

Research Article

Patterns of Allocation CSR Plant Functional Types in Northern Europe

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Morphological and physiological parameters of 76 vascular plant species typical for Northern Europe were analyzed using Grime's classification. *C* species (competitors) have high levels of canopy height, leaf dry weight, and maximal lateral spread. *R* species (ruderal) have low leaf dry weight, longer flowering period, high rate of photosynthetic capacity and respiration, and high nitrogen content in the leaves. Stress-tolerant (*S*) species prevailing in habitats with limited resources are small and have low rate of photosynthetic activity and respiration. Principal component analysis (PCA) ordination showed a clear separation of species of different plant functional types according to their morphological and physiological parameters. The first PCA axis showed close relationship with the rate of respiration and photosynthetic activity and allowed us to differentiate *S* from *R* species. The second PCA axis correlated with morphological parameters associated with the size of plants and allowed us to differentiate *C* species from *S* and *R* species. Using PCA ordination, we developed a model that determines plant functional types in Northern Europe and analyzed plant functional types of several species that are not presented in Grime's classification. The proposed model has higher accuracy (84%) compared to similar models designed for other climatic zones.

1. Introduction

Prediction of response of individual species, communities, and ecosystems to the global climate changes and anthropogenic impact is one of the main problems of modern ecology [1, 2]. In such studies, it is expedient to consider the plant functional groups of assemblages of species with similar responses to changes in environmental conditions. Conception of life strategies developed by Ramenskii and Grime (the CSR theory) is an example of such generalization [3, 4]. According to the CSR theory, there are three main types of life strategies: competitors, ruderals, and stress-tolerators.

Species of different plant functional types have different biomass structure, intensity, and duration of growth processes, photosynthetic capacity and respiration rate, use of assimilates, and features of protective, and adaptive mechanisms and reactions [5–10].

Grime's system of plant functional types includes many species of vascular plants (more than 1000 species) that are typical for the herbaceous flora of Great Britain [2, 11].

The flora of the higher latitudes includes many arctic and alpine species that are not presented in Grime's system. Thus, the CSR classification cannot be used effectively to analyze ecosystems of the northern territories. Moreover, many species have high plasticity and demonstrate different strategic features depending on the environmental conditions (climatic, edaphic, and eco-coenotic), especially on the borders of their distribution areas [12].

Currently, there are several models that identify practical ordination of wild plants within the CSR space. Such models were developed for meadow vegetation of England, Ireland, and France [13]; alpine and subalpine vegetation of Italy [14, 15]; and flora of the Great Britain [11, 16].

Hodgson et al.'s [11] and Pierce et al.'s [15] models are the most known. These models were used to determine life strategies in different climate zones from alpine meadows in Italy [17] to desert vegetation in Turkey [18]. However, there are no data of these models being used in northern latitudes.

In these models, morphological predictors are used. In our view, morphological parameters are easier to measure

than other parameters. However, in some cases, these cannot be used for allocating plant functional types. For example, specific leaf area (SLA) is a key element of the “world-wide leaf economics spectrum” [19]. SLA corresponds to soil fertility and marks stress-tolerant species. However, in Northern Europe where many of the habitats are shaded, the leaf economics spectrum breaks down [20]. We attempt to provide a methodology that gets around this problem using functional (physiological) along with morphological predictors. Functional traits such as photosynthetic capacity, respiration rate, and concentration of carbon and nitrogen in leaves reflect processes of energy transformation and are closely related to plant activity, growth, and productivity [7, 9]. Thus, these are closely linked to the plant functional types.

The aim of the present study was to develop mathematical model allocating CSR functional type of vascular plants in Northern Europe based on morphological and functional parameters.

2. Materials and Methods

2.1. Plant Material. In our investigations, 76 species of herbs were used (57 have CSR status in Grime's system; see Appendix 1 in Supplementary Material available online at <http://dx.doi.org/10.1155/2016/1323614>) from 69 genera, 30 families. Nomenclature is given according to Cherepanov [21].

2.2. Study Sites and Data Source. Investigations were carried out during 2013–2015 in the middle taiga subzone (near Syktyvkar city, 61°34'N, 50°33'E), in the northern taiga (Ilych River basin, 63°13'N, 58°34'E), and far northern taiga (near Seida village, 67°3'N, 62°36'E). Studies of morphological and physiological parameters were performed during the flowering period (July) in typical communities. Most of the data on physiological parameters (photosynthetic capacity and respiration rate) were obtained previously [10].

In addition, we used the data from the TRY DB database (<https://www.try-db.org/>) [22] in order to eliminate differences in species morphology related to specific habitats. Among all the received data, records from the territory of Central and Northern Europe and Great Britain (more than 17,000 primary records) were selected. The average parameters from all sources (arithmetic mean) were used in the succeeding analysis.

2.3. Trait Measurement

2.3.1. Canopy Height. Canopy height was measured from the ground to the top of the generative parts of plants [2]. Measures were conducted with a 30-time replication.

2.3.2. Leaf Dry Weight and Dry Matter Content. Leaf area and dry weight were measured in mature leaves from the middle of stems. Leaf area was measured using photo images by using ImageJ (<https://imagej.nih.gov/ij/>). Measures of leaf wet weight were made in the field during 1–2 h after sampling.

Sampled leaves were placed in hermetically sealed plastic bags to reduce the evaporation of water. Leaf dry weight was measured in the laboratory after the leaves were dried for 24 h at a temperature of 80°C. Dry matter content was calculated as percent ratio of leaf dry weight to leaf wet weight. Measurements of 30–120 samples were replicated according to size and weight of leaves.

2.3.3. Lateral Spread and Phenological Data. Lateral spread of the species is determined by root system, life form, and distance between the ramets (vegetative individuals) of the plant [11]. We used Raunkjær's life-form systems to determine the type of lateral spread of each species. Phenology of the model species was studied using <http://www.plantarium.ru/> (open atlas of vegetation of Russia and bordering countries).

2.3.4. Functional Parameters. CO₂ exchange of the leaves was measured using LI-7000 (LI-COR, Inc., Lincoln, NE, USA) and LCPro+ (ADC BioScientific Ltd., Hoddesdon, UK) systems based on the IR analyzer. Small leaves (smaller than the chamber area) were measured in groups. Large leaves (length or width does not fit in the chamber) were cut from the middle without large veins. Gas exchange of excised leaves was measured. Photosynthetic capacity was measured at saturating photosynthetically active radiation (800–1200 $\mu\text{mol}/\text{m}^2\text{c}$); respiration rate of the leaves was measured in the dark at a temperature of 18–20°C. Leaves were sampled from 10 to 15 individual plants. The results for photosynthesis and respiration are presented based on the leaf dry weight.

The content of total nitrogen and carbon was measured in dry ground biomass using elemental CHNS analyzer EA-1110 (Italy) in the ecoanalytical laboratory of the Institute of Biology of Komi SC UB, RAS. Samples were collected in double replication, and each sample was analyzed in double or triple replication.

2.4. CSR Classification. The basis of the CSR classification is three axes that are related to competition, stress tolerance, and ruderality of species (Figure 1(a)). Grime allocated 19 types of primary, secondary, and tertiary plant functional types [2]. It is common to use letter designations for plant functional types (Figure 1(b)). However, in modeling, it is easier to use digital coordinates of species in the three axes (Figure 1(c)).

2.5. Model Building Scheme. In the first step, the CSR status of species (which are presented in the classification) was determined according to Grime's classification [11].

Then species were divided into four groups: species with domination of competitor strategy (C, C/CR, C/CS, and C/CSR), ruderal strategy (R, R/CR, R/SR, and R/CSR), and stress-tolerators (S, S/SC, S/SR, and S/CSR). In addition, we defined a group of species as intermediate types (CSR, CR/CSR, SC/CSR, SR/CSR, CR, SC, and SR) (Figure 1(b)).

Furthermore, we used the analysis of variance to select traits with significant difference ($p < 0.05$) between these four groups. These parameters were included in the model.

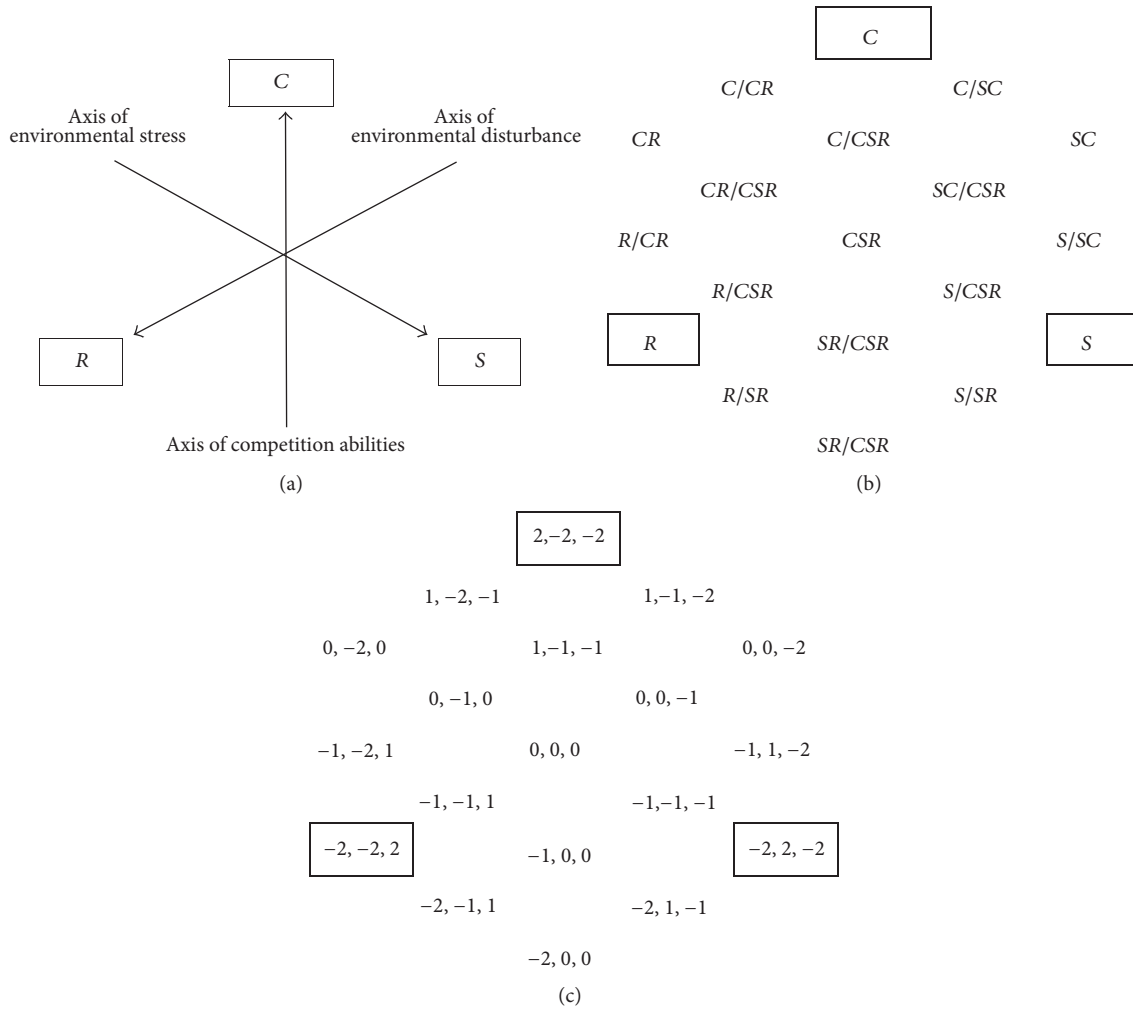


FIGURE 1: The basic classification of CSR plant functional types [11]. (a) Main axes: C axis of competition (ability of plants to displace the other species under favorable environmental conditions); S axis of stress tolerance (ability to withstand long-term adverse environmental conditions); and R axis of ruderality (ability to grow faster in disturbed sites). (b) Primary, secondary, and tertiary functional types (a total of 19 types). (c) Triple coordinates of the types.

The model was based on multivariate analysis by principal component analysis (PCA) according to their morphological and physiological traits selected in the previous step. The obtained two-dimensional PCA coordinates for all species were then allocated to three axes of CSR space. The axes of CSR space were presented using lines connecting the center of PCA ordination with centroids (mean values of coordinates of species allocated to one group) for C, S, and R groups, respectively.

The projection of PCA coordinates of all species to these three axes was considered as new (adjusted) coordinates in CSR space.

In the last step, we identified the CSR strategy for each species as a one of 19 plant functional types that have a minimum distance to the CSR coordinates of species. The distance is calculated by the formula $SS = (C_u - C_m)^2 + (S_u - S_m)^2 + (R_u - R_m)^2$, where C_u , S_u , and R_u are the coordinates of species and C_m , S_m , and R_m are the possible strategies [11].

All analyses were performed for transformed data (Table 1).

The relationship between parameters was assessed using Spearman's nonparametric rank correlation. Variance analysis, PCA ordination, and correlation analysis were performed using IBM SPSS Statistics 19. Model allocation for plant functional types was realized in Microsoft Excel.

3. Results

3.1. Morphological and Physiological Parameters of Plant Species of Different Functional Types. Most of the morphological and physiological traits showed significant differences between species of different functional types (Table 2). Mean CH and LDW of C species were 2-3 times higher than those of R and S species. Typical competitors in our studies were perennial grasses (*Bromopsis inermis*, *Calamagrostis*

TABLE 1: Definition (units) of the predictor variables and method for its transformation in models.

Code	Trait name (units)	Transformation
CH	Canopy height (mm)	Natural logarithm*
LDMC	Dry matter content in the fully hydrated leaves from the middle of stem (%)	Square root
FS	Flowering start ((1) first flowering in March; (2) April; (3) May; (4) June; (5) July; and (6) August)	—
FP	Normal duration of flowering period (months)	—
LS	Lateral spread. Six-point classification [11]	—
LDW	Leaf dry weight of the fully hydrated leaves from the middle of stem (mg)	Natural logarithm plus 3
SLA	Specific leaf area is area/dry weight (mm ² /mg)	Square root
PN	Photosynthetic capacity (mg CO ₂ /g dry weight per hour)	Square root
RD	Respiration rate in dark (mg CO ₂ /g dry weight per hour)	Square root
LNC	Leaf nitrogen concentration (mg/g)	Square root
LCC	Leaf carbon concentration (mg/g)	Square root

*Hodgson et al. [11] used a point system to assess height. However, we used continuous transformation of natural logarithm in order to reduce the information losses.

TABLE 2: Morphological and physiological traits of plant species of different functional types.

Trait	Mean values				ANOVA	
	C	S	R	CSR	F	p
CH	920.8 ± 83.9	296.2 ± 50.4	383.9 ± 39	398.9 ± 49.8	13.924	0.000
LDW	379.4 ± 179.8	76.3 ± 28.2	109.5 ± 51.7	100.3 ± 26.6	3.377	0.025
SLA	25.6 ± 1.3	34.6 ± 4.4	32.9 ± 2.3	27.9 ± 2.4	2.507	0.069
LDMC	26.2 ± 1.5	22.5 ± 1.9	17.1 ± 1.1	21.5 ± 1.8	5.509	0.002
LS	4.3 ± 0.3	2.9 ± 0.3	2.2 ± 0.4	3.4 ± 0.3	6.108	0.001
FS	3.8 ± 0.1	3.7 ± 0.2	3.6 ± 0.2	3.9 ± 0.2	0.509	0.678
FP	2.7 ± 0.2	2.7 ± 0.4	3.8 ± 0.3	2.4 ± 0.2	5.379	0.003
PN	14.5 ± 2.3	8.5 ± 1.8	22.3 ± 3.2	11.4 ± 1.6	6.027	0.001
RD	2 ± 0.2	1.3 ± 0.3	2.6 ± 0.2	1.8 ± 0.2	4.658	0.006
LNC	29.4 ± 1.7	22.9 ± 1.8	31 ± 2.1	28.5 ± 1.7	3.005	0.038
LCC	437.9 ± 8.2	439 ± 7.6	417.7 ± 4.2	443.2 ± 4.2	3.530	0.021

Traits are given like in Table 1.

The arithmetic mean and the error of the arithmetic mean are given. C - species competitors ($n = 15$), R: ruderals ($n = 10$), S: stress-tolerators ($n = 14$). CSR: intermediate species ($n = 18$). Results of ANOVA (F-test, p : significance level).

epigejos, and *Dactylis glomerata*) and nitrophilous plants of rich habitats (*Artemisia vulgaris*, *Urtica dioica*, *Arctium lappa*, and *Angelica sylvestris*). These species were characterized by a height more than 1 m.

SLA did not demonstrate significant differences among plant functional types (Table 2). The maximal SLA values at 50–60 mm²/mg were revealed for S species preferring spruce forests (*Oxalis acetosella* and *Trientalis europaea*) and ruderal species *Stellaria media* and *Myosotis arvensis* (40–50 mm²/mg). Minimal SLA values were found for species from the competitor group (15–30 mm²/mg). S species preferring mire and mountain tundra communities (*Rubus chamaemorus*, *Saussurea alpina*, and *Hedysarum arcticum*) demonstrated low SLA levels.

LDMC increased in the R-S-C species order. The highest LDMC (32–38%) was found for grasses from the competitor group (*Bromopsis inermis*, *Calamagrostis epigejos*, and *Elyt-rigia repens*). Ruderal species demonstrated minimal LDMC values at 9–13% (*Capsella bursa-pastoris*, *Stellaria media*, and *Taraxacum officinale*). Stress-tolerators included species with

both low (*Oxalis acetosella* and *Trientalis europaea*) and high (*Melica nutans* and *Pyrola rotundifolia*) levels of LDMC.

The functional traits (PN, RD, and LNC) also show a significant difference between functional types. PN and RD of leaves increased in the S-C-R species order (Table 2). The highest level of LNC was revealed in the leaves of species from R and C plant functional types (3% in dry weight), and this was higher than in leaves of S species (Table 2).

The group of CSR species according to most of the traits (except for FP, FS, and LCC) is in the intermediate position in the CSR system (Table 2). This fact allows us to use CSR group as the “starting point.” Differences in morphological and functional parameters from this “starting point” were interpreted as a “shift” of the species location in Grime’s triangle relative to the central CSR point.

3.2. Allocating CSR Functional Types in Northern Europe. PCA ordination showed a clear separation of species from different plant functional types according to their morphological and functional traits (Figure 2). PCA axis 1 and

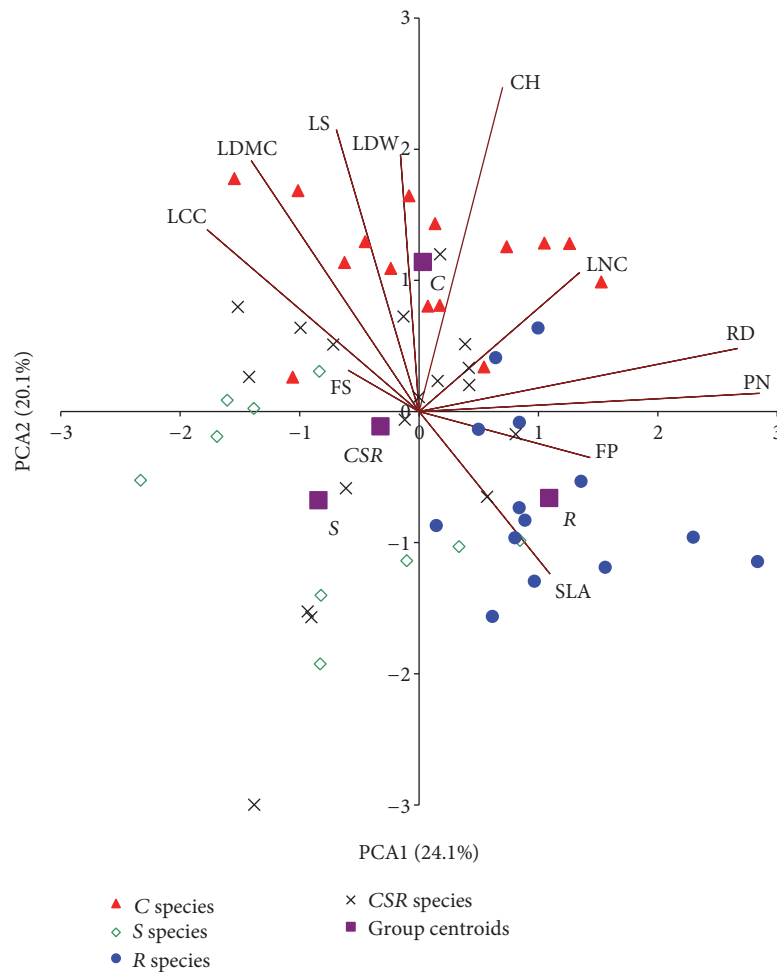


FIGURE 2: Principal component analysis (PCA) ordination of species of different plant functional types. Predictors morphological and physiological traits that differed significantly for different groups of species (Table 2). Lines show a correlation between parameters and PCA axes. C, species competitors; S, stress-tolerators; R, ruderals; CSR, intermediate species. Squares with letters are centroids of groups of species.

axis 2 accounted for 44.2% of total variation. PCA 1 was closely correlated with RD and PN that reflected the rate of metabolism (Table 3, Figure 3) and showed distinct grouping of S and R species. Typical S species are located in the left part of the PCA 1 and demonstrated low levels of PN and RD. Opposite positions of the PCA 1 axis are occupied by R species (*Capsella bursa-pastoris*, *Lepidotheca suaveolens*, and *Stellaria media*) with maximal values of PN and RD. C species are in intermediate position.

PCA 2 axis was positively correlated with the following morphological traits: CH, LDW, LS, and LDMC (Table 3, Figure 2). C species of large physical size are located in the upper part of the PCA ordination: *Angelica sylvestris*, *Elytrigia repens*, *Filipendula ulmaria*, *Urtica dioica*, and *Vicia sylvatica*. Small-size R species (*Myosotis arvensis*, *Poa annua*) and S species are moved to the bottom part of the ordination diagram (*Campanula rotundifolia*, *Oxalis acetosella*).

The next step was to convert the two-dimensional PCA ordination to the relevant C, S, and R axes in Grime's triangle. For this purpose, we projected points to the lines connecting

the center of PCA ordination with centroids of C, S, and R groups. The projections of species on these lines were considered as new coordinates in CSR space. For example, the species *Dactylis glomerata*, with PCA coordinates (0.734 and 1.257), after such projection will receive new coordinates (1.277, -1.360, and -0.022) in the C, S, and R axes, respectively (Figure 3). These values have a minimum distance to the point (1, -1, and -1), which corresponds to C/CSR plant functional type.

The developed model is provided in Excel spreadsheet in Supplementary Material Appendix 1.

The coordinates of species in CSR space of our model were closely correlated with their coordinates in Grime's classification. The C axis showed a correlation of 0.78 and S and R axes 0.64 ($p < 0.01$) (Table 3).

4. Discussion

4.1. Analysis of Morphological and Functional Traits and Their Correlation with CSR Axes. Physical size of plants and

TABLE 3: Correlation between species traits, PCA axes score, and species coordinates in “Grime’s triangle.”

	PCA 1	PCA 2	Axis C	Axis S	Axis R
Traits ($n = 76$)					
CH	0.2 n.s.	0.71**	0.71**	-0.59**	-0.18 n.s.
LDW	-0.04 n.s.	0.56**	0.56**	-0.28*	-0.3**
SLA	0.31**	-0.35**	-0.35**	-0.06 n.s.	0.46**
LDMC	-0.4**	0.55**	0.54**	-0.01 n.s.	-0.64**
LS	-0.2 n.s.	0.61**	0.61**	-0.22 n.s.	-0.48**
FS	-0.17 n.s.	0.09 n.s.	0.09 n.s.	0.11 n.s.	-0.17 n.s.
FP	0.41**	-0.1 n.s.	-0.1 n.s.	-0.27*	0.35**
PN	0.82**	0.04 n.s.	0.06 n.s.	-0.66**	0.66**
RD	0.76**	0.14 n.s.	0.16 n.s.	-0.68**	0.57**
LNC	0.38**	0.3**	0.32**	-0.51**	0.14 n.s.
LCC	-0.51**	0.4**	0.39**	0.14 n.s.	-0.66**
Species coordinates in the CSR triangle ($n = 57$)					
C	-0.14 n.s.	0.78**	0.78**	-0.38**	-0.47**
S	-0.59**	-0.26*	-0.27*	0.64**	-0.35**
R	0.54**	-0.44**	-0.43**	-0.15 n.s.	0.64**

*Denote significance at the $p < 0.05$ level, ** $p < 0.01$, and n.s.: no significance.

PCA 1 and 2: first two axes of PCA ordination.

Axis C, axis S, and axis R: coordinates of species in the space of new model.

Morphological and functional traits are given as in Table 2.

C, S, and R: coordinates of species in the space of Grime’s classification.

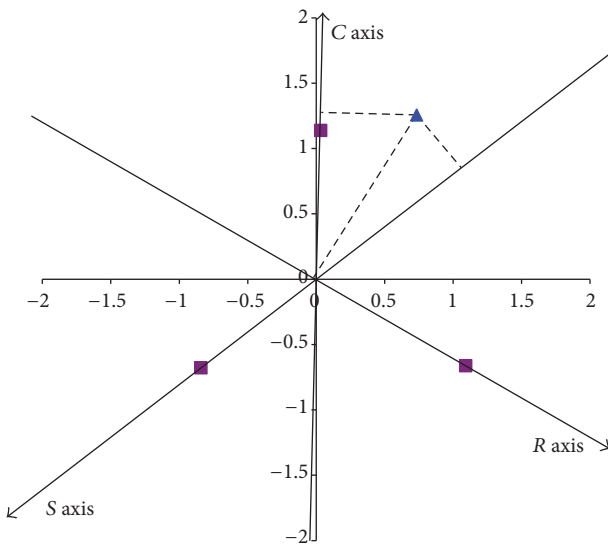


FIGURE 3: Converting the coordinates of *Dactylis glomerata* from principal component analysis ordination to CSR coordinates (projection of the species on C, S, and R lines).

their relative growth rate are considered as key traits in the classification of plant functional types [2]. Competitor species more often establish intact habitats with favorable environmental conditions [2, 11]. These plants capture most of the resources and invest them into its own biomass. Leaves of competitor plants are high and/or have large area and weight (Table 2). Markers of C type could be such traits (Table 3) as CH (correlation coefficient with the C axis in our model –

0.71), LDW (correlation coefficient – 0.56), and high LS values of 0.61

In Grime’s model, competitors are considered as fast-growing species with low LDMC values. On the contrary, according to our data, C species demonstrate the highest LDMC values. This observation is likely connected with the fact that most of the Northern C species cease active growth in July (the month when we take samples) and begin flowering. As growth ceases, cell wall thickening occurs, leading to an increase in the LDMC values.

Stress-tolerators, prevailing in conditions with limited resources, are slow-growing plants with low rate of metabolism [2, 5, 10, 11, 23]. Stress-tolerators are small plants with the lowest values of photosynthetic activity and respiration rate that reveal minimal content of nitrogen and maximal content of carbon in the leaves. The highest negative correlations with S axis were found for CH, PN, RD, and LNC (Table 3).

It is considered that low SLA values indicate stress-tolerant species with relatively low growth rate [24, 25]. SLA indicates acquisitive economics of the leaf area development. Low SLA values are typical for plants of S type with low metabolism and growth rate [19, 26, 27]. However, the use of this parameter leads to several issues, called the “Oxalis” effect [16]. The key aspect of this effect is that a group of S species includes plants growing under different kinds of stress; therefore, they have different adaptive reactions [28]. In our study, species of tundra and mire communities (*Epilobium palustre*, *Eriophorum vaginatum*, *Carex dioica*, and *Potentilla crantzii*) growing in an environment with waterlogging and limited nutritional elements were often characterized by thick leathery leaves and demonstrated low

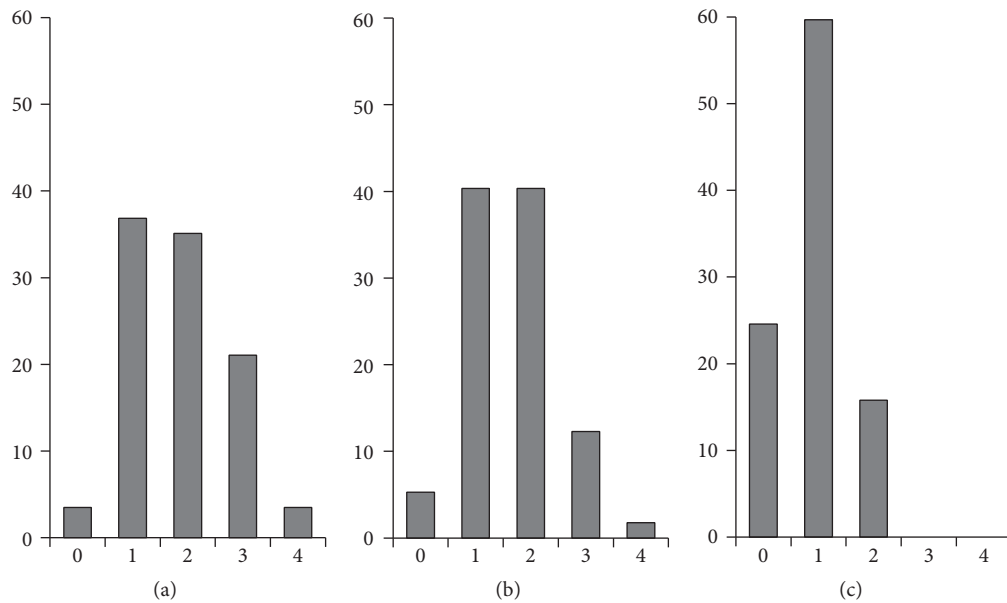


FIGURE 4: Frequency diagrams showing the percentage of matching model results with original Grime's classification. On the horizontal axis is the deviation between positions in the original CSR classification and given by the model ((a), Hodgson et al.'s model; (b), Pierce et al.'s model; (c), our model). The percentage of species is presented on the vertical axis.

SLA values (10–30 mm²/mg). However, species preferring spruce forests with limited light (*Fragaria vesca*, *Oxalis acetosella*, and *Trientalis europaea*) had high SLA values (up to 50–60 mm²/mg). Therefore, following Gross et al. [29], we considered that SLA should ideally not be used as a marker of S plant functional type.

Ruderals prefer rich habitats with weak competition caused by certain disturbance of the vegetation cover. These species demonstrate high growth rate provided by increased metabolic activity: intensive respiration and high nitrogen content in leaves [8, 10, 23, 26, 30]. Usually, ruderals are annual and biennial species with seed reproduction, investing most of their resources to reproduction. They occupy disturbed habitats owing to their accelerated ontogenetic development (ephemeroids) and/or extended period of flowering and fruiting [4]. According to our data, low values of lateral spread (LS) and long flowering period (FP) could be markers of R plant functional type. Ruderals also demonstrated low LDMC values, high SLA values, and maximal level of PN and RD (Tables 2 and 3).

4.2. Validation of the Developed Model Allocating Plant Functional Types in Northern Europe. Table 4 shows a comparison of Grime's functional types [2] with plant functional types allocated using Hodgson et al.'s model [11], Pierce et al.'s model [15], and our model. The number of steps (points of tertiary CSR classification, Figure 1(b)) was determined between the species location in our model and that in Grime's system. If functional types matched, there were no steps. Maximal four steps were noted when the coordinates of functional types were in the opposite sides of Grime's triangle.

In Hodgson et al.'s model, only 40% of species (23 from 57) showed high matching (distance 0 or 1) (Table 4,

Figure 4(a)). Of the species, 35% demonstrated low matching (distance 2) and 21% strong deviation (distance 3). Two species (*Melica nutans* and *Oxalis acetosella*) demonstrated extremely distant locations (distance 4).

In general, in Hodgson et al.'s model, the highest deviation (distances 3 and 4) was found for S species typical for spruce forests (*Oxalis acetosella*, *Trientalis europaea*, *Fragaria vesca*, and *Geum rivale*). All these species demonstrated high SLA and low LDMC values and, according to the modeling, were allocated as CR, R/CR, or C/CR type (Table 4). Obtained difference may be explained by the "Oxalis" effect. Only species with low SLA values (20–30 mm²/mg and lower) and high LDMC values (over 30%) may be potentially considered as stress-tolerators based on the analysis of regression equations of Hodgson et al.'s model. In the northern environment, there are species typical for tundra and mire communities, for example, *Rubus chamaemorus*. It should also be noted that functional types of almost all species allocated using Hodgson et al.'s model were moved to increasing C and R points and decreasing S points (Table 4).

Comparing the model of Pierce et al. [15] with the reference position showed high matching (distances 0 and 1) for 46% of the species (Table 4, Figure 4(b)). Low similarity (distance 2) was revealed for 40% of the species. High deviation (distances 3 and 4) was noted for 14% of the species, including stress-tolerators (*Oxalis acetosella* and *Trientalis europaea*) and grass competitors (*Bromopsis inermis* and *Elytrigia repens*).

The analysis of the model developed in our research showed the highest matching with the reference species positions given in Grime's classification. Distance between relevant and reference position of species was 0 or 1 for 84% of species. Nine species (16%) demonstrated low matching

TABLE 4: Comparison of reference plant functional type [2] and determined by Hodgson et al. [11], Pierce et al. [15], and our model for northern conditions.

Species	Reference plant functional type	Hodgson et al.'s model		Pierce et al.'s model		Our model	
		Strategy	Distance*	Strategy	Distance	Strategy	Distance
<i>Achillea millefolium</i>	CSR	CR	2	CR/CSR	1	CSR	0
<i>Aconitum septentrionale</i>	—	C/CR	—	C/CR	—	C/CR	—
<i>Alisma plantago-aquatica</i>	R/CR	C/CR	2	C/CR	2	CR/CSR	1
<i>Amoria repens</i>	CR/CSR	CR	1	R/CSR	1	CSR	1
<i>Angelica sylvestris</i>	C/CR	C	1	C/SC	2	C/CSR	1
<i>Antennaria dioica</i>	SR/CSR	R/CR	2	R/SR	1	S/SR	1
<i>Arctium lappa</i>	C/CR	C/CR	0	C	1	CR	1
<i>Artemisia vulgaris</i>	C/CR	CR	1	CR	1	CR/CSR	1
<i>Astragalus frigidus</i>	—	CR	—	R/CSR	—	CR/CSR	—
<i>Bartsia alpina</i>	—	CR	—	R/CSR	—	S/CSR	—
<i>Bistorta vivipara</i>	—	CR	—	SR/CSR	—	S/CSR	—
<i>Bromopsis inermis</i>	C	SC/CSR	2	S/CSR	3	C/CSR	1
<i>Calamagrostis epigeios</i>	C/SC	C	1	S/CSR	2	C/CSR	1
<i>Caltha palustris</i>	CSR	CR	2	C/CR	2	CSR	0
<i>Campanula rotundifolia</i>	S/CSR	CR	3	R	3	S/CSR	0
<i>Capsella bursa-pastoris</i>	R	R/CR	1	R/CR	1	R	0
<i>Centaurea jacea</i>	—	CR	—	CSR	—	CSR	—
<i>Chamaenerion angustifolium</i>	C	C/CR	1	CR/CSR	2	C/CSR	1
<i>Comarum palustre</i>	—	C/CR	—	C/CSR	—	C/CSR	—
<i>Cortusa matthioli</i>	—	CR	—	CR	—	S/CSR	—
<i>Crepis sibirica</i>	—	CR	—	CR	—	R/CSR	—
<i>Dactylis glomerata</i>	C/CSR	C	1	CSR	1	C/CSR	0
<i>Deschampsia cespitosa</i>	SC/CSR	C/CSR	1	S/CSR	1	SC/CSR	0
<i>Elytrigia repens</i>	C/CR	SC	3	S/SC	3	C/SC	2
<i>Epilobium palustre</i>	S/CSR	CR	3	R/CSR	2	R/CSR	2
<i>Epipactis atrorubens</i>	S	C/CSR	3	CSR	2	S/CSR	1
<i>Erysimum cheiranthoides</i>	R	CR	2	R/CSR	1	R/CSR	1
<i>Filipendula ulmaria</i>	C/SC	C	1	C/CSR	1	C/SC	0
<i>Fragaria vesca</i>	S/CSR	C/CR	3	CSR	1	S/CSR	0
<i>Galeopsis speciosa</i>	R/CR	CR	1	CSR	2	CR/CSR	1
<i>Geranium albiflorum</i>	—	CR	—	CR/CSR	—	CSR	—
<i>Geranium sylvaticum</i>	CSR	C/CR	2	C/CR	2	C/CSR	1
<i>Geum rivale</i>	S/CSR	C/CR	3	C/CSR	2	SC/CSR	1
<i>Gymnadenia conopsea</i>	SR	C/CSR	3	CR	4	S/CSR	2
<i>Hedysarum arcticum</i>	—	CR	—	CR/CSR	—	C/CSR	—
<i>Hypericum maculatum</i>	CR/CSR	SC/CSR	2	SR/CSR	2	SC/CSR	2
<i>Lathyrus pratensis</i>	CSR	C/CR	2	SR/CSR	1	C/CSR	1
<i>Lathyrus vernus</i>	—	C/CR	—	CR/CSR	—	SC/CSR	—
<i>Leontodon autumnalis</i>	R/CSR	R/CR	1	CR	2	R/CSR	0
<i>Lepidotheca suaveolens</i>	R	R/CR	1	R/CR	1	R/CSR	1
<i>Leucanthemum vulgare</i>	CR/CSR	CR	1	CR	1	SR/CSR	2
<i>Maianthemum bifolium</i>	—	CR	—	R/CR	—	CSR	—
<i>Melampyrum pratense</i>	R/SR	R/CR	2	R/CSR	1	R/CSR	1
<i>Melica nutans</i>	S/SC	R/CR	4	SR/CSR	2	S/CSR	1
<i>Myosotis arvensis</i>	R	CR	2	R/CR	1	R/CSR	1
<i>Oxalis acetosella</i>	S/SR	CR	4	R/CR	3	S/SR	0
<i>Paeonia anomala</i>	—	C/CR	—	C/CR	—	SC/CSR	—
<i>Paris quadrifolia</i>	SR/CSR	R/CR	2	R/CR	2	S/SR	1
<i>Pimpinella saxifraga</i>	SR/CSR	C/CR	3	SC/CSR	2	SC/CSR	2

TABLE 4: Continued.

Species	Reference plant functional type	Hodgson et al.'s model		Pierce et al.'s model		Our model	
		Strategy	Distance*	Strategy	Distance	Strategy	Distance
<i>Pinguicula vulgaris</i>	SR	R/CR	3	R	2	S/SR	1
<i>Plantago major</i>	R/CSR	CR	2	CR	2	SR/CSR	1
<i>Plantago media</i>	S/CSR	CR	3	CR	3	SR/CSR	1
<i>Poa annua</i>	R	R/CR	1	SR	2	SR	2
<i>Polygonum aviculare</i>	R	CR	2	SR/CSR	2	CR/CSR	2
<i>Pyrola rotundifolia</i>	S	SC	2	S/CSR	1	S/SC	1
<i>Ranunculus propinquus</i>	—	CR	—	R/CR	—	SR/CSR	—
<i>Ranunculus repens</i>	CR	C/CR	1	CR	0	CR/CSR	1
<i>Rhodiola rosea</i>	—	R/CR	—	R	—	R/CSR	—
<i>Rubus chamaemorus</i>	SC/CSR	C/SC	1	SC/CSR	0	SC	1
<i>Sanguisorba officinalis</i>	C/CSR	C/CR	1	CSR	1	SC/CSR	1
<i>Saussurea alpina</i>	—	CR	—	CR/CSR	—	S/CSR	—
<i>Stellaria media</i>	R	CR	2	R/CR	1	R	0
<i>Tanacetum bipinnatum</i>	—	CR	—	CR	—	CSR	—
<i>Tanacetum vulgare</i>	C/CSR	CR	2	CR/CSR	1	C/CSR	0
<i>Taraxacum officinale</i>	R/CSR	CR	2	C/CR	2	CSR	1
<i>Thalictrum simplex</i>	—	CR	—	SR/CSR	—	SC/CSR	—
<i>Trientalis europaea</i>	S/CSR	CR	3	R/CR	3	SR/CSR	1
<i>Trifolium medium</i>	SC/CSR	C/CR	2	SC/CSR	0	CSR	1
<i>Tripleurospermum perforatum</i>	R	R/CR	1	CR/CSR	2	R/CSR	1
<i>Trollius europaeus</i>	SC/CSR	CR	3	CR	3	CSR	1
<i>Urtica dioica</i>	C	C	0	SC/CSR	2	C/CR	1
<i>Valeriana wolgensis</i>	CSR	CR	2	CR	2	CR/CSR	1
<i>Veronica longifolia</i>	—	C/CR	—	CSR	—	C/CSR	—
<i>Vicia cracca</i>	C/CSR	C	1	CSR	1	C/CSR	0
<i>Vicia sepium</i>	C/CSR	C/CR	1	CSR	1	CR	2
<i>Vicia sylvatica</i>	C/CSR	C/CR	1	CR/CSR	1	C/CSR	0

*Distance: number of tertiary types between reference strategy and determined by models.

(distance 2). Distances 3 and 4 were not revealed at all (Table 4, Figure 4(c)).

Some species demonstrated high deviation between the reference strategy and our model (distance 2 in Table 4). *Epilobium palustre* has S/CSR type in Grime's classification. However, in our case study, it was allocated in R/CSR type. Shifting the species position to the ruderal type was caused by relatively high values of PN (17 mg CO₂/g dry weight per hour) and RD (3.1 mg CO₂/g dry weight per hour), which is typical for C and R species (Table 2). Change of functional type of *Hypericum maculatum* from CR/CSR to SC/CSR was caused by low values of PN (6.5 mg CO₂/g dry weight per hour) and RD (1 mg CO₂/g dry weight per hour), which is typical for plants of S functional type.

Some species demonstrating changes in their functional types (*Poa annua*, *Polygonum aviculare*, *Pimpinella saxifraga*, and *Vicia sepium*) have known not only the position in Grime's classification but also the "area of variability" [2]. For example, *P. annua* has R type in Grime's CSR system. However, its potential "area of variability" (noted by a dotted line in Figure 5(a)) covers the area of CR-CSR-SR types. In

our model, *P. annua* was allocated in SR functional type, which is in the area of possible types. Similar results were found for *Polygonum aviculare*, *P. saxifraga*, and *V. sepium* (Figure 5).

Therefore, our model allows to us consider a wide variety of species establishing different habitats with different ecological backgrounds. Averaging of morphological and functional traits for large variety of plants from Russia and Central and Northern Europe allowed us to clarify the impact of specific environment and to analyze the traits determined by genotypic specificity. It should be noted that, by using functional traits closely related to the rate of metabolism, we improved the determination accuracy for stress-tolerators. Comparison of the developed model against other models showed its higher accuracy for the species of Northern Europe. It was revealed that the differences between our model and the reference position were within the limits of potentially possible plant functional types in Grime's triangle. Obtained data on morphological and functional parameters can be used as markers for allocating plant functional types of northern species not presented in Grime's classification.

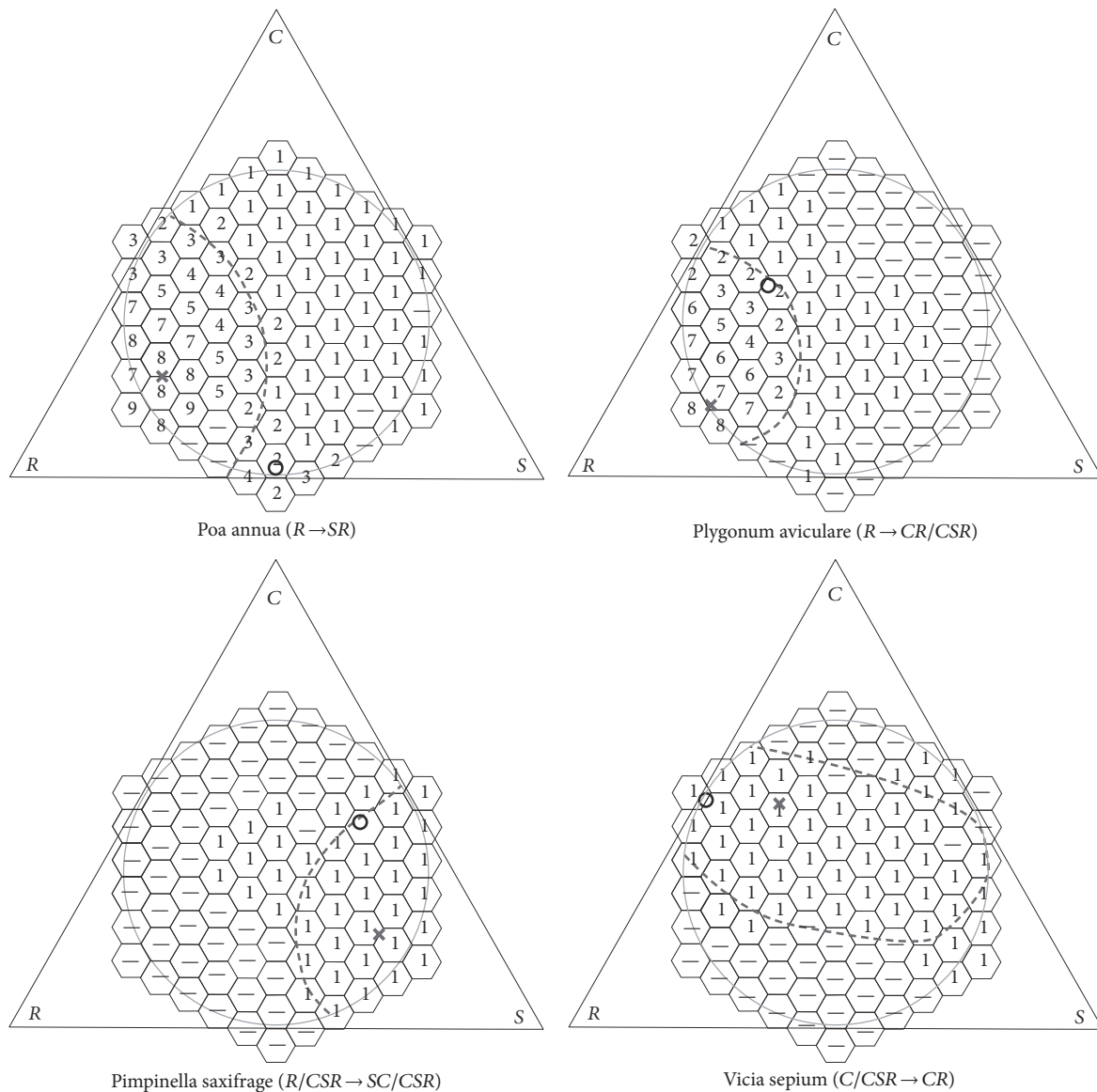


FIGURE 5: Allocation of species in Grime's triangle. Crosses, reference plant functional type according to Grime; noughts, functional type, revealed by our model; dotted line, potential area of changes of the plant functional type ("area of variability"). Figures are taken from [2] with add-ons. Species with the largest deviation from reference position were selected (distance 2).

Competing Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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