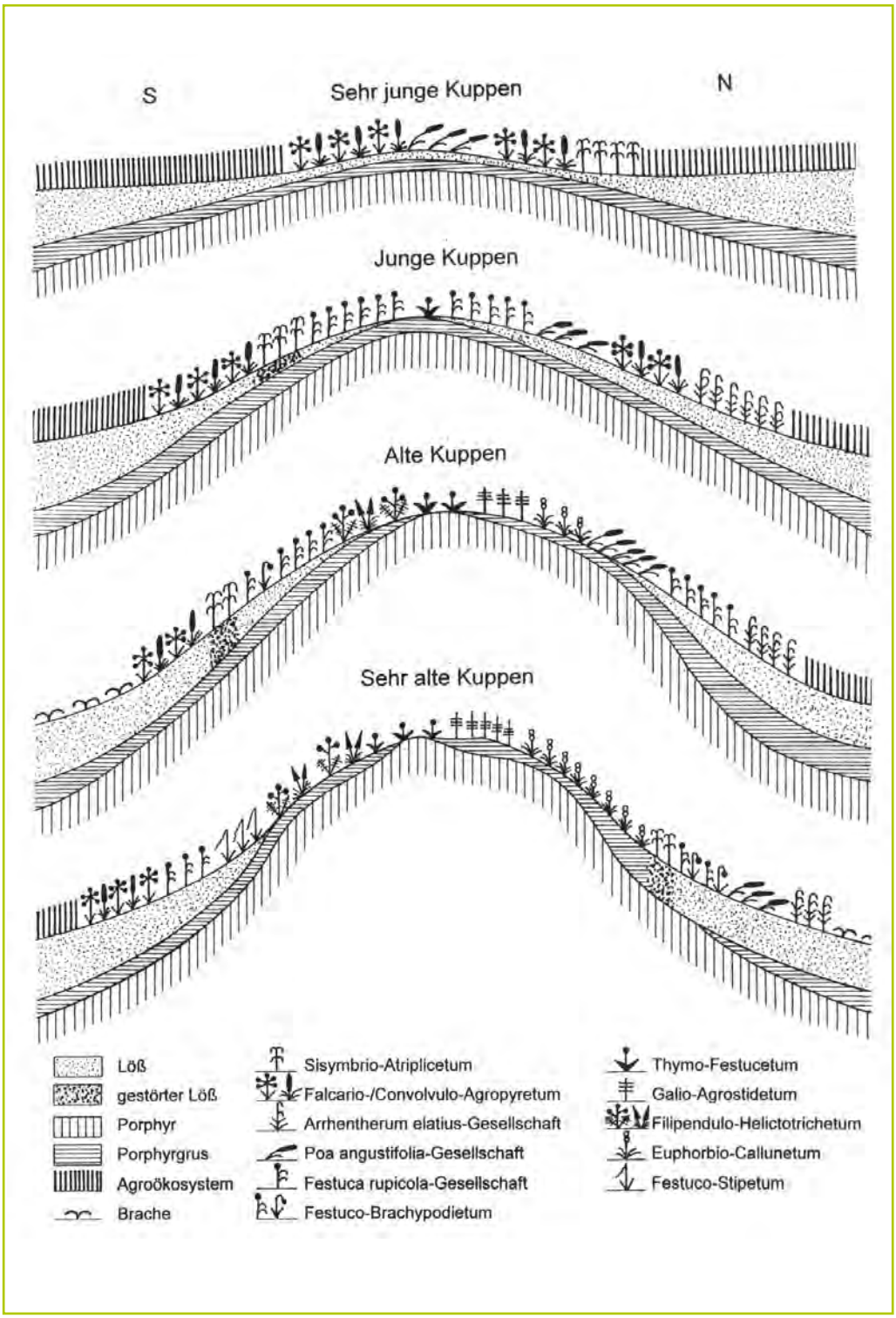

Fig. 3:
Vegetation mosaics of the porphyry outcrops dependent on the genesis of the locations (above: very young outcrops; middle: young and old outcrops; below: very old outcrops; from PARTZSCH 2001).

3.2 Succession on small outcrops

On smaller outcrops, after disturbance and regardless of age, succession starts with annual ruderal communities such as *Sisymbrio-Atriplicetum oblongifoliae* or remains of weed communities like *Matricaria inodora*-stands as pioneer stages (Fig. 4). Over time, development proceeds through more long-lived ruderal communities, such as differing stands dominated by *Elytrigia repens, Poa angustifolia* and *Arrhenatherum elatius*. The preliminary final stage of succession ends with species-poor stands of *Festuca glaucina, F. rupicola* and *F. valesiaca*, which can act as initial stages of (sub) mediterranean or (sub)continental dry and semi-dry grassland communities. For the development of species-rich communities, a transfer of seeds from the surrounding larger and older porphyry outcrops that support higher levels of biodiversity must take place.

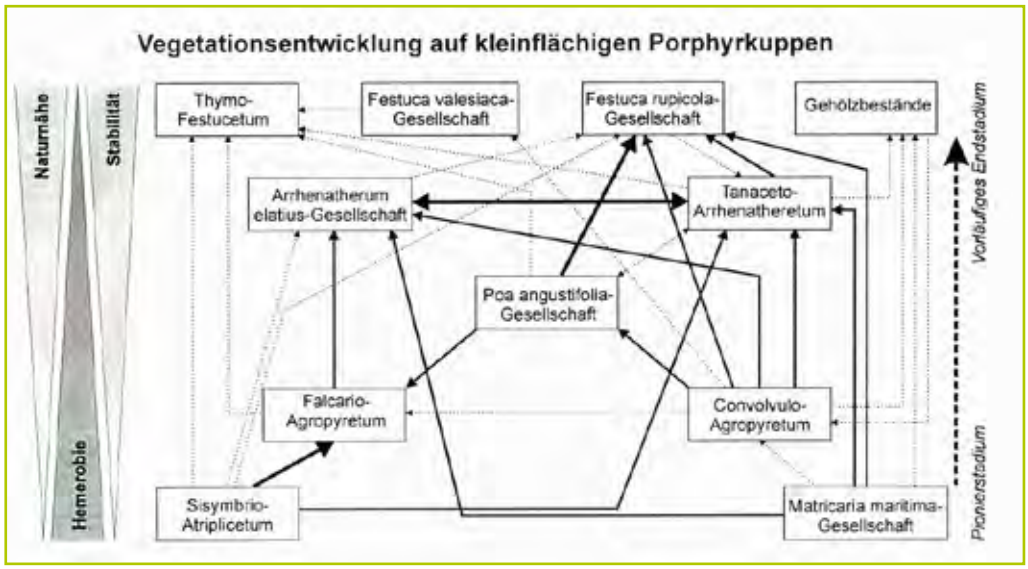

Fig. 4:
Succession on the small porphyry outcrops (from Partzsch et al. 2003).

3.3 Chance of establishment of xerothermic species

Both study species *D. carthusianorum* and *S. ochroleuca* germinated equally well between 65 and 75% in climate chambers and under outdoor conditions (data not shown). The survival analysis showed that the survival likelihood of the species was different: *D. carthusianorum* with small-sized seeds did not significantly differ in dependence on grass density, and seedling mortality varied between 37 and 44% after 330 days (Fig. 5). With its large-sized seeds, *Scabiosa ochroleuca* showed highly significant differences in survival, which decreased with increasing density of *F. rupicola*. Mortality ranged between 30% (without grass) and 85% (with the highest grass density).

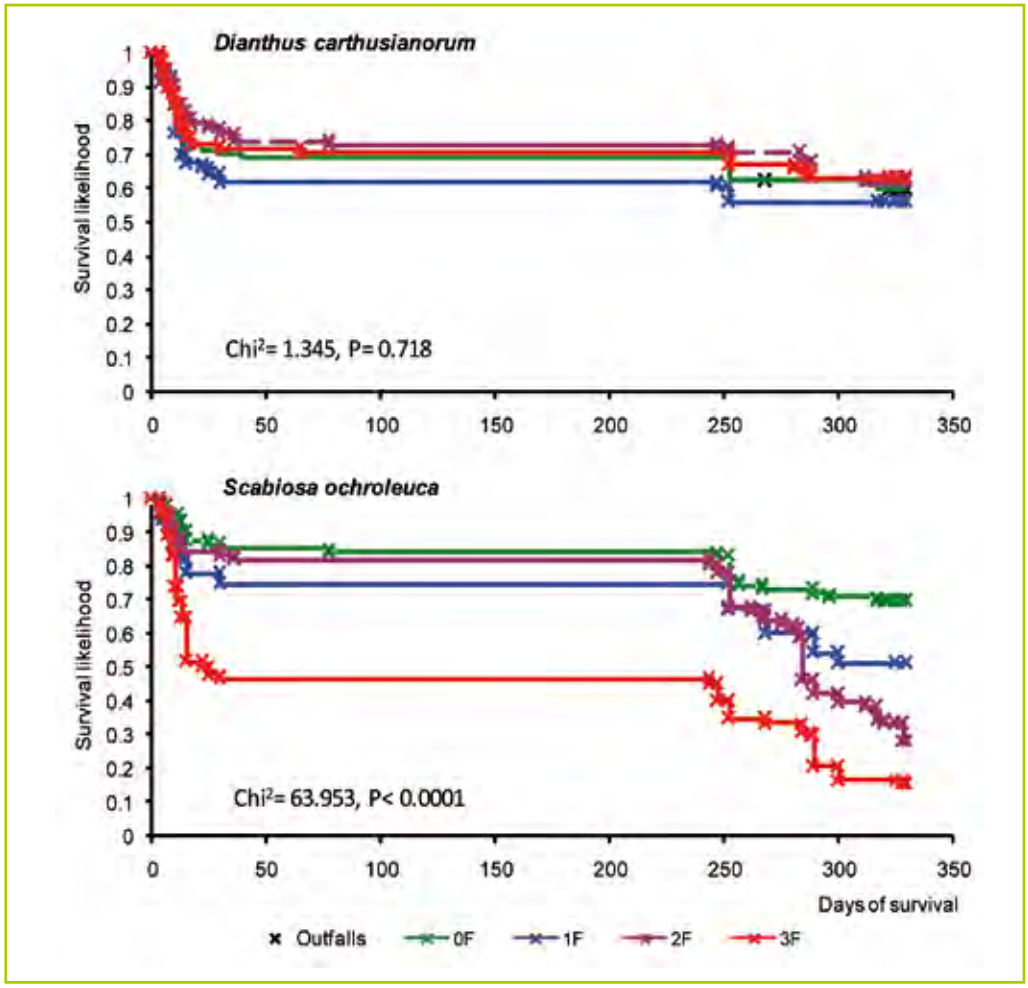

Fig. 5:
Survival likelihood of *Dianthus carthusianorum* and *Scabiosa ochroleuca* in stands of *Festuca rupicola* with different densities over 330 days.

The performance of the plant parameters growth height and number of leaves of both species differed significantly between the treatments with and without grass individuals in the pot (Fig. 6). However, even the subsisting individuals remained at the seedling stage in the presence of grass, even after 330 days, while both species reached the reproductive stage in the pots without *F. rupicola*.

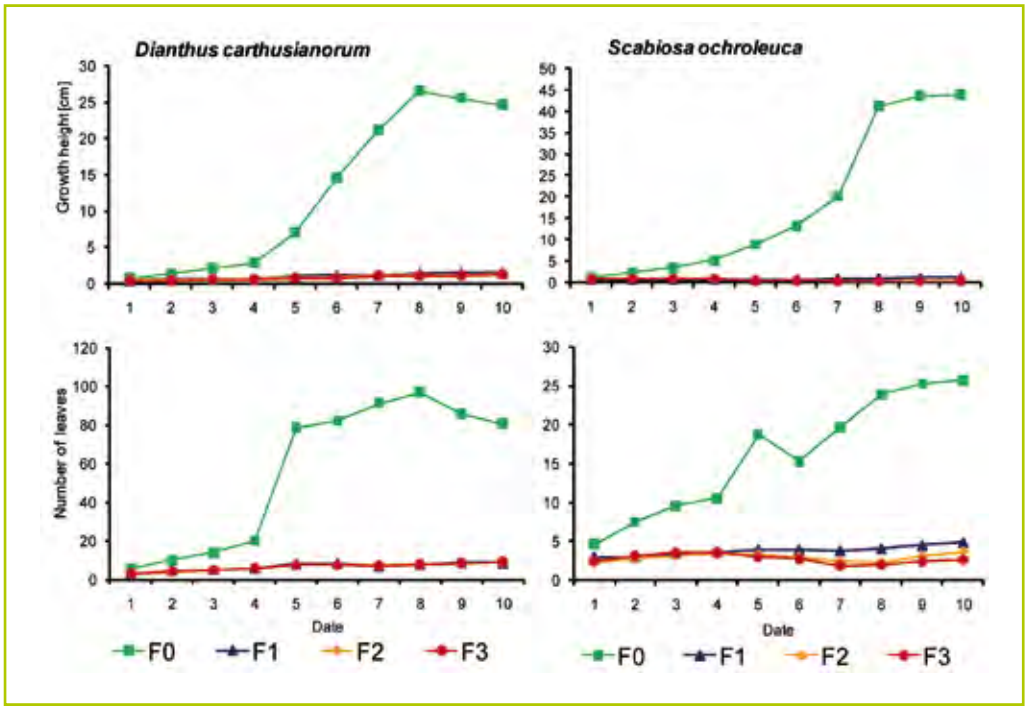

Fig. 6:
Performance of the plant parameters growth height and leaf number of *Dianthus carthusianorum* and *Scabiosa ochroleuca* in grass stands with different densities over 330 days.

4 Discussion

The results of the floristic-phytocoenological analysis show that the diversity of species and communities increases with size of outcrop. This suggests that the area size-species-relation of the Island theory of MacArthur & Wilson (1967) is valid for the distribution of species and communities on the porphyry outcrops, with level of diversity being dependent on the heterogeneity of the location. This confirms the area size-habitat diversity-hypothesis of Sugihara (1980) (Partzsch & Mahn 1998). With increasing size and age of the outcrops, the proportion of rare and endangered plant species and the species-rich dry and semi-dry communities increases in line with decreasing edge effects (Partzsch 2001).

Franz (1952/53) described the biocoenological basic principle that the species richness of plant communities results from the long-term continuous development of environmental factors, which leads to balanced and stable communities. As such, well developed species-rich stands of the *Thymo-Festucetum*, the *Filipendulo-Helictotrichetum*, the *Festuco-Brachypodietum* and the *Euphorbio-Callunetum* were found on the oldest outcrops (Partzsch 2001). Several authors described indicator species for historical old woodlands (Heinken 1998, Otte 1996, Wulf 1994, Zacharias 1994). Based on the present study, the following species are analyzed as indicator species of historical old dry and semi-dry grasslands: *Antennaria dioica, Astragalus danicus, Biscutella laevigata, Campanula glomerata, Carex humilis, Gagea bohemica, Muscari tenuiflorum, Orchis morio, Pseudolysimachion spicatum, Pulsatilla vulgaris, Ranunculus bulbosus, Seseli hippomarathrum, Thesium linophyllon, Viola canina* (Partzsch 2001).

One of most important environmental factors is the traditional land use by grazing with sheep or goats, which shaped these grassland communities from the early Middle Ages. Ongoing abandonment of traditional land use measures leads to a decline of biodiversity due to the changing conditions governing plant species coexistence (Balmer & Erhardt 2000, Poschlod & WallisDeVries 2002, Zobel 1992). Land use change alters structure, composition and dynamics of ecosystems, as well as the survival of plant populations (Donohue et al. (2000). In the landscape of porphyry outcrops, this process started with the political upheaval in 1990 due to economic reasons. Since then, former species-rich grassland communities have declined in biodiversity resulting in the expansion of grass species such as *Festuca rupicola* and *Poa angustifolia* and the increasing decline of dicotyledonous herbs (Frank & Neumann, 1999, Partzsch 2000, 2011, Wesche et al. 2005). However, the

conversion of formerly species-rich grasslands into species-poor communities dominated by various grass species such as *Arrhenatherum elatius*, *Brachypodium pinnatum, Bromus erectus, Festuca* ssp. or *Stipa* ssp. seems to be a widespread phenomenon (Bobbink et al. 1988, Bornkamm 2006, Dostálek & Frantík, 2012, Enyedi et al. 2008, Klimaschewski et al. 2006).
The potential natural restoration of species-rich grassland communities from seed banks is hindered by the fact that most dry and semi-dry grassland species develop only a transient or short-term persistent seed bank in the soil. In addition, seed banks under old semi-dry grasslands and heaths are very pure (Partzsch 2005). A successful establishment of new species depends on different plant traits such as seed size or mass (Moles & Westoby 2002). For the two dicots of the present study, results indicate that as opposed to affecting germination, grass density has strong effects on survival and development. While the survival likelihood of the large-seeded species *S. ochroleuca* significantly decreased with increasing density of *F. rupicola*, it did not significantly differ for the small-seeded species *D. carthusianorum*. Ryser (1993) found in *Mesobrometum* that large-seeded species have lower mortality, because higher amounts of resources in large seeds support etiolation of seedlings in shaded conditions (Leishman & Westoby 1994). The survived individuals in our experiment showed strong differences in performance of the investigated plant parameters with dependence on grass density. The survivors of both species developed into adult flowering individuals in the pots without *F. rupicola* and, in the sense of Mahn (1996) and Kowarik (2003), they became fully established after ca. one year. In all treatments with *F. rupicola,* the individuals of both dicots did not advance beyond the seedling stage, irrespective of seed size. It seems that differing seedling morphology is responsible for variations in establishment success (Xiong et al. 2001). *Dianthus carthusianorum* seedlings are more similar to grass seedlings, while the seedlings of *S. ochroleuca* have a more horizontal rosette growth. In accordance with Jensen & Gutekunst (2003), we conclude that success in seedling establishment is more a species-specific trait and seed size and mass are not generally good predictors for establishment ability (Leishman 1999). On the other hand, the growth form of *F. rupicola* as a tussock grass suggests that it can act as a nurse plant for the seedlings and shelter them from extreme climate conditions, even though it acts as a strong competitor.

5 Conclusions

The landscape of porphyry outcrops near Halle (Saale) accommodates valuable species-rich dry and semi-dry grasslands. The communities with the highest diversity are found on the largest and oldest outcrops caused by reduced edge-effects and a long-term continuous development of environmental factors. The minimum size of the outcrops with well developed communities was found to be ca. 1,500 m². The small-sized outcrops are often disturbed by the intensive agricultural land use of the surroundings, which induce successional processes. The preliminary final stage of succession ends with species-poor stands of *Festuca glaucina, F. rupicola* and *F. valesiaca*, which can act as initial stages of (sub)mediterranean or (sub)continental dry and semi-dry grassland communities. However, the establishment of dicots is hampered by increased grass density and it takes long time, as demonstrated in our establishment experiment. A successful new development or restoration of intact steppe-like ecosystems would be facilitated by the reintroduction of traditional land-use practices such as extensive grazing, as sheep are able to hamper the competitiveness of dominant grass species such as *F. rupicola* (Partzsch 2011). Moreover, through trampling, sheep create small gaps that are important as regeneration niches for other species (Watt & Gibson 1988, Bullock et al. 1994).

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