ISSN 1062-3590, Biology Bulletin, 2018, Vol. 45, No. 3, pp. 255–264. © Pleiades Publishing, Inc., 2018.
Original Russian Text ©A.P. Korablev, V.E. Smirnov, V.Yu. Neshataeva, L.G. Khanina, 2018, published in Izvestiya Akademii Nauk, Seriya Biologicheskaya, 2018, No. 3, pp. 290–300.

BOTANY

Plant Life-Forms and Environmental Filtering during Primary Succession on Loose Volcanic Substrata (Kamchatka, Russia)

A. P. Korablev[a, *], V. E. Smirnov[b, c], V. Yu. Neshataeva[a], and L. G. Khanina[c]

[a]*Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg, 197376 Russia*
[b]*Center for Forest Ecology and Productivity, Russian Academy of Sciences, Moscow, 117997 Russia*
[c]*Institute of Mathematical Problems of Biology, Branch of the Keldysh Institute of Applied Mathematics, Russian Academy of Sciences, Pushchino, Moscow oblast, 142290 Russia*
**e-mail: akorablev@binran.ru*

Received April 17, 2017

Abstract—Peculiarities of the forest vegetation dynamics and the main factors and mechanisms of environmental filtering were studied on loose deposits of the Tolbachinskii Dol Volcanic Plateau (Kamchatka) by means of plant life-form analysis. It was found that, in the earlier stages of plant succession, polycarpic herbs, acrocarpous mosses, and fruticulose lichens dominated. Forest communities of 35 years old differed from the old-growth ones by the proportions of plant life-forms and the total coverage. Environmental filtering is manifested by the most successful development of plants having special morphological adaptations of belowground systems to loose unstable substrata.

DOI: 10.1134/S106235901803007X

INTRODUCTION

The formation of vegetation cover (VC) on newly formed juvenile substrata, or primary succession, could be subdivided into the following stages: the drift of propagules, their germination and rooting, growing of individuals and associations, closing of belowground and above-ground organs, and the formation of phytocoenoses. Conventionally, there are two processes (Shennikov, 1964): at early stages, before the closure of above- and below-ground plant organs, environmental filters prevail and abiotic factors are the leading factors in the regulation of floristic composition. Then, biotic factors prevail. It is shown that at the early stages of primary succession the species composition may be very diverse and fairly random (Walker and del Moral, 2003; del Moral et al., 2005). The selection of species that could survive in the certain environmental conditions takes place not at the taxonomic level, but at the functional level (Prach et al., 1997; Diaz et al., 1998). We have chosen for the analysis plant life-forms (LFs) because they reflected biomorphological adaptations of species to environmental conditions.

This study aims at the analysis of changes in the spectra of plant LFs during the succession of forest vegetation; identification of species and LFs specifics for various succession stages; statistical modelling the distribution of different plant LFs depending on the environmental factors that may play the role of environmental filters.

MATERIALS AND METHODS

The study area is the Tolbachinskii Dol Volcanic Plateau (55°41′ N, 160°16′ E) slightly rising from 70 up to 3000 m above sea level (*Bol'shoe*..., 1984). The plateau is formed by lava flows and tephra (mainly ash and scoria) deposits of mostly Holocene age; it is covered by stratified volcanic ash soils (Zakharikhina and Litvinenko, 2011). The climate is moderately continental; the mean annual precipitation is 700 mm. At altitudes of 100 and 900 m, the mean monthly temperatures are 14.6 and 11.4°C in July and –19.6 and –23.6°C in January, respectively (Grishin et al., 2013). On the plateau, three altitudinal vegetation belts are distinguished: forest belt (up to 900 m), krummholtz belt (800–1000 m), and mountain tundra belt (up to 1900 m) (*Rastitel'nyi*..., 2014). In 1975–1976, the Great Tolbachinskii Fissure Eruption occurred on the plateau, which resulted in the formation of two lava fields with a total area of about 45 km^2, four scoria cones, and a vast ash–scoria plain (*Bol'shoe*..., 1984). According to our estimates, during the eruption and in the years following, vegetation was eliminated over an area of about 170 km^2 and was significantly damaged over an area of >400 km^2 (*Rastitl'nyi*..., 2014).

We analyzed 73 relevés carried out in 2006–2010 on sample plots (SPs) laid within the forest belt in primary habitats, formed in 1975–1976 on ash and scoria deposits. Relevés were conducted using standard methods (*Methods*..., 2002) on SPs of 400 m^2 in dense communities and 100 m^2 in open aggregations.

It is known that under the conditions of unstable and heterogeneous environment, VC is formed by the patch dynamics model (Pickett et al., 1999; Cutler et al., 2008). We analyzed VC on the 30–35 years old substrate; heterogeneity of the environment was manifested by the various rates of loose substrate (tephra) stabilization and different distances to the sources of diasporas. As a result, vegetation in different sites was developed unequally, from nude ash and scoria fields almost without vegetation (closer to the centre of the eruption) up to closed communities near the borders of surviving forest communities. For the subdivision of the successional stages of VC, we used its generalized characteristics: total coverage, the development of community structure, and Lfs of dominant plants (Walker and del Moral, 2003; Walker et al., 2010). We distinguished the following successional stages of forest vegetation, which we consider as a generalized hypothetical trajectory of vegetation development toward forest communities: 1—primary colonization (single individuals or sparse moss–lichen and scarce herb aggregations); 2—stabilization of the substrate and development of herbs and mosses (moss–lichen and grass aggregations with total coverage >5%, moss–grass (*Leymus interior*) communities); 3—wood species establishment and initial differentiation of the vertical structure (shrub and creeping shrub aggregations); 4—closure of creeping shrubs layer and development of tree species (creeping shrub aggregations and communities); and 5—formation of forest communities (larch, poplar, and birch forests and open woodlands).

Plant LFs were identified based on the system of I.G. Serebryakov (1962) in accordance with the classification given by T.G. Polozova (Yurtsev et al., 2010), with some modifications. At the first level of the classification, we distinguished trees, creeping shrubs, tree and shrub young growth, shrubs, dwarf-shrubs, poly- and monocarpic herbs, mosses, liverworts, and lichens. LFs represented by only one species were excluded from the analysis. At the second level of the classification, we distinguished 21 LFs. For arboreal species, we considered the features of the aboveground shoot architecture and for herb species we used the morphology of below-ground organs. Moss species were divided into acrocarpous and cladocarpous ones, lichens—into fruticulose, foliose, and crustose ones. The species were attributed to a particular LF according to the published data (Bezdelev and Bezdeleva, 2006; Yurtsev et al., 2010) and by our own observations.

For the different successional stages, the spectra of LFs at the first level of the classification were constructed using percentage coverage (PrC) and the number of taxa (Fig. 1). For vascular plants we considered species, but for the mosses and lichens we considered genera because of difficulties in identification of some species. To construct the spectra for the successional stages, the summarized values of PrC of taxa for each LF were obtained, and then the sum was divided by the number of SP related to the each stage, and finally received the mean of PrC of LF per 1 SP (100 or 400 m^2). The number of taxa was estimated using the mean number of species (or genera) of each LF per one SP in the stage.

Statistical analysis and plotting were performed in the R environment for statistical computing and graphics (R Core Team, 2016). For identifying the characterizing species for the successional stages, we used Indicator Species Analysis (ISA) (De Cáceres and Legendre, 2009) performed using the function *multipatt* from the INDICSPECIES package. Indicator value (*IndVal*) was calculated between the species and each stage as well as between the species and each combination of stages.

The impact of environmental factors on LFs was examined using canonical ordination by the method of redundancy analysis (RDA). To minimize the influence of interactions among plants, we selected 46 SPs with sparse VC: PrC of mosses and lichens <30%, herbs <15%, shrubs and creeping shrubs <10%, trees <5%, and sum PrC <34%. For these SPs we summarized PrC of species of each LF by two levels of the LF classification, thus receiving two matrices of dependent variables (responses). We used the following characteristics as independent variables (predictors): the distance to the surviving forest communities; the thickness of the tephra of 1975–1976 eruption (hereinafter, the thickness of tephra); the altitude above sea level; the intensity of erosion (hereinafter, erosion); % of outcropping lavas; presence or absence of lava outcrops; % of woody debris on the surface of tephra; the size of tephra particles; microrelief; for LF of herbs, as predictors, we also considered the sum PrC of trees and shrubs. For the first variant of the analysis (by LFs at the first level of the classification) we used all LFs as response variables at this level; for the second variant of the analysis, we used five LFs of the most common polycarpic herbs. The RDA was performed using the VEGAN package (functions *rda, ordiR2step,* etc.) taking into account recommendations of Legendre, P. and Legendre, L. (2012). Variables (predictors and responses) were transformed according to the requirements of the RDA statistical model. We have built a parsimonious model selecting "best" explanatory variables by the method of forward selection of predictors (function *ordiR2step*).

RESULTS

LF spectra during the development of vegetation. They reflect changes in abundance, dominance, species richness and, the vertical structure of plant communities and aggregations at different successional stages.

The first successional stage was characterized by an extremely low total PrC (Table 1); herbs and mosses

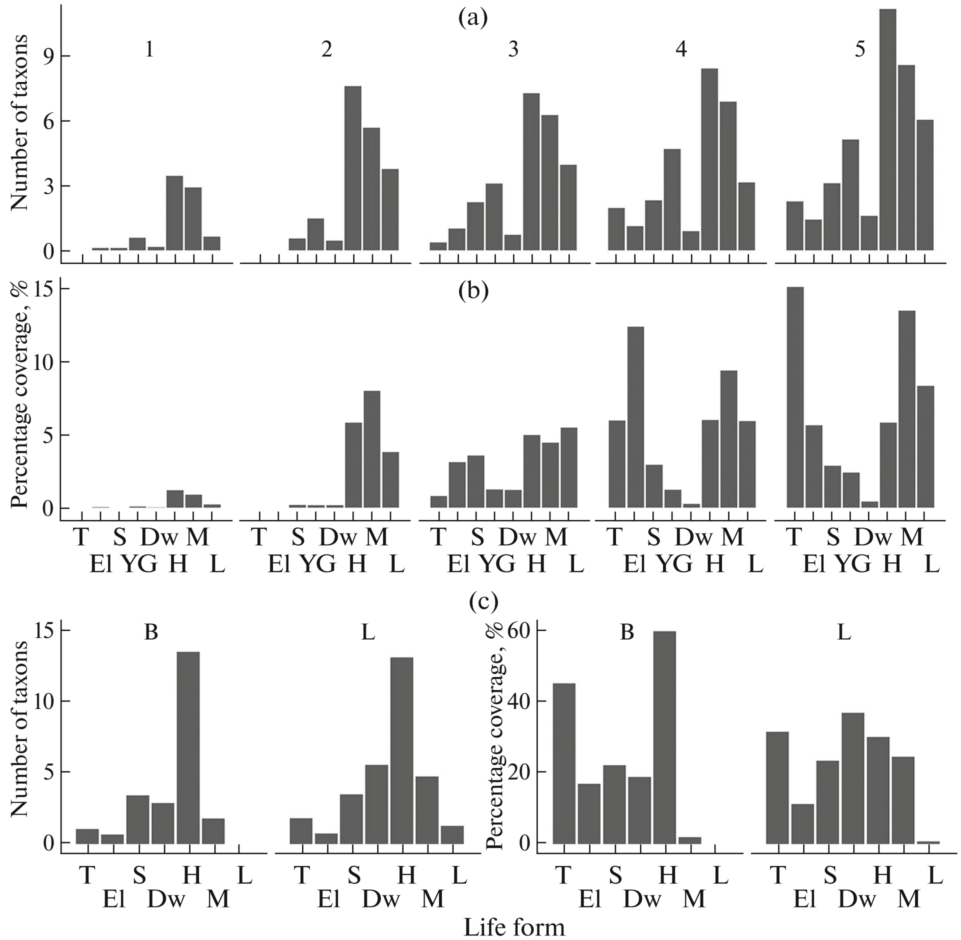

Fig. 1. Life-form spectra for the successional stages of forest vegetation: by percentage coverage (a), by the number of taxa (b), and by the same characteristics for undisturbed communities (c). 1–5, Successional stages. L, larch forests; B, stone birch forests; T, trees; El, creeping shrubs; YG, young growth; S, shrubs; Dw, dwarf shrubs; H, herbs; M, mosses; L, lichens; for Figs. 1 and 2.

prevailed by both PrC and the number of species or genera. Creeping shrubs, shrubs, and young growth of arboreal species occurred sparsely, but the vertical structure was not developed yet: VC was sparse, formed by single specimens of plants.

At the second stage, the vertical structure still was lacking, but the PrC and species richness of mosses, herbs and lichens increased significantly. As at the first stage, under the conditions of unstable substrata, lichens were unable to develop normally; at the second stage, under stabilization of the substrate, they represented a typical component of the pioneer aggregations, like herbs and mosses.

At the third stage, all LFs were presented; PrCs of herbs and mosses was insignificantly reduced, while PrCs of other LFs increased. At this stage, the forming of a vertical structure begun: VC was represented by separate patches of creeping shrubs and shrubs; sparse sinusia of herbs, mosses and lichens were found in the ground layer.

Table 1. Mean (standard deviations in parentheses) values of percentage coverage of plants and species richness per sample plot by the successional stages of forest vegetation

Variables	Successional stages				
	1	2	3	4	5
Number of relevés	19	11	14	17	12
Percentage coverage, %	2.4(1.8)	17.9(18.8)	24.7(13.1)	44.1(30.8)	53.8(25.9)
Number of species and genera	7.9(4.7)	19.6(13.6)	25.1(13.4)	29.7(13.2)	40(16.3)

The fourth stage was characterized by the higher total coverage and the higher species richness of all LFs being compared to the previous stages, mostly by the increase of PrC of LFs with long duration of life cycle (creeping shrubs and trees). In the communities of dwarf alder (*Alnus fruticosa*) and Siberian dwarf pine (*Pinus pumila*), the vertical structure (layers) was well-defined.

At the fifth stage, the PrC of trees, mosses, and lichens as well as species richness, especially of the subordinate layers, were higher than at the fourth stage. At this stage, we can find all layers typical for forest communities. As the age of communities does not exceed 35 years, total PrC remained low and the percentage ratio of dominants and the species composition of communities differed significantly from the mature ones (*Larix cajanderi* and *Betula ermanii* forests) of undisturbed habitats (Fig. 1c). In mature forests, the species diversity of herbs was significantly higher than that of mosses and lichens and lower than in young forest communities formed on ash and scoria fields. Dwarf-shrubs codominated in mature larch forests and herbs codominated in mature stone birch forests. High PrC of lichens was typical for primary communities and aggregations.

Indicator species and life-forms for the successional stages of forest vegetation. The indicator species analysis (ISA) showed that species of the following LFs: acrocarpous moss, long-rhizome grass, and taproot cushion-shaped herb, had a high constancy for all stages (Table 2). While *L. interior*, a long-rhizome grass common in pioneer communities and aggregations (occurrence on the SP is 35%) was not included in the table due to its absence on the third stage and non-significant *IndVal*, $p = 0.34$.

For the first two stages, ISA also showed high *IndVal* for polycarpic herbs (two taproots and one long-rhizome–taproot) with the semi-rosette and rosette shoot types (Table 2). They are all cushion-shaped petrophytes adapted to the growth on unstable substrata and were distributed mainly in the krummholtz and mountain tundra altitudinal belts. At the second stage indicator, albeit with a low *IndVal*, were pioneer acrocarpous mosses of the genus *Tortella*. Since the second stage, the constant indicators of communities were fruticulose pioneer lichens and polycarpic herbs, mainly without rosettes (turf grasses, long-rhizome–taproot and taproot cushion-shaped herbs). In addition, from the second to the fifth stage with *IndVal* = 49.1%, the young growth of low tree *Salix bebbiana* was recorded.

At the third successional stage with *IndVal* = 27.4%, the shrubby form of poplar *Populus suaveolens* was presented. In the undisturbed conditions, it is a tree up to 30 m high, forming flood-plain forest communities on young alluvia. On the Tolbachinskii Dol Plateau, poplar is a pioneer species on ash and scoria fields; in the conditions of movable substrate and snow corrasion, it has shrubby LF. At stages 3–5 *P. pumila* became more frequent in communities. LFs with woody stems were also typical; among them young growth of trees and orthotropic shrubs occurred. For these stages pioneer acrocarpous mosses and fibrous short-rhizome herbs were also characteristic; among them *Dryopteris fragrans* was often associated with lava outcrops and *Hieracium umbellatum* was one of the pioneers on ash and scoria fields (*Rastitel'nyi*..., 2014).

In the communities of the fourth stage, the young growth of the willow *Salix caprea* and the herb *Cardaminopsis lyrata*, that was characteristic of primary habitats, were present with low *IndVal*. For the fourth and fifth stages, two species of tall trees, one species of low tree *Sorbus sibirica*, one species of creeping shrub *A. fruticosa*, orthotropic shrubs, young growth of trees and creeping shrubs were found. Also at this stage with a low *IndVal*, the prostrate dwarf-shrub *Vaccinium uliginosum* occurred. The fourth and fifth stages had the similar floristic composition of arboreal species that distinguishes them from the earlier stages. At the fourth stage, the composition of the understorey was not similar yet to the same of the mature forests.

At the fifth stage, as forest communities form, an environment becomes more suitable for the growth of forest species that prefer shading and the stable substrate. This stage was characterized by a group of indicator species. Firstly, there were a tall tree, forest-forming species *L. cajanderi*, some forest species of cladocarpous mosses *Sanionia uncinata* and *Pleurozium schreberi*, and foliose lichens of the genus *Peltigera*. At the fifth stage with a lower *IndVal* we registered the prostrate shrub *Juniperus sibirica*, characteristic of the exposed middle-aged (270–1300 years) lava flows. Orthotropic and prostrate shrubs which are characteristic species of forests and krummholtz (creeping shrubs communities); polycarpic herbs, occurring in mature forests and krummholtz, as well as scoria fields in the forest belt; and acrocarpous mosses and foliose, fruticulose, and crustose lichens also occurred with low *IndVal*. Only at the fifth successional stage, indicators were liverworts, preferring shaded and moist habitats.

Environmental factors affecting the distribution of plant life-forms. Results of the analysis (for parsimonious models) are presented in Table 3 and Fig. 2. In the variant 1 (LFs at the first level of the classification), the first three axes were significant and explained more than 40% of the total variance (the adjusted R^2 was 0.411). Predictors were (in order of decreasing importance) the thickness of tephra, erosion, and woody debris. The first canonical axis explained 35% of the total variance and indicated a complex environmental gradient coupled with increasing of the thickness of tephra, the distance to the surviving forest communities, and partly the altitude above sea level. PrC of all LFs negatively correlated with this axis (Table 3). The axis also reproduced the successional

Table 2. Indicator species and plant life-forms, by the successional stages of forest vegetation

Stages	Species	LF-1	LF-2	*C*	*IndVal*	*p*
1–5	*Niphotrichum canescens*	M	M–Ap	75	–	–
	Poa malacantha s. l.	H	H–Lr	53	–	–
	Papaver microcarpum	H	H–T	37	–	–
1–2	*Ermania parryoides*	H	H–LrT	63	54.4	0.013
	Eritrichium kamtschaticum	H	H–T	20	20	0.028
2	*Saxifraga funstonii*	H	H–T	64	51.6	0.003
	Tortella spp.	M	M–Ap	27	17.9	0.031
2–5	*Salix bebbiana*	YG	YG–T	50	49.1	0.013
	Calamagrostis purpurea s. l.	H	H–B	59	58.7	0.001
	Trisetum spicatum s. l.	H	H–B	43	42.6	0.007
	Chamerion angustifolium	H	H–LrT	87	86	0
	Saxifraga cherlerioides	H	H–T	52	50.6	0.008
	Campanula lasiocarpa	H	H–LrT	26	25.9	0.057
	Cladonia spp.	L	L–Fr	80	78.9	0
	Stereocaulon spp.	L	L–Fr	67	66.4	0.003
3	*Populus suaveolens*	S	S–O	29	27.4	0.010
3–5	*Pinus pumila*	El	El–E	67	66.9	0
	Spiraea beauverdiana	S	S–O	42	40.9	0.003
	Salix bebbiana	S	S–O	35	34.6	0.027
	Rubus sachalinensis	S	S–O	28	27.9	0.064
	Populus suaveolens	YG	YG–T	79	72.9	0
	Pinus pumila	YG	YG–El	74	71.3	0
	Dryopteris fragrans	H	H–SrF	33	32.6	0.005
	Hieracium umbellatum	H	H–SrF	26	23.9	0.061
	Ceratodon purpureus	M	M–Ap	91	86.4	0
	Pohlia spp.	M	M–Ap	81	72.1	0
4	*Salix caprea*	YG	YG–T	29	23.5	0.046
	Cardaminopsis lyrata	H	H–T	18	17.6	0.023
4–5	*Populus suaveolens*	T	T–H	90	86.8	0
	Betula ermanii	T	T–H	28	27.6	0.015
	Sorbus sibirica	T	T–L	28	27.6	0.018
	Alnus fruticosa	El	El–D	59	54	0
	Ribes triste	S	S–O	38	37.4	0.012
	Salix caprea	S	S–O	28	24.7	0.037
	Lonicera caerulea	S	S–O	17	17.2	0.072
	Rosa amblyotis	S	S–O	14	13.8	0.090
	Larix cajanderi	YG	YG–T	48	46.3	0.001
	Betula ermanii	YG	YG–T	35	31	0.007
	Sorbus sibirica	YG	YG–T	31	26.8	0.015

Table 2. (Contd.)

Stages	Species	LF-1	LF-2	*C*	*IndVal*	*p*
	Populus tremula	YG	YG–T	24	23.2	0.036
	Alnus fruticosa	YG	YG–El	28	27.6	0.010
	Spiraea beauverdiana	YG	YG–S	17	17.2	0.058
	Vaccinium uliginosum	Dw	Dw–P	21	20.7	0.063
5	*Larix cajanderi*	T	T–H	50	47.5	0
	Juniperus sibirica	S	S–P	17	15.4	0.073
	Pyrola minor	Dw	Dw–O	17	16.7	0.043
	Vaccinium vitis-idaea s. l.	Dw	Dw–O	17	16.7	0.049
	Ledum palustre s. l.	Dw	Dw–P	25	19.8	0.092
	Saussurea pseudo-tilesii	H	H–Lr	33	29.7	0.006
	Artemisia arctica	H	H–SrF	25	25	0.006
	Aster sibiricus	H	H–Lr	25	24.6	0.007
	Mertensia pubescens	H	H–T	25	20.4	0.034
	Moneses uniflora	H	H–T	17	16.7	0.049
	Hedysarum hedysaroides	H	H–LrT	17	16.7	0.045
	Sanionia uncinata	M	M–Cl	58	45.6	0
	Pleurozium schreberi	M	M–Cl	33	30	0.005
	Aulacomnium spp.	M	M–Ap	42	29.8	0.008
	Dicranum spp.	M	M–Ap	33	28.7	0.013
	Brachythecium spp.	M	M–Cl	25	22.7	0.018
	Hepaticae	Lw	Lw	25	25	0.006
	Peltigera spp.	L	L–Fl	75	57.7	0
	Baeomyces spp.	L	L–Fr	33	24.8	0.008
	Cetraria spp.	L	L–Fl	25	21.9	0.012
	Flavocetraria spp.	L	L–Fl	25	20	0.026
	Thamnolia vermicularis	L	L–Fr	17	16.7	0.049
	Pertusaria spp.	L	L–Cr	17	16.7	0.043

In the table, only species with $p < 0.1$ are presented. LF-1, life-forms at the first level of the classification: T, tree; El, creeping shrub; S, shrub; YG, young growth; Dw, dwarf-shrub; H, polycarpic herb; M, moss; Lw, liverworts; L, lichen; LF-2, life-forms at the second level of the classification: T–H, high tree; T–L, low tree; El–E, evergreen creeping shrub; El–D, deciduous creeping shrub; S–O, orthotropic shrub; S–P, prostrate shrub; YG–T, young growth of tree; YG–El, young growth of creeping shrubs; YG–S, young growth of shrub; Dw–O, orthotropic dwarf-shrub; Dw–P, prostrate dwarf-shrub; H–B, turf herb; H–Lr, long-rhizome herb; H–SrF, fibrous short-rhizome herb; H–T, taproot herb; H–LrT, long-rhizome-taproot herb; M–Cl, cladocarpous moss; M–Ap, acrocarpous moss; L–Fr, fruticulose lichen; L–Fl, foliose lichen; L–Cr, crustose lichen. *C*, constancy, %; *IndVal*, indicator value, %; *p*, *p*-values calculated by permuting the data 999 times.

gradient. The second canonical axis explained 6.4% of the total variance; it mostly associated with weak erosion. Lichens and mosses, vulnerable to erosion, positively correlated with this axis. PrC of various LFs was higher in habitats where erosion was local, and patchy structure of VC was represented. PrC of woody debris had the highest correlation with the third canonical axis (it explained 3.3% of the total variance) and had a high negative correlation with the first axis; i.e., the presence of woody debris on the surface of ground had a positive effect to the VC forming.

In the variant 2 (polycarpic herbs), the first two axes were significant and explained more than 50% of the total variance (the adjusted R^2 was 0.515). Predictors were the presence of lava outcrops, the thickness of tephra, and woody debris. The contribution of the first canonical axis to the total variance was 33.9%.

Table 3. Correlations of variables with significant canonical axes

Variables	RDA 1	RDA 2	RDA 3	Variables	RDA 1	RDA 2
Variant 1				Variant 2		
Predictors				Predictors		
tephra thickness	0.894	0.076	0.195	presence of lava	–0.83	0.449
weak erosion	–0.045	0.957	0.019	woody debris	–0.48	–0.875
medium erosion	–0.639	–0.261	–0.345	tephra thickness	0.864	–0.011
intensive erosion	0.656	–0.577	0.317			
woody debris	–0.626	0.291	0.723			
Responses				Responses		
T	–0.531	–0.331	0.295	H–Lr	0.129	0.405
El	–0.652	0.07	0.238	H–B	–0.733	0.105
S	–0.594	–0.074	–0.201	H–Sr	–0.888	–0.087
Dw	–0.339	–0.231	–0.156	H–LrT	0.246	0.556
YG	–0.782	0.007	–0.135	H–T	–0.201	0.73
H	–0.464	–0.35	–0.149			
M	–0.45	0.318	0.065			
L	–0.643	0.327	–0.015			

RDA 1, RDA 2, RDA 3 are canonical axes.

The group of environmental characteristics associated with the thickness of tephra (the distance to the surviving forest communities, the altitude above sea level) positively correlated with this axis, whereas the presence of lava outcrops correlated negatively with it. The successional gradient along this axis was detected. Fibrous short-rhizome and turf herbs showed a high negative correlation with this axis because these herbs prefer habitats with a low thickness of tephra and the presence of lava. The second canonical axis explained

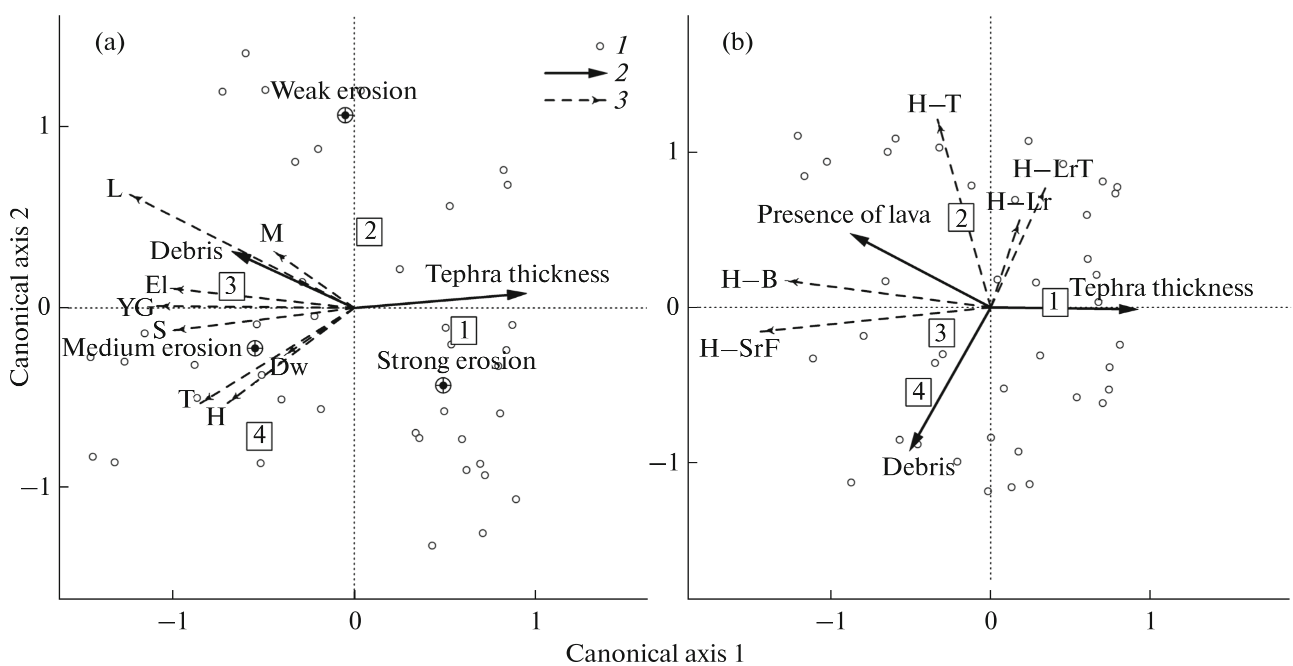

Fig. 2. RDA triplot of the life-forms data: for the first level of the classification (a) and for polycarpic herbs (b). *1*, Relevés; *2*, environmental characteristics; *3*, life-forms. Crossed circles represent centroids of the relevés for the erosion levels. 1–4, The successional stages of forest vegetation. Polycarpic herbs: H–B, turf; H–Lr, long-rhizome; H–SrF, fibrous short-rhizome; H–T, taproot, H–LrT, long-rhizome–taproot.

19.4% of the total variance. PrC of woody debris negatively correlated with the axis. Taproot, long-rhizome–taproot, and long-rhizome herbs had high positive correlations with this axis because of these LFs dominate in most open habitats on ash and scoria fields in the absence of woody debris. They were little affected by the thickness of tephra deposits.

DISCUSSION

LF spectra in the series of forest vegetation succession correspond to the classic concepts of primary succession trends: the increase of species richness and coverage, and the invasion of larger plants with a longer lifespan (Shennikov, 1964; Walker and del Moral, 2003). On one hand, the obtained distribution of the LF spectra depended partly on the method of identification of stages; on the other side, it reflected patterns characterized in some other studies of primary succession in different regions (Rydin and Borgegård, 1991; Prach et al., 1997; Lichter, 1998; Poli Marchese and Grillo, 2000).

On the Tolbachinskii Dol Plateau, at the first three successional stages, besides mosses and lichens, polycarpic herbs often developed successfully, as was estimated by their coverage and the number of species. Many researchers have noted the dominance of herbs at early stages of primary successions (Rydin and Borgegård, 1991; del Moral and Poli Marchese, 2010; Dimopoulos et al., 2010). However, in these studies, annual herbs represented the most part of dominant species. In our case, annual herbs did not occur at all, this can be explained by their extremely low distribution in cool-temperate regions (Goryshina, 1979). This is confirmed by the rare occurence of annual herbs in primary habitats on the volcanos Usu (Japan) and Mount St. Helens (United States) (Tsuyuzaki and del Moral, 1995). In addition, human-disturbed habitats and settlements, which could serve as a source of ruderal species were absent in the territory adjacent to the study area.

In the most severe conditions at the first successional stage of forest vegetation, mosses had lower coverage and species richness being compared with herbs. The previous researchers who studied the recovery of vegetation on the ash and scoria fields of the Tolbachinskii Dol in 1978–1979 did not find mosses at all (Sidel'nikov and Shafranovskii, 1981). Grishin et al. (2013) explained this phenomenon by the fact that mosses could appear on ash and scoria fields only after the stabilization of the substrate. According to our observations, in the areas with intensive erosion, mosses *Niphotrichum canescens, Polytrichum piliferum*, and *Racomitrium lanuginosum* were represented by singular specimens growing on the particles of tephra. The success of pioneer species in the colonization of new territories is due to dispersal of a large number of diasporas over long distances (Walker and del Moral, 2003). Mosses meet this criterion, but at the time of eruption a vast area was disturbed, so a long time (>4 years) was necessary for disperse spores from adjacent areas ("donor control") (Fuller and del Moral, 2003), establishment of mosses, and their local dispersion ("local control"). Currently, the constancy of mosses on tephra deposits according to our data is 93%.

The biomorphological features of species persisting under stressful conditions (erosion, mechanical damage, deficiency in water and nutrients, temperature fluctuations) are of great interest because they reflect adaptive strategies of plants, that allow them to survive under environmental filters. For the first two successional stages of VC on the Tolbachinskii Dol Plateau, the long-rhizome–taproot herb *Ermania parryoides* (pubescent, with a many-headed caudex) and the taproot herbs *Eritrichium kamtschaticum* (pubescent, with branched caudex) and *Saxifraga funstonii* (forming large turfs) were characteristic. They are characterized by a cushion-like growth form protecting them from the damage by tephra mooved by wind or water. They produce many small seeds (0.5–2 mm), which are resistant to low temperatures; their germination is stretched in time (Voronkova et al., 2008). According to the dispersal mode, they can be attributed to the group of "tumblers" (Fuller and del Moral, 2003). On pumice stone deposits of Mount St. Helens Volcano, in the first decade of succession "parachutists" prevailed. They had seeds carried by wind due to pappus or other long hairs, but the "tumblers" had gradually increased their abundance over 18 years (Fuller and del Moral, 2003). Nevertheless, the data obtained by Sidelnikov and Shafranovsky (1981) indicate that, in the first years after the eruption, "tumblers" also occurred more frequently than "parachutists" on the tephra of the Tolbachinskii Dol Plateau.

The morphology of below-ground organs of pioneer species was analyzed at the Usu and Mount St. Helens volcanoes (Tsuyuzaki and del Moral, 2003). It was found that long-rhizome herbs were the most successful pioneers on both volcanoes, but on Mount St. Helens taproot species of the genus *Lupinus* predominated (del Moral and Bliss, 1993). According to our data, the most adapted to unstable substrate were taproot, long-rhizome–taproot, and long-rhizome herbs (Table 2); they were distinguished into separate groups on the RDA triplot (Fig. 2b). The taproot system gives advantages in the conditions of a movable substrate. It allows plants to anchor firmly and to resist strong winds, to accumulate nutrients for rapid growth, and penetrate deeply into the soil for obtaining water (del Moral and Bliss, 1993; Voronkova et al., 2008). Long-rhizome herbs successfully tolerate erosion and other disturbances; they are able to disperse rapidly over long distances. This ability allows them to occupy the surrounding areas (Tsuyuzaki and del Moral, 1995). Apparently, there were also species with fibrous short-rhizome and turf systems of below-ground organs. These herbs were distinguished into a separate group (Fig. 2b) and they were negatively correlated to the thickness of tephra.

At the second stage, herbs and mosses occupied most of the surface. This contributes to retention of the substrate, thereby increasing the chances of other species to settle and creating favourable conditions for the development of the fruticulose lichen cover formed by lichens of genera *Cladonia* and *Stereocaulon*. At this stage, the facilitation effect of early colonists appears (Walker and del Moral, 2003). For the second stage and later stages, a more diverse group of herbs, including turf grasses and taproot herbs, and young growth of the willow *Salix bebbiana*, was identified. They all are anemochores. Beginning from the third stage, there was a diverse group of shrubs and young growth of trees, as well as fibrous short-rhizome herbs. Among them *P. pumila* and *Rubus sachalinensis* were zoochores, while others were anemochores. Beginning from the fourth stage trees and shrubs became constant components of communities. Among the indicator species of the fourth and fifth stages, the number of zoochores increased but anemochores were still dominant. Thus, during the succession, there was a tendency towards the increase in plant size, the proportion of arboreal species, and the ratio of zoochores. The larger the plant the stronger it changes the habitat. At the fifth stage, cladocarpous mosses, liverworts, and foliose lichens appeared among the indicator species. Apparently, these LFs were not adapted to the colonization of open habitats.

Previously it was shown that the floristic composition of ash and scoria fields closely correlated with the distance to surviving forest communities and the thickness of tephra deposits, which reflects the erosion intensity (Korablev and Neshataeva, 2016). Thirty-five years after the eruption, larch open woodlands formed mostly about 1 km from forest refuges; creeping shrubs communities and tree aggregations formed within 1.5 km. The dispersal of plants on the ash and scoria plain was limited by the remoteness from the sources of diasporas and by erosion of substrata. In the most isolated areas by the time of the next eruption, succession may not have progressed beyond the stage of pioneer herb and shrub vegetation. Before the eruption of 1975–1976, these communities had been grown in the central part of the Plateau on the deposits of the 850-years-old eruption (*Rastitel'nyi*..., 2014). On the stage when the species became a community-forming dominant (e.g., *P. pumila*), the succession could be interrupted or retarded; such a phenomenon was described as "arrested trajectories" (Walker and del Moral, 2003). In addition, the early stages of succession may follow different trajectories depending on the ecological and biological features of established species (Tsuyuzaki, 2009; del Moral et al., 2012; Mudrak et al., 2016).

ACKNOWLEDGMENTS

We are sincerely grateful to D.E. Himelbrant and I.S. Stepanchikova for the identification of lichens; I.V. Chernyad'eva and E.Yu. Kuz'mina for the identification of mosses; and V.V. Yakubov for the identification of vascular plants.

The investigation was supported by the Russian Foundation for Basic Research (projects 17-04-01754 and 16-34-50229); the field studies were supported by the Program of the Presidium of the Russian Academy of Sciences no. 17 "Evolution of the Organic World. The Role and Influence of Planetary Processes." This study was carried out within the framework of the projects of the Komarov Botanical Institute (project no. 01201458800), the Institute of Mathematical Problems of Biology (project no. 0017-2016-0103 (part 3)), and the Center for Forest Ecology and Productivity (project no. 0110-2014-0004) of the Russian Academy of Sciences.

REFERENCES

Bezdelev, A.B. and Bezdeleva, T.A., *Zhiznennye formy semennykh rastenii rossiiskogo Dal'nego Vostoka* (Life Forms of Seed Plants of the Russian Far East), Vladivostok: Dal'nauka, 2006.

Bol'shoe treshchinnoe Tolbachinskoe izverzhenie (1975–1976 gg., Kamchatka) (The Great Fissure Tolbachik Eruption (1975–1976, Kamchatka)), Fedosov, S.A., Ed., Moscow: Nauka, 1984.

De Cáceres, M. and Legendre, P., Associations between species and groups of sites: indices and statistical inference, *Ecology*, 2009, vol. 90, no. 12, pp. 3566–3574.

Cutler, N.A., Belyea, L.R., and Dugmore, A.J., The spatiotemporal dynamics of primary succession, *J. Ecol.*, 2008, vol. 96, pp. 231–246.

Diaz, S., Cabido, M., and Casanoves, F., Plant functional traits and environmental filters at a regional scale, *J. Veget. Sci.*, 1998, vol. 9, pp. 113–122.

Dimopoulos, P., Mucina, L., and Tsiripidis, I., Vegetation patterns and primary succession on sea-born volcanic islands, *Phytocoenologia*, 2010, vol. 40, no. 1, pp. 1–14.

Fuller, R.N. and del Moral, R., The role of refugia and dispersal in primary succession on Mount St. Helens, *J. Veget. Sci.*, 2003, vol. 14, pp. 637–644.

Goryshina, T.K., *Ekologiya rastenii* (Plant Ecology), Moscow: Vyssh. Shk., 1979.

Grishin, S.Yu., Krestov, P.V., Verkholat, V.P., Shlyakhov, S.A., Yakovleva, A.N., and Yakubov, V.V., Dynamics of vegetation cover of Tolbachinskii Dol (Kamchatka) in recent decades, *Komarovskie Chteniya*, 2013, no. 61, pp. 119–158.

Korablev, A.P. and Neshataeva, V.Yu., Primary plant successions of forest belt vegetation on the Tolbachinskii Dol Volcanic Plateau (Kamchatka), *Biol. Bull.*, 2016, vol. 43, no. 4, pp. 307–317.

Legendre, P. and Legendre, L., *Developments in Environmental Modelling*, vol. 24: *Numerical Ecology*, 3rd Engl. ed., Amsterdam: Elsevier Science BV, 2012, xiv + 990 p.

Lichter, J., Primary succession and forest development on coastal Lake Michigan sand dunes, *Ecol. Monogr.*, 1998, vol. 68, pp. 487–510.

Poli Marchese, E. and Grillo, M., Primary succession on lava flows on Mt. Etna, *Acta Phytogeogr. Suecica*, 2000, vol. 85, pp. 61–70.

Metody izucheniya lesnykh soobshchestv (Methods of Study of Forest Communities), Yarmishko, V.T. and Lyanguzova, I.V., Eds., St. Petersburg: NIIkhimii SPbGU, 2002.

del Moral, R. and Bliss, L.C., Mechanism of primary succession: insights resulting from the eruption of Mount St. Helens, *Adv. Ecol. Res.*, 1993, vol. 24, pp. 1–66.

del Moral, R. and Poli Marchese, E., Floristic change during primary succession on lava, Mount Etna, Sicily, *Braun-Blanquetia*, 2010, vol. 46, pp. 225–234.

del Moral, R., Wood, D.M., and Titus, J.H., Proximity, microsites, and biotic interactions during early succession, in *Ecological Responses to the 1980 Eruption of Mount St. Helens,* Dale, V.H., Swanson, F.J., and Crisafulli, C.M., Eds., New York: Springer, 2005, pp. 93–110.

del Moral, R., Thomason, L.A., Wenke, A.C., Lozanoff, N., and Abata, M.D., Primary succession trajectories on pumice at Mount St. Helens, Washington, DC, *J. Veget. Sci.*, 2012, vol. 23, pp. 73–85.

Mudrak, O., Doležal, J., and Frouz, J., Initial species composition predicts the progress in the spontaneous succession on post-mining sites, *Ecol. Engi.*, 2016, vol. 95, pp. 665–670.

Pickett, S.T.A., Wu, J., and Cadenasso, M.L., Patch dynamics and the ecology of disturbed ground: A framework for synthesis, in *Ecosystems of Disturbed Ground*, Walker, L.R., Ed., Amsterdam: Elsevier, 1999, pp. 707–722.

Prach, K., Pyšek, P., and Smilauer, P., Changes in species traits during succession: a search for pattern, *Oikos*, 1997, vol. 79, pp. 201–205.

R Core Team*, R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria, 2016. https://www.R-project.org/.

Rastitel'nyi pokrov vulkanicheskikh plato Tsentral'noi Kamchatki (Klyuchevskaya gruppa vulkanov) (The Vegetation Cover of Volcanic Plateaus of Central Kamchatka (Kluchevskaya Group of Volcanoes)), Neshataeva, V.Yu., Ed., Moscow: KMK, 2014.

Raunkiaer, C., *Plant Life Forms*, Oxford: Clarendon, 1937.

Rydin, H. and Borgegård, S.-O., Plant characteristics over a century of primary succession on islands, Lake Hjälmaren, *Ecology*, 1991, vol. 72, pp. 1089–1101.

Serebryakov, I.G., *Ekologicheskaya morfologiya rastenii. Zhiznennye formy pokrytosemennykh i khvoinykh* (Ecological Plant Morphology. Life Forms of Angiosperms and Conifers), Moscow: Vyssh. Shk., 1962.

Shennikov, A.P., *Vvedenie v geobotaniku* (Introduction to Geobotany), Leningrad: Izd. LGU, 1964.

Sidel'nikov, A.N. and Shafranovskii, V.A., The impact of the Tolbachik Volcano eruption in 1975–1976 (Kamchatka) on vegetation, in *Lesovodstvennye issledovaniya na Sakhaline i Kamchatke* (Silvicultural Research in Sakhalin and Kamchatka), Vladivostok: Izd. DVNTs AN SSSR, 1981, pp. 107–144.

Tsuyuzaki, S., Causes of plant community divergence in the early stages of volcanic succession, *J. Veget. Sci.*, 2009, vol. 20, pp. 959–969.

Tsuyuzaki, S. and del Moral, R., Species attributes in early primary succession on volcanoes, *J. Veget. Sci.*, 1995, vol. 6, pp. 517–522.

Voronkova, N.M., Kholina, A.B., and Verkholat, V.P., Plant biomorphology and seed germination in pioneer species of Kamchatka volcanoes, *Biol. Bull.* (Moscow), 2008, vol. 35, no. 6, pp. 599–605.

Walker, L.R. and del Moral, R., *Primary Succession and Ecosystem Rehabilitation*, New York: Cambr. Univ. Press, 2003.

Walker, L.R., Wardle, D.A., Bardgett, R.D., and Clarkson, B.D., The use of chronosequences in studies of ecological succession and soil development, *J. Ecol.*, 2010, vol. 98, pp. 725–736.

Yurtsev, B.A., Koroleva, T.M., Petrovskii, V.V., Polozova, T.G., Zhukova, P.G., and Katenin, A.E., *Konspekt flory Chukotskoi tundry* (Synopsis of Chukchi Tundra Flora), St. Petersburg: VVM, 2010.

Zakharikhina, L.V. and Litvinenko, Yu.S., *Geneticheskie i geokhimicheskie osobennosti pochv Kamchatki* (Genetic and Geochemical Characteristics of Soils of Kamchatka), Moscow: Nauka, 2011.

Translated by S. Kuzmin