

Original Research

Applicability of Functional Groups Concept in Analysis of Spatiotemporal Vegetation Changes on Manmade Habitats

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Abstract

The immense variety in plant diversity at the species level might explain why it is so difficult to establish strict generalizations in vegetation dynamics. In the last two decades many published research reports have shown that the introduction of the concept of plant functional groups (PEG) into the analysis of vegetation dynamics might be more informative in explaining spatiotemporal changes of vegetation than analysis based only on species composition.

The spontaneous vegetation development observed on post-industrial manmade habitats (coal-mine heaps in the Silesian Upland, southern Poland), which are different in age provide an excellent opportunity to study the changes of participation of species representing the analyzed PFG. In this study a vast range of life history features were taken into account in order to find which of them are the most explicable (not redundant) in terms of changes in species composition in time during vegetation development. The study showed that during vegetation development in manmade habitats some features undergo variation over time and their importance depends on the developmental phase of succession/colonization processes. The results revealed that the most explanatory PFG's are plant height, leaf shape and area, root system, seed weight, and photosynthetic pathway. It is impossible to recommend one closed set of species feature categories to provide the best explanation of spatiotemporal changes of vegetation on manmade habitats during all developmental stages, because the significance of a different plant's features varies in the following phases of vegetation development.

Keywords: plant functional groups, manmade habitats, spatiotemporal vegetation changes

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Introduction

Spatiotemporal changes in vegetation have been of great interest in plant ecology for a long time. The patterns of vegetation dynamics have been described for many natural and semi-natural habitats [1, 2]. Many generalizations have been made about what to expect during the development of vegetation, including an increase in evenness, a high degree of predictability in the sequence of different life forms [3], a tendency for introduced species to decline [4, 5] and a decrease in the rate of change as the system approaches a “mature” state [6].

However, debate continues, in part related to the variation in species diversity from site to site [7, 8]. The above statements indicate that knowledge is still far from creating a comprehensive theory of vegetation dynamics [9]. The cited contributions are mostly based on studies of particular species present in specific vegetation complexes. The enormous variety of plant species might be why it is so difficult to come to more comprehensive generalizations. In the last two decades many published research reports have shown that the introduction of the concept of plant functional types into the analysis of vegetation dynamics processes might be more informative in explaining spatiotemporal changes in vegetation than analysis based only on species composition [10-13].

The study of spontaneous vegetation development on post-industrial sites, apart from its scientific aspect, is important for developing reclamation practice. Most of the research on the vegetation of post-coalmining spoil heaps has focused on the diversity of specific vegetation types [14-17]. Only a few studies have attempted to analyze the changes in participation of plant functional

groups in vegetation patches over time on a comprehensive selection of the coal-mine spoil heaps across a whole industrial region [18]. The application of these concepts may help to reveal the mechanisms of the operating processes as well making it possible to predict and monitor future changes.

A functional group (FG) is defined as a group of unrelated species that can be characterized by one common feature [11, 13, 19, 20] that responds in a common way to diverse environmental conditions [21-24]. Some of the modifications can be reflected in a plant's morphology, e.g. a smaller leaf area for limiting lost water. Some others can cause only physiological changes, e.g. in photosynthesis [11, 13, 23-27].

Most often the functional groups are established on the basis of easily measured features. These include: growth form, plant height, leaf area, morphological and anatomical structure, seed bank type, seed weight, and dispersal type, all of which are involved in determining a plant's colonizing ability. Many of these features are obviously correlated with each other due to causal or coincidental relationships.

To analyze all potentially important plant functional features would be time consuming. It would be useful to have a list of features, that are tested in terms of their significance for explaining the changes in plant composition during vegetation development.

The aim of our study is to determine which of the considered plant functional features are the most explicable (not redundant) for the vegetation changes in manmade habitats. The expected result will be a list of plant functional features that give a high probability of providing useful results in further studies in similar habitats.

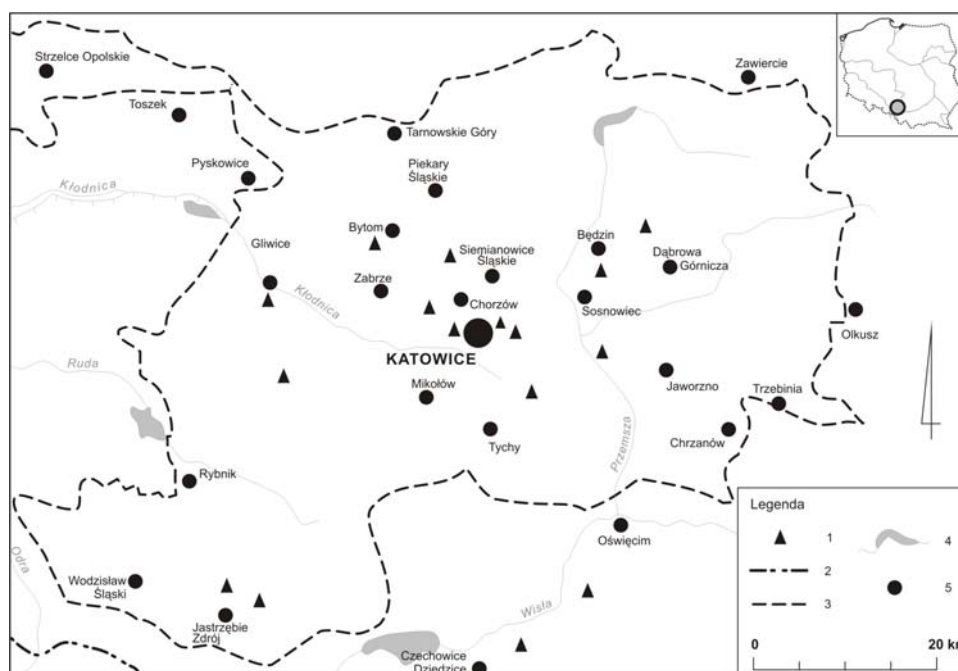


Fig. 1. Location of studied heaps in the area of the Silesian Upland.

1 – heaps, 2 – state border, 3 – borders of Silesian Upland, 4 – rivers and lakes, 5 – towns and cities

Table 1. Categories of analyzed plan functional groups.

Characteristic	Values
Height [cm] typical maximum	<50 50-100 >100
Leaf shape	compound simple
Leaf area [cm ²]	<10 10-100 >100
Root depth type	deep shallow deep+shallow
Root depth [cm]	< 10 10-50 >50
Photosynthetic pathway	C3 CAM C4
Mono/poly-carpic	monocarpic polycarpic facultatively polycarpic+monocarpic facultatively polycarpic
Vegetative reproduction/persistence (method)	rhizomes stolons rhizomes+stolons branching root stocks buds rooting stems stolons+rooting stems root buds root buds+rhizomes suckers suckers+none none
Vegetative reproduction/persistence (pattern)	diffuse ramets patch-forming patch-forming+diffuse ramets no ramets
Seed weight mean [mg]	<0.2 0.21-0.5 0.51-1.0 1.01-2.0 2.1-20 20.1-100 100.1-500 500.1-1,000 >1,000
Seed production typical range per flower	<1,000 >1,000
Time of germination (season)	spring autumn/summer twice many
Seedbank longevity	<1 yr 1yr- 5 yrs >5 yrs

Table 1. Continued.

Characteristic	Values
Seedbank type	short-term persistent long-term persistent transient many
Mean seedbank density [m ²]	<100 >100
Clonality normal state	tussock forming graminoid rhizome shortly/far creeping clones formed by suckering from roots far creeping stolons extensively creeping and rooting at nodes tip rooting (stems often turn downwards) little or no vegetative spread

Methods

Vegetation samples were taken from coalmine heaps throughout Poland's Upper Silesia (Fig. 1). The heaps were divided into four different age classes (A – up to 10 yrs. old; B – from 11 to 30 yrs. old; C – from 31 to 60 yrs. old; D – more than 60 yrs. old). In each of the four age classes 12 permanent plots were established and annual records were made of species composition and species cover. As a result, the vegetation of heaps in each age class was described by 120 vegetation samples that were recorded throughout ten years (1998-2007) of vegetation development. Species cover was assessed on a scale with intervals of 10% except that below 10% cover (levels of 1% and 5% were distinguished). Species cover was assessed once a year in August.

All the plant species recorded were allocated to functional groups drawn from the following categories:

- (i) typical maximum height,
- (ii) leaf shape,
- (iii) leaf area,
- (iv) root depth,
- (v) photosynthetic pathway,
- (vi) mono- poly-carpic,
- (vii) vegetative reproduction persistence method and pattern,
- (viii) mean seed weight,
- (ix) seed production (typical range),
- (x) time of germination,
- (xi) seed bank longevity,
- (xii) seed bank type,
- (xiii) mean seed bank density,
- (xiv) mean and intensity of vegetative spread (Table 1).

Information about the functional characteristics of each plant species were obtained from databases [28, 29].

In order to ascertain which features are the most applicable for study, principal components analysis (PCA) dimension reduction was employed. The vegetation data

Table 2. Comparison of cumulative percentage variance of species data for PCA 1 axis and eigenvalues of plant traits in each time series of vegetation development in coal-mine heaps in Silesian Upland. The highest values in each time series are in bold.

Variable	Time series 1	Time series 2	Time series 3	Time series 4	Entire period
Cumulative variance of species data for the first Axis in %	47.4	56.9	71.6	58.6	39.5
Typical maximum height >100 [cm]	-	-	0.9327	0.975	-
Compound leaf shape	-	0.9845	-	-	-
Simple leaf shape	0.9792	-	0.9747	0.975	0.9770
Leaf area (up to 10 cm ²)	-	-	0.9327	-	-
Leaf area (up to 100 cm ²)	-	-	0.9224	-	-
Photosynthetic pathway C3	0.9792	0.9156	0.9849	0.921	0.9772
Root depth type (deep)	-	0.9845	-	-	-
Mean seed weight (1.01-2.0 mg)	-	0.9845	-	-	-
Mixed seed bank type	0.9337	-	0.9731	0.926	-
Mean seed den sity [<100/m ²]	-	-	0.9461	-	-
Rrhizome shortly/far creeping	-	-	0.9505	-	-
Far creeping stolons	-	-	0.9505	-	-
Little or no vegetative spread	-	0.9845	-	0.975	-
Polycarpic	0.9011	-	0.9325		0.918

from 120 vegetation plots using cover data of species for each time series (age classes) were subjected to four separate PCA analyses. Additionally, PCA was used to analyze the entire period (whole data set). For the purpose of this analysis, the eigenvalues of the first axis with values higher than 0.9 for each feature in each time series were taken into account arbitrarily as the most explanatory. In the next step a Kruskal-Wallis test was used to compare medians of the most explanatory variables between age classes. *Apost-hoc* Conover test was employed for multiple comparisons.

Results

The cumulative variance for the first principal component varied between 47% and 72% in particular time series. As the whole period (all data set) is concerned, the cumulative explained variance only amounted to 39% for the first axis (Table 2).

In each age class time series the cover of plants representing the photosynthetic pathway C3 was one of the strongest explanatory variables and in the third age class time series (plots initially 31-60 years old) it was the most important. In the first age class time series (plots initially 10 years old or less), only four variables scored higher values than 0.9, but in the third age class as many as ten plant traits turned out to be highly explanatory (Table 2). The features that turned out to be the most explicable were leaf shape (compound and simple), seed bank type, typical maximum height, and the last listed PFG attribute – little vegetation spread (Table 2). In the intermediate time series, addition-

ally root depth and seed weight were important features. In relation to all age classes combined, then only simple leaf shape, photosynthetic pathway, and polycarpic features turned out to be the only so highly explanatory traits (Table 2). The remaining features are redundant.

Concerning the differences in the cover of plants with simple leaf shape in the different age classes, in the two

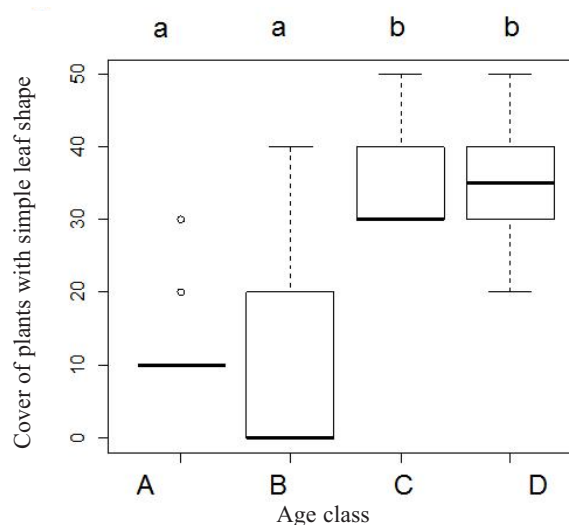


Fig. 2. Comparison of percentage plant cover with simple leaf shape between age 4 classes. Kruskal-Wallis test followed by Conover test. Age classes: A – up to 10 yrs. old; B – from 11 to 30 yrs. old; C – from 31 to 60 yrs. old; D – more than 60 yrs. old. The same small letters above whisker-boxes mean that medians do not differ significantly at $p < 0.05$.

later ones higher values can be observed when compared with the first two (Fig. 2). The cover of plants with the deep root type was the highest in first and the fourth age classes (Fig. 3). The cover of plants with the C3 photosynthetic pathway was the highest in first age class and the lowest in second and also in the third age class time series (Fig. 4). In the oldest age class time series (initially more than 60 years old) an increased value for the typical height of the plants can be observed. The differences between all age classes are statistically significant (Fig. 5).

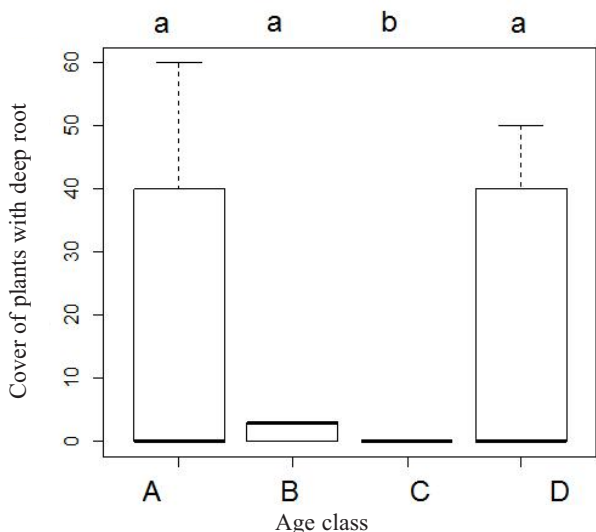


Fig. 3. Comparison of percentage plant cover with deep root type between age 4 classes. Kruskal-Wallis test followed by Conover test. Age classes: A – up to 10 yrs. old; B – from 11 to 30 yrs. old; C – from 31 to 60 yrs. old; D – more than 60 yrs. old. The same small letters above whisker-boxes mean that medians do not differ significantly at $p < 0.05$.

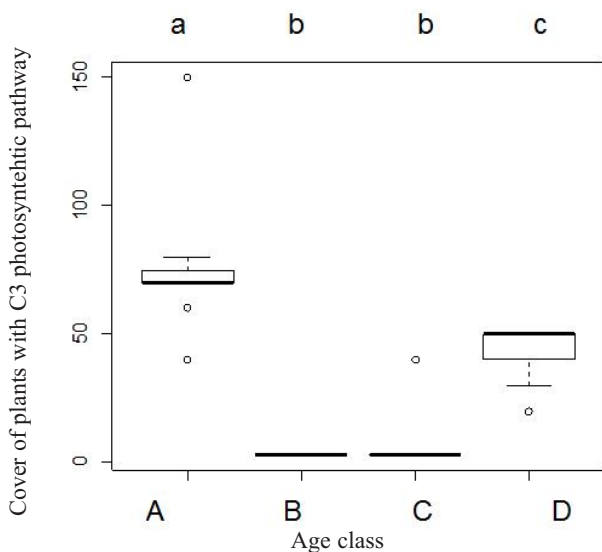


Fig. 4. Comparison of percentage plant cover with C3 photosynthetic pathway between age 4 classes. Kruskal-Wallis test followed by Conover test. Age classes: A – up to 10 yrs. old; B – from 11 to 30 yrs. old; C – from 31 to 60 yrs. old; D – more than 60 yrs. old. The same small letters above whisker-boxes mean that medians do not differ significantly at $p < 0.05$.

Discussion

Plant functional groups (PFGs) are defined according to the problem which has to be solved. No universal criteria for distinguishing PFGs exist. The concept of plant functional groups has been used in the analysis of meadow [12] and grassland [30] vegetation. Those analyses were performed in order to assess the trends in character of PFGs (changes in the number and cover of species) representing the stages of development distinguished in the course of vegetation development after meadow and grassland abandonment.

The changes in the balance between species that controls the feature of maximal height of plants appeared to be important in vegetation development on the heaps belonging to the two oldest age classes. The maximum height a plant can achieve has been underlined by many authors as being very important. Weiher et al. [31] claimed that the competitive ability of a plant is determined by the maximum height and biomass of the plant. Bullock et al. [32] stated that maximum height, biomass, and relative growth rate of a plant are crucial for measuring its competition abilities. Gaudet and Keddy [33], in their study of tall herbaceous vegetation, considered plant height to be the main measure of competition ability. An analysis of changes in the participation of species different in terms of their maximum height was performed in an experiment conducted by Moog et al. [34], who presented evidence that the participation of tall species increased along with the decrease in the level of disturbance. A similar relationship between disturbance level and maximum plant height was reported by Crawley [35], who explained his result in terms of the increasing competition for light in which species with the highest maximum height are the superior competitors.

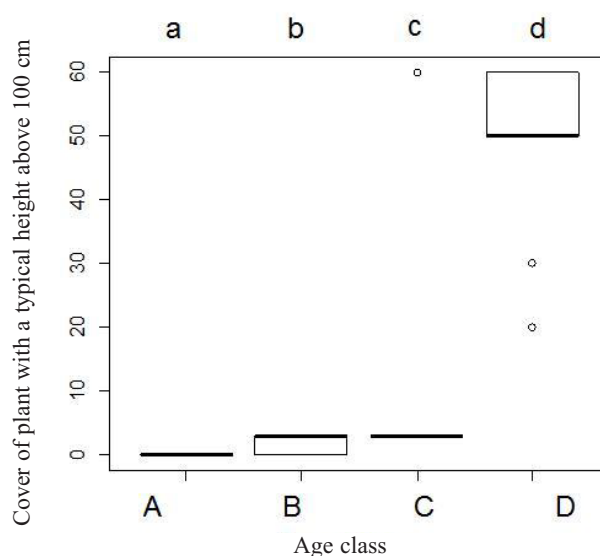


Fig. 5. Comparison of percentage plant cover typical height > 100 cm between age 4 classes. Kruskal-Wallis test followed by Conover test. Age classes: A – up to 10 yrs. old; B – from 11 to 30 yrs. old; C – from 31 to 60 yrs. old; D – more than 60 yrs. old. The same small letters above whisker-boxes mean that medians do not differ significantly at $p < 0.05$.

In Moog's experiment [34] small plants were more abundant in plots with treatments of regular grazing and biomass removal. Under such circumstances, small plants with leaves close to the ground (rosettes) were favoured. Grazing was also found by Noy-Meir et al. [36] to be a factor that favours a higher abundance of small plants. An increasing abundance of tall species characterized patches undergoing succession. These results are consistent with those obtained by Kahmen and Poschold [12], who studied the development of abandoned grasslands. The presented results, in which the plant height feature only becomes important in vegetation initially more than 30 years old, imply that it is possible, at least on coal spoil heaps, to suggest that it is some considerable time before plant height becomes an important competitive trait. The reason might be harsh environmental conditions.

The shape of leaves is an explanatory feature. In the presented results participation of species with simple and compound leaves differ between the first and second time series. Simple leaf shape is an important feature during vegetation changes in the first period of development and the compound leaf shape is useful for analyzing the second time series. Apart from the shape of leaves, the leaf area is also explanatory, particularly for the third time series. Traiser et al. [37] give a detailed analysis of European vegetation distribution depending on the tree species leaf physiognomy characteristics. Some generalisations were described regarding the changes in leaf area sizes in relation to environmental gradients. There is a trend of increasing leaf size with increasing temperature and precipitation. Coal-mine heaps provide habitats that are temporarily extremely wormy compared with the surroundings, but with no differences in precipitation [18]. The discussed generalizations consider the distribution in space while the objectives of the presented study are focused on changes in time. However, the presented results are focused on leaf area and there is another aspect of leaf physiognomy broadly discussed – specific leaf area. The importance of specific leaf area in vegetation analysis has also been recognized by other authors. The scheme of life strategies (LHS) proposed by Westoby [38] is based on three easy measurements of plant functional features: height (H), leaf area (L), and seed mass (S). Studies of factors influencing the participation of species of different plant leaf areas have shown that shade species with bigger leaves tend to obtain higher cover because plants with such features have a better chance of capturing more light [34, 39]. In habitats without disturbance, species with bigger leaves are superior competitors when light is the crucial factor. It has been stated that trees have lower photosynthesis levels than herbaceous plants [40]. Many studies have shown that the level of photosynthesis decreases along with vegetation development. Under optimum conditions the level of photosynthesis in the early successional species has been estimated as being as high as $50 \text{ mg} \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$ [41]. Westoby [38] regarded the specific leaf area as the best way to characterize optimal growth conditions while plant height and seed weight are important when species have to respond to disturbances. The ecological importance of leaf area was also underlined

by Weiher et al. [31] and Wilson et al. [39]. There are also some authors who are convinced that leaf area (along with a plant's height and canopy area) presents the best basis for predicting the competitive abilities of a species [33, 42, 43]. On the studied sites a higher cover of C3-species in the first and fourth age class was observed. The C3 and C4 plants respond differently to variations in environmental factors, such as temperature and moisture availability. The C4 plants are physiologically more adapted to moisture deficits than C3 plants. The detailed analysis of changes in vegetation composition during development on coal-mine heaps [18] showed that in the first age class herb plants were abundant and in the fourth age class dominance of trees was recorded. This suggests that the photosynthesis pattern found on the coal-mine heaps is related to the abundance of grasses, which was recorded in the second and third age classes.

Root system type appears as an explanatory variable in vegetation development in the third age class time series. Different root system types have different efficiency in resource capture at different soil levels. The shallow rooting grasses and deep rooting shrubs in cold steppe vegetation and the cold and warm season grasses in prairie vegetation, or combinations of nitrogen fixing plants together with species demanding nitrogen, are examples of species sharing the same habitat by the complementary exploitation of different space or time zones of resources [21, 44]. Among the many PFGs distinguished in the present study, the deep and shallow rooting plants present a significant level of complementarities [13, 45, 46]. The question arises why root system type became significant in the third age class, and why not in the others? Some authors present the opinion that the intermediate stages of vegetation development are the richest in species because they include, apart from species typical for the intermediate stage, some of those from earlier and later stages [8]. The species richness in the intermediate stages might be the reason why the importance of deep rooted species was not as evident as in the first and fourth age classes.

Seed weight appears as an explanatory variable in the second age class time series (Table 2). Analysis of participation of species with different seed weights revealed that a constant increase of cover of species with heavier seeds took place during the vegetation development on coal-mine heaps [8].

In studies in which seed weight was analyzed in relation to vegetation development it has been shown that with time the participation of species with heavier seeds increases [34]. In one experiment [34] it was also shown that with a treatment of controlled burning, the seed weight rose with decreasing frequency of disturbance. Reader [47] stated that disturbance favours the recruitment of species with small seeds. However, Lavorel et al. [48], did not confirm such a relationship between disturbance and colonization by species with a small seed mass. The results obtained by Dzwonko and Loster [30] revealed that in the grasslands studied, the participation of species with heavy seed increased with the development of the vegetation. Research on the relationship between total vegetation cover and the

participation of species with different seed weights showed that low total cover (i.e. much open ground) favoured the occurrence of species with small seed mass, while species with heavy seeds are more successful in shaded habitats, because it is easier for them to penetrate the litter layer and they are more resistant to fungus infection [47, 49]. Moreover, Reader [47] and Grime [49] stated that seedling survival in undisturbed habitats is higher for species with heavy seeds. The same result was obtained by Leishman [50], Kidson and Westoby [51], Westoby et al. [52], and Moles and Westoby [53]. All the results show that with vegetation development the participation of species with heavy seeds increases and that in shaded habitats species with small seed gain reproductive advantage. According to Reader [47] and Eriksson and Eriksson [54], seedlings established from small seeds are more abundant when gaps and open sites are present. It was also recorded that seed mass is a feature that might be related to the method of seed dispersion, growth form, and specific leaf area [38]. In Reader's [47] study the removal of vegetation cover caused intense seedling establishment of species with seed weights less than 1.4 mg. Nevertheless, Reader [47] concluded that seed mass is a weak basis for predicting a species ability to colonize open habitats and to persist in habitats in which herbivore and vegetation cover influence seedling establishment. Seed mass is inversely related to seed number in an evolutionary trade off [54, 56, 57]. Seed mass has long-term ecological implications. Jakobsson and Eriksson [57] proved that the variance of the per capita number of seeds inside one vegetation type can be important and significant. Heavy seeds produce established seedlings of high competitive abilities [58-60]. These two statements lead to the conclusion that a competition-colonization relationship exists. Species with smaller seed are good colonizers but worse competitors, while species with heavy seed are bad colonizers (small number of seeds) but good competitors (a lot of nutrients in seeds). Jakobsson and Eriksson [57] were able to explain only 40% of the overall variance in per capita seed production in terms of seed mass. The remaining 60% of variance might be the result of between-species differences in allocation strategies, habitat requirements, and plant architecture.

Vegetative spread appeared to be another feature that can explain spatiotemporal changes during vegetation development on coalmine heaps. The increase of species with the ability of intensive vegetative spread was reported from many vegetation development observations [12, 61, 62].

Conclusions

The application of the concept of PFGs in highly human-transformed habitats allows more explanatory results to be obtained, and the results may be more applicable than observation of changes in the species composition of vegetation patches that are relatively variable. Species with some particular features are more important (i.e. their cover undergoes explicable changes) in the early stages of development, others during the later stages. The results

reveal that the most explanatory PFGs are plant height, leaf shape, leaf area, root system type, seed weight, and photosynthetic pathway. These categories are not equally important at all phases of vegetation development. It is impossible to recommend one closed set of species feature categories to provide the best explanation of spatiotemporal changes of vegetation on manmade habitats during all developmental stages. The coal-mine heaps as well as other post-industrial sites provide very specific and changeable (in terms of chemical and physical properties) habitat for plants and other organisms. This might be a reason why a set of plant features explains the changes in vegetation only in a restricted period of time and not for the entire development process.

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