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Variations in the Growth Rate of *Cladonia* Lichens during Long-Term Postfire Successions in the North of West Siberia

S. U. Abdulmanova and S. N. Ektova

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences,
ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia
e-mail: svabdulmanova@e1.ru

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Abstract—This paper presents the results of studying the *Cladonia* lichen postfire growth-rate dynamics in different zonal units of West Siberia. The relative growth rate of lichens in forest-tundra and taiga zones was assessed with regard to the pyrogenic factor. The growth rate varied from 1.2 mm/year at the early stage of recovery succession to 11.9 mm/year at the stage of the closed lichen cover. The variations in lichen growth rates at different stages of recovery were reliable in southern and middle taiga communities. In open forests and forest-tundra communities of northern regions, the growth rate of lichens was not characterized by significant changes.

Keywords: fruticose lichens, relative growth rate, postfire recovery, taiga, forest-tundra, West Siberia

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INTRODUCTION

The study of fruticose lichen growth has a high value for understanding the features of distribution and functioning of lichen communities and for assessing their productivity. It is shown that in climax and sub-climax communities the lichen growth rate depends on a large number of environmental factors (temperature, humidity, structure of upper layers of the forest, ratio of mosses and lichens in living aboveground cover, and so on) and is very sensitive to changes in them (Andreev, 1954; Tolpysheva et al., 2003; Ćabrajić et al., 2010; Abdulmanova, 2013; etc.). At present, the vast territory of West Siberia is affected by natural and anthropogenic impacts (fires, reindeer grazing, and industrial development) (Moskalenko, 1999; Magomedova, 2006). Against this background, the study of fruticose lichen growth rate features is important to assess the resource potential of lichen-dominated communities during recovery successions and to predict the probability of lichen cover recovery and period for achieving maximum production.

Boreal and tundra ecosystems of West Siberia are convenient territories for studying the variability of the fruticose lichen growth rate in various natural and anthropogenic environment, since communities where lichens are dominant in the aboveground cover are widespread from the southern taiga to the arctic tundra and play an important role in the composition of vegetation cover (Il'ina et al., 1985). Therefore, in the zonal gradient in climax and subclimax communities, the fruticose lichen growth rate significantly decreases from south to north with increasing of severity of hydrothermal conditions and changes in the structure of communities (Abdulmanova, 2013). An analysis of our own observations and literature data allowed us to formulate the hypothesis that the identified features will be disrupted or leveled against various external influences.

Postfire successions in the communities on dry sandy substrates are a convenient object for studying the features of lichen cover recovery. They are widely distributed in taiga and tundra ecosystems, can be dated quite easily, and are characterized by a considerable period without fire, and serial communities are characterized by a typical composition and structure of lichen synusias (Ahti and Oksanen, 1990; Gorshkov and Stavrova, 2005; Neshataev, 2002; Kukurichkin and Neshataev, 2004). Analysis of the fruticose lichen growth rate dynamics during long-term postfire succession makes it possible to estimate the growth rate of lichens in their main periods of life (Andreev, 1954; Armstrong, 1974), as well as the relationship of the lichen growth rate with recovery-associated changes in the community structure, trophicity, and moisture of habitats (Neshataev, 2002). Data about lichen growth rate variety obtained during the study of postfire successions make it possible to model the dynamics of the growth rate and productivity of lichens and predict the features of recovery of lichen communities on the pastures of reindeer, where it is impossible to exclude grazing and observe natural recovery succession. It is most important for the north of West Siberia, where the aboveground cover is damaged by reindeer over-grazing as much as strong fires: the lichen cover is destroyed, fruticose species are replaced by pioneer species of crustose and foliose lichens (Magomedova et al., 2006).

The purpose of this work was to study the shrub-fruticose *Cladonia* lichen growth rate dynamics during postfire recovery in the north of West Siberia and identify major biotic environmental factors affecting the growth rate.

MATERIALS AND METHODS

This study was carried out on four key areas within the southern taiga, middle taiga, and northern open forest subzone of the taiga and forest-tundra zones (Table 1), which were destroyed by natural fire. On the key areas lichen communities occur mainly on high terraces of rivers and watersheds which characterized by substrates of light mechanical composition and phytocenoses are formed by light coniferous species (larch in the north and pine in the south).

Within the forest-tundra, the key area is located on the eastern macroslope of the Polar Urals and is characterized by a severe climate, high influence of winds, and close bedding of permafrost. Forest-tundra lichen open forests are interspersed with dwarf birch and willow tundra communities and in wetlands of interfluves with hummocks and polygonal bogs. The slightly closed tree canopy has no significant impact on the grass-dwarf-shrub and moss covers (Il'ina et al., 1985).

In the gradient of the taiga zone, the key areas were selected in three subzonal divisions:

(1) the northern open forest is a narrow subzone of the taiga zone of West Siberia on the border with the forest-tundra, which has been distinguished according to soil complexes, types of bogs, combination of vegetation types in the landscape, and the structure of forest vegetation (Chertovskii, 1987). Taiga lichen open forests are always in combination with forest communities or communities of boreal hummocks bogs (Il'ina et al., 1985).

(2) the middle taiga subzone is characterized by domination of pine forests, which is due to widespread sand and sandy-loam substrates of various genesis. The most drainy locations—tops and upper parts of hills with automorphic podzolic illuvial-ferruginous-humus soils—are occupied with dwarf shrub–lichen pine forests, while depressions are occupied with bogs. Bogs are mainly oligotrophic, with pines with the dwarf shrub-sphagnum cover (Il'ina et al., 1985).

(3) pine forests in the southern taiga subzone occupy the high terraces of rivers. Large territories are occupied with the most widespread grass–dwarf shrub pine forests of the slopes and tops of low hills and ridges. Lower parts of slopes are covered with grass forests. Lichen pine forests occupy the driest habitats—tops of dunes and hills with deeply lying groundwaters (more than 4 m) and poor soils—and occur as small areas among other forest types (Il'ina et al., 1985).

Sample areas (100–400 m) were established in the uneven-aged postfire communities dominated by lichens (5–100 years after the fire) for making general geobotanical descriptions (*Polevaya geobotanika*, 1964) and descriptions of lichen synusiae, as well as to sample lichens for determining the growth rate. To study the structure of the moss–lichen cover, we used geobotanic methods adapted for lichens to determine abundance, cover, occurrence, and vitality. The descriptions were made at areas of 0.625 m^2 with the use of grids (25 × 25 cm) in 10- to 25-fold replications to fully identify the species composition (Magomedova, 2006).

The lichen growth rate was calculated according to the method of K.N. Igoshina (1939), when we determined the total height and age (number of internodes) of lichen podetia. The measurements were carried out at extremely humid thalli of the four model species of the *Cladonia* genus: *C. arbuscula* (Wallr.) Flot, *C. rangiferina* (L.) F.H. Wigg, *C. stellaris* (Opiz) Pouzar & Vĕzda, *C. stygia* (Fr.) Ruoss). From each sample, 15–25 podetia of each species were measured, totaling 4660 lichen thalli. The total amount of the work carried out is shown in Table 1.

The importance of the factors expressed in the nominal scale, as well as differences in the growth rate of lichen species and at different levels of spatial association and recovery stages, was assessed by ANOVA (using Fisher's test) and cluster analysis using the STATISTICA v. 6.0 software package. The contribution of environmental factors measured in the continuous quantitative scale was assessed by making regression models.

RESULTS AND DISCUSSION

To analyze the variability of the shrub fruticose lichen growth rate in environmental gradients, we started our investigation with evaluation of the structure of the upper layers and the aboveground cover of uneven-aged postfire communities (Table 2).

In the forest-tundra zone, the vegetation cover of the key area is represented by a combination of larch shrub–moss–lichen open forests and *Ledum–Betula*–dwarf shrub–lichen tundra. The tree canopy of the open forest is formed by *Larix sibirica* Ledeb. (h = 10–12 m) rarely with *Betula pubescens* Ehrh.; the closeness of the canopy is 0.1–0.2. The shrub layer is composed of *Betula nana* L. and *Ledum palustre* L. The grass–dwarf shrub layer is formed by *Vaccinium uliginosum* L. and *Empetrum hermaphroditum* Hagerup. Grasses are sporadic. Green mosses occupy 5–20% of plots. The lichen cover is 60–80% and has low species diversity: *Cladonia arbuscula*, *C. rangiferina*, *C. stygia*, and *C. stellaris*; in depressions, *Cetrariella delisei* (Bory ex Schaer.) Kärnefelt & A.Thell, *Alectoria nigricans* (Ach.) Nyl., and *Cetraria erice-*

Table 1. Characteristics of key areas and amount of collected material

Parameters/Zonal area	Forest-tundra		Open forests of northern taiga	Middle taiga	Southern taiga
	Tundra areas	Forest areas			
Key areas	5–20 km northeast Labytnangi town (66°41′ N, 66°20′ E)		Neighborhood of N. Urengoy city (66°11′ N, 76°42′ E)	Natural Park Sibirskie Uvaly (62°26′ N, 81°40′ E)	Natural Park Pripyshminskie Bory (57°16′ N, 64°23′ E)
Administrative division	Yamal-Nenets Autonomous Okrug		Yamal-Nenets Autonomous Okrug	Khanty-Mansi Autonomous Okrug	Sverdlovsk region
Ecological features of key areas	Eastern macroslope of Ural Mountains, high diversity of substrates and habitat conditions, mosaicity of vegetation cover, impact of winter reindeer grazing		Homogeneous vegetation cover, sandy and loamy substrates, impact of winter reindeer grazing and oil and gas industry	Dominance of zonal vegetation types on dry sandy substrates, homogeneous habitat conditions over large areas, regular impact of wildfires	Intrazonal vegetation type, lichen communities cover small areas in watersheds with sandy substrates
Dominant vegetation type	Shrub (*Ledum palustris*, *Betula nana*) dwarf shrub–lichen tundras	Larch (*Larix sibirica*) shrub (*Betula nana*) dwarf shrub–moss–lichen open forests	Larch (*Larix sibirica*) shrub (*Betula nana*) dwarf shrub–lichen open forests and flat–hilled bogs	Pine (*Pynus sylvestris*) lichen forests	Pine (*Pynus sylvestris*) lichen forests
Days with active temperatures	114◆		119◆◆	130◆◆◆	165◆◆◆◆
Sum of active temperatures*, °C	1331.8		1493.5	1838.7	2357.8
Precipitation**, mm	424.7		340.4	329.8	528.0
Relative air humidity***, %	75		76	69	71
Years of research, collectors	2005, L.M. Morozova, N.Yu. Ryabitseva; 2011–2013, S.Yu. Abdulmanova, S.N. Ektova		2005, M.A. Magomedova, S.N. Ektova,	2007–2008, S.N. Ektova, S.Yu. Abdulmanova	2003, M.A. Magomedova; 2011, S.Yu. Abdulmanova
Ages of burnt areas	5, 12, 20, 30, 45, 85		1, 5, 20, 35, 45, 65	5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 100	9, 10, 11, 20, 30, 35, 40, 55, 80, 100
Number of geobotanical descriptions (100–400 m^2)/Number of descriptions of lichensynusias (0.625 m^2) / Number of measurements of lichen thalli					
Amount of material	24/65/680	20/55/550	28/90/920	40/115/1250	21/105/1260

* Active average daily temperatures for fruticose lichens range from 5 to 25°C; ** precipitation on days with active average daily temperatures; *** relative air humidity on days with active temperatures.

◆, Meteorological station of Salekhard; ◆◆, meteorological station of Novy Urengoy; ◆◆◆, meteorological station of pos. Raduzhnyi; ◆◆◆◆, meteorological station of Tugulym. Analysis includes data from the sites "Russia's Weather" (http://meteo.infospace.ru) and "Reliable Prognosis" (http://rp5.ru/)

torum Opiz. Mosaicity of the cover is clearly expressed as mosses, lichens, shrubs, and its combination, depends on the nanorelief and the degree of soil shading. After the ground fire, the surface of the burnt area is nonuniform due to hillosks burning out in varying degrees. The lichen cover is destroyed unevenly, species of the original community stay preserved, and species of the genera *Peltigera* and *Stereocaulon*, as well as cup-shape *Cladonia*, expand (Morozova et al., 2007).

In the tundra communities, the shrub layer is sparse (covering 20–25%) and is formed by *Betula nana* (h = 20–30 cm) with a considerable amount of *Ledum palustre* (h ~ 20 cm). The grass–dwarf shrub layer covers 50% and is formed by *Vaccinium uliginosum*, *V. vitis-idaea* L., *Empetrum hermaphroditum*, and *Carex arctisibirica* (Jurtz.) Czer. The moss–lichen layer is dense with predominance of *C. rangiferina*, *C. arbuscula*, *Cetraria islandica* (L.) Ach., percentage cover is 40–95%. The overall mat thickness is 4–7 cm. The moss cover varies from 1 to 60% in some areas, dominated by *Aulacomnium turgidum* (Wahlenb.) Schwaegr., *Dicranum angustum* Lindb., and *Polytrichum strictum* Brid. Burning of the vegetation is not uniform; there are small patches where lichens have been damaged by fire but not burned. During the recovery, the aboveground cover pass the main stages of postfire succession of lichens cover (Magomedova, 2006), but on the third stage of recovery the continuous cover with *C. stellaris* is not formed, which is associated with intense winter reindeer grazing.

A key area in the subzone of open forests, the canopy of the *Betula*–dwarf shrub–moss–lichen open forest is formed by *Larix sibirica* (h = 10–15 m) with birch and sporadically *Pinus sibirica* Du Tour. The undergrowth includes larch, birch, cedar, and sporadically spruce. The shrub layer is formed by *Betula nana* (h = 50 cm) and *Ledum palustre*. The grass–dwarf shrub layer contains *Empetrum hermaphroditum*, *Arctous alpine* (L.) Niedenzu, *Vaccinium uliginosum*, *V. vitisidaea*, and *Calamagrostis langsdorfii* (Link.) Trin. Lichens percentage cover is 60–75%. The most abundant species is *C. stellaris*; less abundant are *C. arbuscula* and *C. rangiferina*. The aboveground cover is formed by fragments with different composition of lichens.

After the fire the percentage cover of the vegetation is less than 20%. Lichens remain under shrubs and some fragments on the border of the burnt area. Preservation of the pieces of original vegetation leads to combination of pioneer postfire lichens (Magomedova, 2006) and species typical for the original communities. In the latest stage of postfire succession, the structure of the lichen cover is influenced by the winter grazing of reindeer, which prevents the formation of a closed homogeneous cover.

Within the middle taiga, lichen pine forests are formed by *Pinus sylvestris* L., sparsely with *Betula pubescens*, and sporadically with *Pinus sibirica*. The tree canopy is closed only for 0.2–0.7, height is 9–17 m. The estimated productivity class is V. Undergrowth is not evenly distributed. Underwood is not developed. The shrub layer is not developed (up to 0.1); shrubs *Ledum palustre* and *Betula nana* occur sporadically, mainly in depressions. The total percentage cover of the vegetation is up to 100%. The grass–dwarf shrub layer covers 5–30% and is formed by *Vaccinium vitis-idaea* with the addition of *Empetrum hermaphroditum* and *Vaccinium myrtillus* L.; rarely, *Andromeda polifolia* L. Grasses (*Calamagrostis epigeios* L. Roth) occur sporadically. In upper parts of the hills, lichens percentage cover is 80–100%. The mat is monodominant and is formed by *C. stellaris*. *C. arbuscula* ssp. *mitis*, *C. rangiferina*, *C. cornuta*, *C. crispata*, *C. deformis*, and *C. uncialis* are characterized by high occurrence and low percentage cover. The moss percentage cover is not more than 5%, with the predominance of forest mesophytes *Dicranum polysetum* and *Pleurozium schreberi*. Dwarf shrubs grow in depressions; the percentage cover is 40%. Grasses are found sporadically. The dense moss cover (covering 95%) is formed by green moss. Lichens (*Cladina stellaris* and *C. rangiferina*) are rare, and lichen cover is less than 5%.

After the fire, the aboveground cover is mainly dead, lichens are found only on dead wood. Further recovery of lichen mat passes all stages of classical lichen postfire succession (Ahti and Oksanen, 1990; Neshataev, 2002; Magomedova, 2006), including the stages of predominance of cup-shape, tubulose, and crustose lichen species, then predominance of shrub-fruticose *Cladonia* (*C. arbuscula* and *C. rangiferina*) and monodominant *C. stellaris*.

In the southern taiga, study forests are dominated by *Pinus sylvestris*, *Betula pubescens* is common. The tree canopy closeness is 0.2–0.7. The estimated productivity class is IV–V. The shrub layer is not developed. The grass–dwarf shrub layer is formed mainly by grasses, coverage is from 5 to 80%, h = 25–60 cm. The moss–lichen layer of the main territories is formed mainly by mosses, covering from 50 to 90%, lichens may cover 55–95% of other territories. In general, the coverage of lichens may vary from 1 to 95%. The lichen cover at different stages of recovery is formed by the main species of the pioneer postfire lichens (Magomedov, 2006) or is dominated by *C. stellaris*.

Zonal features of plant communities, characteristics of the fires, and differences in the structure of aboveground cover lead to the average growth rate of the fruticose lichens in the postfire communities to vary widely (from 1.2 to 11.9 mm/year) (Table 3).

Maximum values of the *Cladonia* growth rate were observed in the northern open forests. The minimum growth rate in zonal gradient is observed in the forest–tundra zone. However, after fire the smallest lichen growth rate is observed on the early stages of recovery in the middle taiga communities. The middle taiga burnt areas are situated on watershed with sandy substrates and characterized by dominance of pine lichen or green moss-lichen forests. These territories are characterized by thin litter and low rates of accumula-

Table 2. Structure of living aboveground cover of postfire communities

Age of burnt area, years	5–20	25–35	40–60	>70
Forest-tundra zone				
Grass–dwarf shrub layer cover, %	Up to 60	40–80	50–70	50–70
Moss cover, %	25–80	30–80	1–80	5–80
Lichen cover, %	5–15 (in spots)	15–50	10–95	11–80
Dominant species	*Stereocaulon paschale* (L.) Hoffm., *Cladonia borealis* S. Stenroos, *C. fimbriata* (L.) Fr.	*Stereocaulon paschale, Cladonia cornuta-gracilis, C. deformis-sulphurina*	*Cladonia arbuscula, C. subfurcata* (Nyl.) Arnold., *C. uncialis* (L.) F.H. Wigg.	*Cetraria islandica* (L.) Ach., *C. laevigata* Rass., *Cladonia arbuscula, C. rangiferina*
	Model species cover, %			
C. arbuscula	Up to 5	Up to 15	10–50	10–50
C. rangiferina	Around 1	Up to 5	0.5–55	0.5–10
C. stellaris	Less than 1	Up to 7	Up to 10	Up to 10
Lichen mat thickness, cm	3–6.5	5–8	3–10	5–14
Northern open forests				
Grass–dwarf shrub layer cover, %	Less than 10	Around 30	Around 30	n/a
Moss cover, %	Up to 5	Around 20	Around 21	n/a
Lichen cover, %	~5 (in spots, die off)	70	60–75	n/a
Dominant species	*Cetraria* (muricata, odontella), *Cladonia cyanipes* (Sommerf.) Nyl., *Trapeliopsis granulosa* (Hoffm.) Lumbsch	*Cladonia amaurocraea* (Flörke) Schaer., *C. cornuta* (L.) Hoffm, *C. crispata* (Ach.) Flot., *C. gracilis* (L.) Willd., *C. uncialis*	*Alectoria* (nigricans, ochroleuca), *Arctocetraria andrejevii* (Oxner.) Kärnefelt & Thell, *Cetraria* (islandica, laevigata), *Cladonia arbuscula*, *C. rangiferina*, *C. stellaris*	n/a
	Model species cover, %			
C. arbuscula	0–50	5–50	5–90	n/a
C. rangiferina	0–5	1–25	1–40	n/a
C. stellaris	0–5	3–65	2–100	n/a
Lichen mat thickness, cm	Up to 6	Up to 7	5–9	n/a
Middle taiga subzone				
Grass–dwarf shrub layer cover, %	1–25	Up to 30	5–40	5–30
Moss cover, %	1–50	Up to 10	1–5	Up to 5
Lichen cover, %	30–80	50–90	80–100	80–100
Dominant species	*Trapeliopsis granulosa, Cladonia cariosa* (Ach.) Spreng., *C. coccifera* (L.) Willd., *C. botrytes* (K.G. Hagen) Willd.	*Cladonia crispata, C. cornuta. C. gracilis*	*Cladonia uncialis, Cladina arbuscula*	*Cladonia stellaris*

Table 2. (Contd.)

Age of burnt area, years	5–20	25–35	40–60	>70
	Model species cover, %			
C. arbuscula	2–6	5–40	10–60	Around 1
C. rangiferina	Up to 1	Up to 5	5–40	Up to 3
C. stellaris	0	0	Up to 40	more than 60
Lichen mat thickness, cm	1.5–2	2–4.5	7–13	6–13
Southern taiga subzone				
Grass cover, %	5–80	15–60	10–30	Up to 30
Moss cover, %	50–90	5–80	5–20	10–20
Lichen cover, %	1–90	15–95	50–95	Around 80
Dominant species	*Cladonia botrytes*, *C. verticillata* (Hoffm.) Shaer., *C. cornuta*	*C. arbuscula*, *C. cornuta*, *C. gracilis*	*Cladonia arbuscula*, *C. rangiferina*, *C. stellaris*	*Cladonia stellaris*
	Model species cover, %			
C. arbuscula	20–50	35–70	15–65	Around 1
C. rangiferina	1–30	7–15	7–15	5–7
C. stellaris	Up to 15	2–10	Up to 52	Up to 70
Lichen mat thickness, cm	2–8	8–13	8–10	8–10

Table 3. Variation of fruticose lichen relative growth during postfire succession

Nature zone	Ages of communities after fire							
	5–20 years		20–35 years		40–60 years		older than 70 years	
	$X_{av} \pm$ SD	min–max	$X_{av} \pm$ SD	min–max	$X_{av} \pm$ SD	min–max	$X_{av} \pm$ SD	min–max
Forest-tundra	3.5 ± 1.1	1.7–5.5	3.2 ± 0.4	2.7–4.3	3.6 ± 0.8	2.1–5.5	3.8 ± 0.8	2.8–5.0
Open forest subzone	7.6 ± 0.1	7.5–7.7	6.4 ± 1.9	5.1–8.5	6.0 ± 2.5	3.4–11.9	n/a	n/a
Middle taiga	2.1 ± 0.3	1.8–2.5	3.8 ± 1.4	2.6–6.4	5.9 ± 1.1	3.3–9.3	6.4 ± 1.7	4.7–8.0
Southern taiga	4.4 ± 1.9	1.2–8.5	6.6 ± 1.5	4.0–9.1	6.8 ± 1.4	4.4–9.8	7.2 ± 1.5	5.1–9.5

tion of nutrients in the soil (Neshataev, 2002). Here, fire spreads rapidly and widely, causing complete burning of the lichen cover and the thin soil horizon. Recovery of the ground cover begins from the stage of pioneer mosses and crustose lichens (*Trapeliopsis granulosa* (Hoffm.) Lumbsch), followed by the introduction of cup-shape and tubulose *Cladonia* and slow closure of the lichen cover. Accordingly, the growth rate of fruticose lichens that start to grow on the recently burned areas (less than 35 years) is minimal and is lower than at similar recovery stages in the tundra communities characterized by a thick litter, stable water regime, and higher trophicity of habitats (Morozova et al., 2007). Further postfire succession leads to a significant change in the species composition, structure, and thickness of the lichen mat (Abdulmanova, 2010), and the growth rate of the model fruticose lichen species increases in about five times (from 1.8 to 9.7 mm/year). We detected significant differences and increasing of the lichen growth rate during long-term recovery and between all stages (F(3.37) = 16.67; $p \ll 0.01$). The greatest contribution (31%) in the growth rate variability is introduced by biogenic factors associated with the structure of the aboveground cover, as the lichen mat thickness ($\beta = 0.44$; $R^2_{adj} = 0.31$; $p < 0.01$) and percentage cover of lichens ($\beta = 0.38$; $R^2_{adj} = 0.14$; $p < 0.01$), while the time after fire explains only about 28% of the variability ($\beta = 0.50$; $R^2_{adj} = 0.28$; $p < 0.01$).

Table 4. Variation of growth rate (mm/year) of model lichen species during postfire recovery of middle taiga communities

Species/Age of burnt areas, years	*C. arbuscula*		*C. rangiferina*		*C. stellaris*	
	$X_{av} \pm$ SD	min–max	$X_{av} \pm$ SD	min–max	$X_{av} \pm$ SD	min–max
10–20	2.2 ± 0.2	2.0–2.5	2.1 ± 0.4	1.8–2.5	n/a	n/a
25–35	3.5 ± 0.5	2.8–3.9	3.8 ± 1.7	2.9–6.3	4.5 ± 2.7	2.6–6.4
40–60	5.0 ± 0.6	4.1–6.0	5.9 ± 1.5	3.3–8.1	7.2 ± 1.5	5.7–9.3
Older than 80	4.7 ± 0.5	3.7–5.2	6.6 ± 0.9	5.0–8.6	8.0 ± 0.9	6.5–9.7

Table 5. Variation of growth rate (mm/year) of model species during postfire recovery of southern taiga communities

Species/Age of burnt areas, years	*C. arbuscula*		*C. rangiferina*		*C. stellaris*	
	$X_{av} \pm$ SD	min–max	$X_{av} \pm$ SD	min–max	$X_{av} \pm$ SD	min–max
9–15	4.0 ± 1.4	2.3–6.4	6.0 ± 2.2	2.8–8.5	3.3 ± 2.0	1.2–5.2
20–35	5.8 ± 0.4	5.1–6.5	7.2 ± 1.7	4.0–8.5	5.7 ± 1.1	4.1–6.7
40–50	6.0 ± 0.9	4.4–6.9	7.9 ± 1.7	5.9–9.8	6.6 ± 1.6	5.1–8.3
Older than 80	5.7 ± 0.8	5.1–6.6	7.8 ± 0.1	7.8–7.9	10.2 ± 1.0	9.5–10.9

Species features also introduce additional variability to the lichen growth rate. So, the lowest values of the growth rate during postfire recovery were observed in *C. arbuscula* (Table 4), because this species is more sensitive to abiogenic environmental factors (temperature, light intensity, and growing season duration) (Lechowicz and Adams, 1974) than other model species. During postfire recovery, the growth rate in *C. rangiferina* increases about three times and, in burnt areas older than 40 years after fire, is significantly higher than in *C. arbuscula*. As *C. rangiferina* is most sensitive for moisture conditions (Ahti and Hyvönen, 1985), and a significant increasing of its growth rate correspond to development of a dense lichen mat with a significant proportion of the dead mass which is able to retain moisture of the cover for a longer time. However, in the final stages of the lichen mat recovery (over 70 years), the highest values of the growth rate were found in *C. stellaris*, as this species is the most xerophytic (Ahti and Oksanen, 1990). In the absence of repeated disturbances, this species occupies dominant positions in the structure of the aboveground cover in the dry habitats of the taiga communities on the sandy substrates and forms a monodominant cover. This species replaces other lichen species, and also successfully competes with other groups of plants.

Among the model species, only in *C. arbuscula* we observe typical dynamics of the growth rate for three age periods of lichen thallus life according to the classification of V.N. Andreev (1954). The maximum values of the growth rate in this species were found in communities of middle-aged burnt areas (40–60 years after the fire), and at the terminal stage of lichen cover succession the growth rate slightly decreased; this species is excluded from the ground cover (cover less than 1%) in burnt areas over 70 years and older (Neshataev, 2002; Magomedova, 2006; Abdulmanova, 2010). *C. rangiferina* and *C. stellaris* in the postfire communities older than 60 years are characterized by the stable growth rate without the decreasing phase. These species are later successional lichens (Kershaw, 1978; Ahti and Oksanen, 1990), they invade later and form the cover of stable postfire communities. In sample key areas these species reach only the period of stable growth rate.

In uneven-aged postfire southern taiga communities, the growth rate of lichen genus *Cladonia* varies in the same range as in the middle taiga, from 1.2 to 10.9 mm/year. However, this territory is destroyed by fire less, as a result parts of the initial lichen vegetation can be preserved. It leads to more quickly recovery and closed ground cover. As a result, the lichen growth rate reaches stable values more quickly; thus, the greatest increase of about 1.5–2 times is observed in the recovery of the community within a period from 9–15 to 20–35 years after the fire (Table 5). And the growth rate is stable enough in 20–35 years after the fire.

In the southern taiga, the contribution of environmental conditions to the growth rate variability is higher (40%) than in the middle taiga communities. Therefore, the greatest contribution to the lichen growth-rate variation is introduced by the lichen mat thickness ($\beta = 0.67$; $R^2_{\text{adj}} = 0.40$; $p \ll 0.01$), whereas the time after fire explains only 16% of the variability ($\beta = 0.40$; $R^2_{\text{adj}} = 0.16$; $p < 0.01$). The lichen mat thickness is highly important for the fruticose lichen growth as a factor stabilizing the hydrothermal regime of the ground cover because the climatic conditions of this subzone are characterized by a long growing season

Table 6. Variation of growth rate of model species during postfire recovery of northern open forest subzone communities

Species/ Age of burnt areas, years	*C. arbuscula*		*C. rangiferina*		*C. stygia*		*C. stellaris*	
	X_{av} ± SD	min–max	X_{av} ± SD	min–max	X_{av} ± SD	min–max	X_{av} ± SD	min–max
5–10	7.6 ± 0.1	7.5–7.7	n/a	n/a	n/a	n/a	n/a	n/a
30–45	5.3 ± 0.3	5.1–5.5	7.4 ± 1.5	6.3–8.5	n/a	n/a	n/a	n/a
50–55	5.9 ± 2.7	3.8–10.2	7.0 ± 3.3	4.9–11.9	5.2 ± 1.4	3. 4–6.8	6.5 ± 3.2	4.4–10.2

Table 7. Variation of growth rate of model species during postfire recovery of forest-tundra zone communities

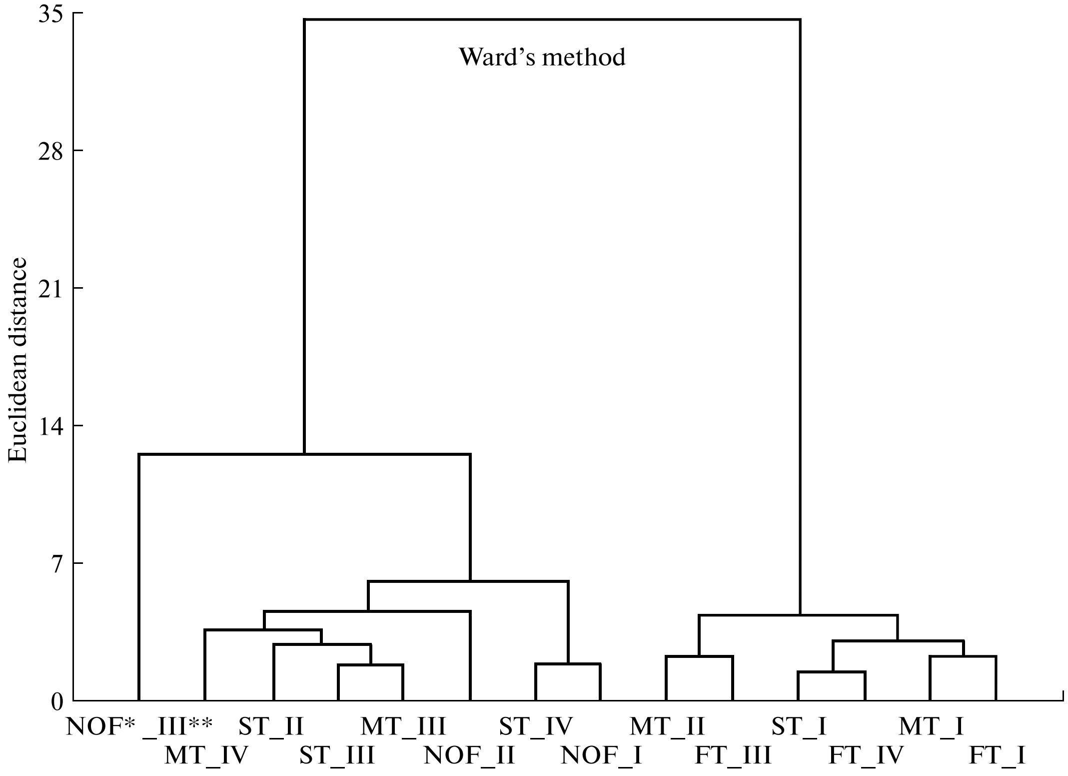
Species/Age of burnt areas, years	*C. arbuscula*		*C. rangiferina*		*C. stygia*		*C. stellaris*	
	X_{av} ± SD	min–max	X_{av} ± SD	min–max	X_{av} ± SD	min–max	X_{av} ± SD	min–max
5–20	2.6 ± 0.8	1.7–3.4	3.9 ± 0.4	3.7–4.2	4.3 ± 0.7	3.7–5.5	2.6 ± 1.3	1.7–3.5
25–35	3.2 ± 0.4	2.7–4.3	n/a	n/a	n/a	n/a	n/a	n/a
40–60	3.2 ± 0.6	2.1–4.2	4.3 ± 0.7	3.7–5.5	n/a	n/a	3.7 ± 0.5	3.3–4.4
Older than 70	3.6 ± 0.8	2.9–4.4	4.2 ± 0.6	3.7–5.0	3.7 ± 1.0	2.8–4.7	3.5 ± 1.0	2.8–4.7

with high daily temperatures (Table 1) and the lack of precipitations during this period.

Thus, during postfire succession in the lichen-rich communities in the southern and middle taiga subzones of West Siberia, the largest increase (1.5–2 times) in the fruticose lichen growth rate was estimated in the initial stages of recovery. And then 35–40 years after the fire when the lichen mat is dense and thick, with a significant proportion of mortmass (leading to the stabilization of microenvironmental conditions), the lichen growth rate reaches maximum values and its further changes are not as significant. It is believed that the growth rate and resource potential accumulated during this period correspond to productivity of lichen postfire communities at a level sufficient for the pasture (Thomas, 1995).

In the northern open forest of the taiga zone and forest-tundra zone, the mosaicity of the ground cover and substrates and the diversity of micro- and nanorelief are high, leading to the preservation of areas with original vegetation. These features of territories have an influence on the ground-cover recovery and, consequently, on the growth rate and potential productivity of fruticose lichens. There are no significant differences in the fruticose lichen growth rate at different stages of postfire succession (($F(2.20) = 0.43$; $p = 0.66$) (Tables 6, 7). Only *C. arbuscula* occurred in the burnt areas of different ages, while other model species, being late-succession ones, were found only in the burnt areas older than 30 years. In the postfire communities of the northern open forest subzone, the highest values of the growth rate were found in *C. rangiferina*. The lichen mat thickness is the only significant biotic environmental factor ($\beta = 0.88$; $R^2_{adj} = 0.82$; $p < 0.01$) affecting the growth rate variation not only in the postfire, but also in the original zonal communities (Abdulmanova, 2013). The dynamics of the composition and structure of lichen synusiae during postfore succession in these territories does not correspond to the classic scheme of recovery of the lichen cover, which is typical of tundra and boreal ecosystems (Ahti and Oksanen, 1990; Neshataev, 2002; Kukurichkin and Neshataev, 2004; Magomedova, 2006). Although the species composition of uneven-aged postfire communities (Morozova et al., 2007; Abdulmanova, 2010) is characterized by a high coverage of pioneer postfire lichens at all stages of succession (Table 2). A feature of the communities of the northern open forest subzone and the forest-tundra zone is that the highest values of growth belong to *C. rangiferina* and *C. stygia*, rather than *C. stellaris*, which can be explained by repeated disturbances of the vegetative cover as a result of the grazing of reindeer or recreation, because these species are more resistant to mechanical stress than *C. stellaris* (Magomedova et al., 2006).

The forest-tundra zone is characterized by the highest number of biotic environmental factors, which have a significant influence on the lichen growth rate variability in both undisturbed (Abdulmanova, 2013) and postfire communities. However, the greatest contribution (43%) in the growth rate variety is introduced by the time after fire ($\beta = 0.64$; $R^2_{adj} = 0.43$; $p \ll 0.01$). In the forest-tundra, where fires destroy smaller areas against high mosaicity of the vegetation cover and drainage or moisture conditions than in homogeneous sandy landscapes of the taiga zone, the most significant



Dendrogram of differences in growth rate of fruticose lichens on uneven-aged burnt areas in zonal gradient.
*Nature zone: FT, forest-tundra; NOF, northern open forests; MT, middle taiga; ST, southern taiga.
**Stages of recovery: I, burnt areas 5–20 years; II, burnt areas 20–35 years; III, burnt areas 40–60 years; IV, burnt areas older than 70 years.

are processes of growth of the lichen thalli in different periods of their lives, which depend on the time factor. However, the correlation with biotic environmental factors is high. The most important biotic factors are the lichen mat thickness ($\beta = 0.49$; $R^2_{\text{adj}} = 0.24$; $p < 0.01$), then the shrub layer closeness ($\beta = 0.40$; $R^2_{\text{adj}} = 0.16$; $p < 0.01$) and the moss coverage ($\beta = 0.35$; $R^2_{\text{adj}} = 0.11$; $p = 0.05$). These biotic parameters stabilize and soften the conditions of open (when compared with typical forest) habitats and contribute to a more rapid growth rate of fruticose lichens, reducing the drying effects of wind and maintaining the humidity of the moss–lichen layer. The high coverage of lichens in the structure of the aboveground cover may adversely affect the growth of fruticose species ($\beta = -0.39$; $R^2_{\text{adj}} = 0.16$; $p < 0.01$), because in open communities the lichen cover heats and dries faster than moss (Ipatov and Tarkhova, 1983; Tolpysheva et al., 2003), which reduces the growth processes in the thalli.

Despite the similar trends in the dynamics of lichen growth rate during of postfire succession between the subzone of open forests and the forest-tundra zone of West Siberia, the fruticose lichen growth rate in the northern open forest communities is significantly higher than in the forest-tundra phytocenoses ($F(1.65) = 2.01$; $p = 0.16$). As a result, we face the problem of identifying the hierarchy of factors causing the relative growth variability in uneven-aged postfire communities of the study zones and subzones, that is, the determination of factors largely causing the *Cladonia* fruticose lichen growth rate variation, namely the zonal/subzonal features or time after fire.

The results of cluster analysis show two large clusters combining lichens with the same growth rate from the taiga zone and forest-tundra zone (see figure).

Only the initial stages of postfire recovery in the middle and southern taiga are characterized by a low lichen growth rate, which is similar to the postfire communities of the forest-tundra zone. In the later stages of recovery, when lichens reach a growth rate most typical for these habitat conditions, no clear separation of the taiga zone into subzones was identified, which is fully confirmed by the results of ANOVA. Therefore, in the middle and southern taiga burnt areas younger than 40 years, the growth rate of the model lichen species is significantly lower than in the northern open forest communities ($F(2, 25) = 9.14$; $p < 0.01$). In communities older than 40 years, the growth rate of fruticose lichens of the taiga zone communities reaches the maximum possible values, and differences in the growth rate of model species of different subzones are not reliable ($F(2, 53) = 1.24$; $p = 0.30$). The species features of the growth rate additionally contribute to the variation but do not change the picture formed by zonal and time factors.

CONCLUSIONS

The *Cladonia* fruticose lichen growth rate varies widely in the zonal gradient and during postfire succession of the aboveground cover in West Siberia. The growth rate of the model lichen species significantly increases from north to south (from the forest-tundra zone to the southern taiga) and as time passes after the fire ends.

To study and extrapolate the growth rate of shrub-fruticose *Cladonia* lichens it is necessary to consider the level of zonal association (taiga–forest-tundra) without distinguishing more fractional subzonal units and the fire features (fire power, burn area, and lichen cover damage degree). As a result of the total destruction of the aboveground cover, lichens of the *Cladonia* genus reach the maximum growth rate values on burnt areas 40 years after the fire. The availability of variants is explained by the degree of disturbance of the territory: the classic scheme of successive changes in the aboveground cover and the long-term recovery of the stable growth rate, which can provide maximum productivity of the lichen cover, in case of the highest fire intensity and complete mineralization of the soil, or rather high growth rates already in the early stages of succession in case of mosaic burning of the vegetation cover. However, the second variant does not provide high productivity of the lichen cover at early stages because the coverage of fruticose lichens in the structure of community is low and does not correspond to highly productive stages of postfire recovery.

In all the zonal units, the greatest contribution in the growth rate variability is introduced by the lichen mat thickness. In the forest-tundra zone it is necessary to consider the factors that stabilize habitat conditions—the closeness of the shrub layer and the percentage cover of mosses in the aboveground cover.

Trends in the variability of growth rate of model lichen species during the postfire succession in different subzonal units are similar. The smallest growth rate was found in *C. arbuscula*, while the maximum growth rate in the absence of repeated disturbances was observed in *C. stellaris*; in the areas with winter grazing of reindeer, the highest growth rate was shown in species more resistant to mechanical stress, *C. rangiferina* and *C. stygia*.

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