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DECOMPOSITION OF TERRICOLOUS LICHENS IN DIFFERENT CLIMATIC CONDITIONS

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Abstract. The dependence of the decomposition of terricolous lichens and that of the model substrate (standard cellulose) on climatic conditions were investigated in three ecosystems of Estonia and the Kola Peninsula (different subzones of the forest zone, and alpine tundra) in 1989—1992. Changes in the chemical composition of lichens (total carbon, total nitrogen, water-soluble carbon compounds, lipids, hemicelluloses), the formation of humic substances, and quantitative and qualitative microbiological indices were compared. The changes in the content of nitrogen in decomposing lichens were caused not only by its resynthesis by microflora. Direct observations of microbial landscapes showed an active growth of blue-green algae in all the samples. The greatest changes in carbon biogenity of decomposing lichens were noticed in the alpine tundra of the Khibiny Mountains: the total biomass of microorganisms per carbon unit had diminished almost 10 times by the second exposition year. On all sites, lichen humification proceeded according to the fulva type. The content of fulvic acids exceeded that of humic acids 7—9 times. Comparative research of lichen decomposition under different climatic conditions showed that the intensity of their mineralization in the Estonian Scotch pine forest was considerably higher than on the investigated plots of the Kola Peninsula. In Estonia the C:N ratio in lichens was 56 after two years (initially in lichens 74), in the Scotch pine forest of the Kola Peninsula it was 61, and in the alpine tundra 63.

Key words: terricolous lichens, decomposition.

INTRODUCTION

Terricolous fruticose lichens dominate the vegetation cover of some forest and tundra communities. They are a part of the total litter turnover. Peculiarities of their decomposition are connected with the absence of real litter and a gradual disappearance of the lower parts of thallus, which are in contact with soil. The decomposition of lichens under natural conditions has not been studied thoroughly enough. In literature data can be found on the rate of the decomposition process of lichens in their natural environment (Frankland, 1974; Pike, 1978; Moore, 1981; Verseghy, 1982; Wetmore, 1982; etc.). Less attention has been paid to the microbiological peculiarities of this process (Щербакова, 1982, 1983; Паринкина & Пийн, 1989, 1991).

In general, the soil lichen cover stimulates the development of microflora in natural conditions providing a more stable moisture regime and a higher content of organic matter for the microorganisms (Пийн et al., 1984). An inhibiting effect of lichens was observed in respect to spore-forming bacteria; however, this phenomenon occurred only in the soil layer that was in close contact with lichens (Паринкина & Пийн, 1984; Parinkina & Piin, 1991). In this contact region of soil and lower parts of lichen thalli natural decomposition of terricolous fruticose lichens takes place. These facts inspired us to study the lichen decomposition under natural conditions. First, we used traditional methods.

Under the conditions prevailing in the Scotch pine forest in Estonia (deciduous-coniferous forest subzone), the decomposition of lichens *Cladina rangiferina* (L.) Nyl., *C. stellaris* (Opiz) Brodo, and *Cetraria islandica* (L.) Ach. was found to proceed slowly; the main destructors of lichens were micromycetes; the usnic acid — a secondary lichen substance with antibiotic properties — was practically absent in the thallus of *C. stellaris* after the second year of exposition in nylon bags (Паринкина & Пийн, 1989).

In order to compare the rate of decomposition of various lichen species under different climatic conditions and to find out differences between species in the decomposition process and changes in the chemical composition of lichens in this process in connection with the successions of microflora we conducted a new series of observations. Taking into account the considerable slow-down of litter decomposition process in the northern taiga forest subzone and alpine tundra (the Kola Peninsula) the observations of lichen decomposition were planned for the period of three years with interval analyses after the first and the second exposition year.

The present article presents only the results of the first two years of research of the decomposition process of *Cladina rangiferina*, *C. stellaris*, and *Cetraria islandica*.

The rest of the findings will be analysed in our further publications.

MATERIALS AND METHODS

Investigation of lichen decomposition was carried out on three stationary plots situated on the Kola Peninsula (the Khibiny Mountains) and in Estonia (Lahemaa National Park).

On the Kola Peninsula, one of the plots (KHIBINY) lies in the alpine tundra belt at the height of 560 m above sea level. A characteristic feature of the sandy soil there (on eluvium of nepheline syenite) is the absence of a clearly formed podzolic horizon. Another stationary plot is situated close to the town of Apatity on foothills (absolute height 140 m) in Scotch pine forest (APATITY). In this case the soil was illuvial-humic sandy podzol on boulder-rich moraines.

In Estonia, the observations were carried out on a plot (ESTONIA) in Scotch pine forest on illuvial sandy podzol (absolute height 45 m).

Some climatic characteristics of the research areas are presented in Table 1.

Air-dried samples of lichens (5 g) in three replicates per year for every lichen species were put into nylon bags with the mesh size of 1×1 mm and laid under lichen cover (in the Khibiny and Apatity under a forest litter layer). The lichens for the experiments were collected in Estonia. The experiments started in September 1989 and the samples were analysed after one and two years of exposition (in 1990 and 1991). Pieces of standard cellulose (100% glucan, ash content 0.04%, size 40×40×3—4 mm) were put as a control substrate close to the bags with lichens.

Table 1

Climatic parameters of research plots

Plot	Air temperature, °C					Precipitation, mm				
	Months				Mean t°	Months				Sum
	Je	Jy	Au	S		Je	Jy	Au	S	
KHIBINY	5.8	9.8	9.1	2.0	6.7	72	78	99	105	354
APATITY	9.8	13.8	12.0	6.6	10.6	51	57	64	62	234
ESTONIA	13.8	16.5	15.4	11.1	14.2	51	70	78	71	270

The decomposition rate of the control substrate was determined in order to estimate the environmental conditions for the transformation of organic matter under various natural conditions. Undoubtedly, hydrothermal, physical-chemical, and edaphic environmental factors affect the decomposition process. The extent of their impact in various climatic conditions should be reflected by the decomposition rate of the control substrate.

The chemical analysis consisted of the determination of total carbon (Пономарева & Плотникова, 1975), total nitrogen according to Kjeldahl (Аринушкина, 1970), and changes in the composition of the organic matter of lichens. The fractioning of the organic matter of the decomposing lichens was carried out by consecutive extraction of samples with reagents. Lipids were extracted with alcohol-benzene in the Soxlet apparatus, after which the samples were treated with 0.1 M solution of NaOH. The total content of carbon was determined in an alkaline extract; the content of carbon of humic acids was fixed after precipitation with an acid. The amount of fulvic acids was determined by difference. The contents of water-soluble organic matter (by carbon) and reducing sugars were determined in separate samples. The content of substances transient to acidic (2% HCl) extract (carbon and reducing sugars) was determined after the extraction of water-soluble fractions. The amount of hemicelluloses was calculated by multiplying the content of the sugars in the acidic extract by a coefficient of 0.9 (Переверзев, 1987). All calculations were made for ash-free matter.

Microbiological observations included the analysis of the total numbers of bacteria and fungi, the counts of ammonifying microorganisms and of those using mineral nitrogen. The total numbers of bacteria were determined by means of Vinogradsky's technique as modified by Shulgina (Разумовская et al., 1960) and the fungal mycelium length on membrane filters with the help of the modified method by Demkina-Mirtshink (Демкина, 1986). Special attention was paid to the determination of the biomass of the microflora allowing us to evaluate the actual amount of living matter of the destructors and observe the changes in the biogenity of the organic matter of lichens during the process of their decomposition. The determination of bacterial biomass was based on the direct estimation of the numbers of microorganisms and on the weight of cells. The measurement of cells was carried out whilst the bacteria were being counted and the weight was calculated on the basis of the volume and the specific weight of 1.0 (Parinkina, 1974; Паринкина, 1989). The weight of 1 m of fungal mycelium was taken as 0.02 mg (Мирчинк, 1988). Direct observations with the help of capillary pedoscopes were used to follow the changes in the appearance of the microbial landscapes (Аристовская & Паринкина, 1961). The pedoscopes were put into the nylon

bags with lichens. This method is very useful for correcting and completing indirect methods of microflora investigation.

All the data received were treated statistically.

As the present paper deals only with the impact of climatic factors on the decomposition process of lichens, we used averaged data of three lichen species for each plot.

RESULTS AND DISCUSSION

The analysis of the decomposition rate of the control substrate (standard cellulose) shows considerable differences in the transformation of organic matter on the observation plots (Table 2).

Table 2

Weight loss of cellulose and lichens during the experiment, %

Object	Year of exposition	KHIBINY	APATITY	ESTONIA
Cellulose	First year	17.2	39.3	85.6
	Second year	26.3	87.6	97.2
Lichens	First year	19.8	33.3	34.1
	Second year	30.4	40.7	50.4

During the first year of exposition, the loss of cellulose weight was insignificant in the alpine tundra of the Khibiny Mountains, but was over 85% of the original in the Scotch pine forest of Estonia. In the Scotch pine forest of Apatity the decomposition of cellulose was quite intensive, the weight loss exceeded that of the alpine tundra more than twice, but was still two times lower than that in Estonia. During the second exposition year, the decomposition of cellulose continued, being especially intensive in Apatity. In Khibiny the process continued to proceed slowly: in two years the weight loss of cellulose amounted to only 26%. Comparing cellulose decomposition intensity in Apatity and Estonia, i. e. similar forest ecosystems on different latitudes, we can note that the weight loss of cellulose in Apatity over two years is close to the value obtained in Estonia over one year's exposition (87.6 and 85.6%, respectively).

The data characterizing lichen decomposition intensity correspond generally to the results obtained for the control substrate: the differences in weight loss of samples decomposing under different climatic conditions were significant. Still, on forest plots the total intensity of lichen decomposition was lower than the rate of cellulose decomposition. At the same time, lichen weight loss in Khibiny was somewhat higher than cellulose weight loss (Table 2). This was, probably, the result of intensive leaching of water-soluble substances from lichens due to abundant atmospheric precipitation common in the alpine tundra belt of the Khibiny Mountains.

Therefore, the obtained results on weight loss of standard cellulose and lichens show notable differences in the intensity of mineralization processes caused by climatic factors. Mineralization process is the most restrained in the alpine tundra.

The analysis of the changes in the chemical composition of lichens during their decomposition shows that the content of total carbon grows considerably after the first exposition year (Table 3). During the second year the changes are not so great.

Table 3

Chemical properties of decomposing lichens (mean data of three lichen species)

Chemical indices	Initial content	KHIBINY		APATITY		ESTONIA	
		1990	1991	1990	1991	1990	1991
Total C, %	43.53	47.68	47.67	48.63	46.83	46.00	47.14
Total N, %	0.59	0.63	0.76	0.72	0.87	0.69	0.90
C : N	74	76	63	69	61	69	56
Water-soluble C, %	6.80	5.28	2.61	4.16	5.81	5.07	3.54
Water-soluble carbohydrates, %	3.52	2.44	0.40	1.61	1.15	2.39	1.16
Hemicelluloses, %	25.14	26.16	16.77	28.59	18.39	24.20	17.17
Lipids, %	8.32	6.84	7.11	7.54	6.87	8.62	7.14
C_{HA}, %*		0.46	0.51	0.48	0.84	0.63	0.91
C_{FA}, %*		3.85	6.48	4.49	6.17	4.32	7.00
$C_{HA}+C_{FA}$		4.31	6.99	4.97	7.01	4.95	7.91
$C_{FA} : C_{HA}$		8.40	12.70	9.30	7.30	6.80	7.60

* HA — humic acids, FA — fulvic acids.

Still, an examination of the decrease of carbon in comparison with the changes in lichen weight during decomposition (Table 4) reveals an obvious regularity: carbon loss increases from the alpine tundra of the Khibiny Mountains to the Scotch pine forest in Estonia. In the second decomposition year the loss of carbon increased proportionally to the weight loss of lichens.

Changes in the content of total nitrogen are somewhat different. The amount of nitrogen in decomposing lichen samples increased considerably, exceeding the original content 1.3—1.5 times in two years. The rise in the content of nitrogen in the decomposing lichens was the biggest in Estonia and the smallest in the alpine tundra.

It could be supposed that the nitrogen accumulation in decomposing lichens is caused mainly by the resynthesis of nitrogenous substances by microorganisms. At the same time, analysis of the biomass of microorganisms (bacteria and fungi) per unit of decomposing lichen material showed that a rise in the nitrogen amount occurred together with a decrease in the amount of the biomass of microflora (Table 5). It is especially high in the alpine tundra, somewhat lower in the Scotch pine forest of Apatity, and practically absent in Estonia.

While in Khibiny the decrease in the biomass of microflora is caused by a sharp decline in the amount of fungi and a somewhat smaller decrease in the amount of bacteria, then in Apatity the fall in fungal biomass is smaller than that of bacteria, but in Estonia the twofold decrease in the amount of bacterial biomass is accompanied even by a slight increase in fungal biomass as a result of which almost no changes occur in the total amount of microbial biomass (Table 5).

Thus, the increase of nitrogen content in decomposing lichens cannot be caused only by its resynthesis by the microflora, but there should also exist additional sources for the input of nitrogen into this decomposing material.

Table 4

Changes in the chemical content of decomposing lichens (mean data of three lichen species

Chemical indices	Initial content, g	CHIBINY				APATITY				ESTONIA			
		1990		1991		1990		1991		1990		1991	
		g	% of initial content	g	% of initial content	g	% of initial content	g	% of initial content	g	% of initial content	g	% of initial content
Total carbon	1.89	1.66	88	1.44	76	1.41	75	1.20	63	1.32	70	1.01	53
Total nitrogen	0.026	0.022	85	0.023	88	0.021	81	0.022	85	0.020	75	0.019	73
Water-soluble carbon	0.30	0.18	60	0.08	26	0.12	40	0.15	50	0.14	48	0.08	25
Water-soluble carbohydrates	0.15	0.08	53	0.01	8	0.05	31	0.03	20	0.07	45	0.02	17
Lipids	0.36	0.24	67	0.21	58	0.22	61	0.18	50	0.25	69	0.15	42
Hemicelluloses	1.09	0.91	83	0.51	47	0.83	76	0.47	43	0.69	63	0.37	34

Table 5

Microbiological data of the decomposing lichens (mean values of three lichen species)

Microbiological indices	CHIBINY		APATITY		ESTONIA	
	1990	1991	1990	1991	1990	1991
Total number of bacteria $\times 10^9$/g o.d.m.*	12.9	13.2	11.1	7.8	17.4	11.5
Bacterial biomass $\times 10^{-3}$ g/g o.d.m.	3.25	1.94	2.57	1.48	4.79	2.20
Fungal biomass $\times 10^{-3}$ g/g o.d.m.	43.8	1.83	55.1	43.9	144.1	145.9
Total microbial biomass $\times 10^{-3}$ g/g o.d.m.	47.05	3.77	57.67	45.38	148.89	148.1
Bacterial biomass $\times 10^{-3}$ g/g C	6.83	4.08	6.3	3.47	10.80	4.70
Fungal biomass $\times 10^{-3}$ g/g C	70.84	3.8	135.7	69.8	318.3	316.0
Total microbial biomass $\times 10^{-3}$ g/g C	77.67	7.88	142.0	73.27	329.1	320.7
Fungal biomass/bacterial biomass	13.5	0.95	21.4	29.6	30.1	66.3
Ammonifying bacteria $\times 10^3$ cells/g o.d.m.	4 587	723	5 550	3 016	1 241	2 848
Spore-forming bacteria $\times 10^3$ cells/g o.d.m.	48	19	5	63	201	40
Bacteria using mineral N $\times 10^3$ cells/g o.d.m.	927	26 000	12 300	65 630	550	31 000
Fungi $\times 10^3$/g o.d.m.	346**	166	847	1 597	5 933	6 919

* o.d.m.: oven dried lichen mass; ** $p < 0.95$.

Investigation of the microbial landscapes of decomposing lichens revealed a considerable growth of blue-green algae (cyanobacteria) in all the subject sites. They were especially abundant in the decomposing lichens in Estonia (*Gloeocapsa*, *Anabaena*, *Dactylococcopsis*, *Microcystis*, *Rhabdoderma*), but occurred often in large amounts also in Apatity and Khibiny, where together with *Gloeocapsa* and *Anabaena* also *Oscillatoria* and *Stigonema* as well as representatives of other genera may be found. As cyanobacteria include many nitrogen-fixing species, the rise in the nitrogen content in decaying lichens may be caused by an intensive development of these autotrophic microorganisms. The existence of additional sources for nitrogen input is apparently proved by the fact that the decrease of the nitrogen content in lichens (taking into account sample weight losses) is slower than the fall in the carbon content. In case of the most intensive decomposition of lichens, which was observed in Estonia, the loss of nitrogen over two years amounted to 25% and that of carbon to 50%.

As the increase in the nitrogen content (% per dry substance) is more notable than that of carbon, the C:N ratio becomes lower in decomposing lichens. The C : N ratio in lichen samples was 56 in Estonia after two years of decomposition, while the initial ratio was 74 (Table 3).

Fresh plant remains contain numerous substances that can dissolve in water. The water-soluble fraction in the subject lichens amounted to about 7% of dry weight (by carbon). In the process of lichen decomposition the content of water-soluble substances diminishes, although a considerable amount of water-soluble fractions of organic matter was preserved in the samples after two-year exposition. Ecological conditions had little effect on the mineralization intensity of these substances.

Carbohydrates make up a considerable part of the water-soluble substances. Their content in decomposing lichens decreased remarkably, especially during the second exposition year. Their disappearance was the most notable in the samples decomposing in alpine tundra. This happened as a result of their intensive leaching from the samples by atmospheric precipitation, the amount of which was relatively high there (Table 1).

Data on the changes in carbon biogenity in decomposing lichens (biomass of microorganisms, g/g C) confirm these results. Undoubtedly, the leaching of the water-soluble fraction, in particular carbohydrates, makes the organic lichen matter less available for microorganisms.

A significant change in carbon biogenity in decomposing lichens was noticed in the alpine tundra of the Khibiny Mountains (Table 5): the total microflora biomass per carbon unit had diminished almost ten times by the second exposition year. The decrease in the fungal biomass was especially remarkable (18.6 times). This is caused by successional changes of microflora in which the weight of the rapidly growing mycelium of "sugar-fungi" diminishes simultaneously with the decrease in the amount of easily available carbohydrates.

A similar tendency towards a decrease in the carbon biogenity in decomposing lichens, though to a lesser extent, was observed in the Scotch pine forest in Apatity, where the total biomass of microorganisms and the biomass of fungi per carbon unit fell two times by the end of the second year. The slightest decrease in the carbon biogenity of lichens by the second decomposition year was observed in the Scotch pine forest of Estonia.

This may be connected not only with the level of leaching, but also with the obviously richer taxonomical composition of soil micromycetes in forest ecosystems than in tundra communities (Widden & Parkinson, 1979; Бабьева Е., 1983; Бабьева И., 1984; Паринкина, 1989). That is why the notable changes in chemical parameters of decaying lichens in Estonia

do not have such a big impact on fungal biomass. The withdrawal of some species of fungi is compensated for by the development of others which are better adapted to the new ecological situation.

These conclusions are indirectly proved by data on fungal and bacterial biomass ratio in the subject regions (Table 5). If the considerable domination of fungi in the first decomposition year in Khibiny disappears completely due to the changed ecological situation in the second decomposition year, then in Estonia even an increase may be observed, reflecting the diversity of micromycetes in this Scotch pine forest.

The intensity of the decomposing processes of lichen organic matter, reflected in their weight loss, is also expressed by the amount of microorganisms taking part in the mineralization process.

The greatest weight loss in lichens on stationary plots of Estonia and Apatity is accompanied by a rise in the amount of saprophytic microorganisms. A contrary picture may be seen in the alpine tundra of the Khibiny Mountains, where the decomposition process is slowed down to a great extent.

In the course of the transformation of lichens numerous microorganisms assimilating mineral nitrogen compounds develop. This occurred in all research areas and is the result of ammonium nitrogen accumulation due to the suppression of the nitrification process in the acidic environment of remains.

The whole microflora of decomposing lichens undergoes certain successional changes. The analysis of these changes in microflora in the course of lichen decomposition on the basis of microbial landscapes in capillary pedoscopes proves the general validity of the obtained results for the amount and biomass of microorganisms.

Rich and diverse microbial communities in the decomposing lichen substrate are characterized after the first exposition year by an almost universal domination of fungi, diverse nonspore-forming bacteria, abundance of blue-green (*Gloeocapsa*, *Anabaena*, *Tetrarcus*, *Dactylococcopsis*, *Calothrix*, *Microcystis*, *Rhabdoderma*, etc.) and green algae, and a great amount of protozoa — mainly amoebas.

The density of growths of microorganisms in the capillary channels of pedoscopes became lower after the second exposition year. Changes occurred both in the qualitative variety of individual groups of microorganisms (blue-green algae, for example, are represented after two decomposition years almost exclusively by *Gloeocapsa*) and in the physiological activity of microflora (expressed by a decrease in the amount of actively vegetating forms, generation of a great amount of spores of bacteria, chlamydospores, and arthrospores of fungi, isolated protoplasms in mycelia and appearance of disruptions of hypha as well as cysts of amoebas and algae).

This corresponds to the data of the chemical analysis of samples, in particular to the considerable decrease of water-soluble carbohydrates.

Components of lichen organic matter which are not so easily available for the transformation by microflora (hemicelluloses and humic acids) favour the development of the corresponding microflora (fungi in the forest site of Apatity and especially in Estonia, simultaneous increase in the number of spore-forming bacteria and microorganisms of the actinomycetes group).

In spite of the high frequency of bacteria in microbocoenoses after the second exposition year, the absolute amount of bacteria diminished (Table 5), probably initiating a considerable decrease in the occurrence of amoebas and other protozoa in the microbial landscape.

Thus, the qualitative composition of microbial communities changes considerably in the course of the decomposition of terricolous lichens,

reflecting changes in their chemical composition which take place under the impact of biotic and abiotic environmental factors.

The analysis of lipids (fats and fatty acids, waxes, and resins) in alcohol-benzene extract showed that their content in the initial lichen samples amounted to more than 8%. After the first exposition year the relative content of lipids dropped, except for the samples decomposing in Estonia in which the amount of lipids even rose slightly (Table 4).

One of the characteristics of lichens is their large content of hemicelluloses. Their mean content in the subject lichens was 25%. During the first decomposition year it showed virtually no change and in Apatity even rose a little. This happened as a result of a decrease in the content of other carbon-containing fractions which were more easily available for microorganisms. After two years of exposition the content of hemicelluloses dropped sharply. Taking into account the weight loss of lichens, their quantity decreased by more than two times in the course of two years after the decomposition of the samples started. An even bigger decrease in the amount of hemicelluloses was observed in the decomposing lichen samples in Estonia (Table 4).

Decomposition of plant remains in natural ecosystems is a combination of two simultaneously occurring processes, mineralization and humification, which causes the formation of specific organic matter, mainly humic and fulvic acids. Such substances are absent in fresh remains of plants.

In the humification process of lichens the formation and considerable accumulation of humic acids take place. Their dynamics can well be traced back year by year, demonstrating a considerable increase in the content of humic acids in the second year (Table 3).

The impact of ecological conditions is also well displayed, showing the maximum accumulation of humic substances in Estonia and the minimum in the alpine tundra of the Khibiny Mountains. This phenomenon is more evident in connection with fulvic acids. At all plots, lichen humification proceeds according to the fulva type: the content of fulvic acids exceeds the amount of humic acids 7—9 times. This type of humification of plant remains is characteristic of the climatic conditions under which podzolic soils are formed.

Therefore, the comparative research of lichen decomposition processes under various climatic conditions showed that the intensity of their mineralization was considerably higher in the deciduous-coniferous (mixed) forest subzone than in the northern taiga forest subzone and the alpine tundra belt (analogous to the tundra zone). This is caused by more favourable climatic factors, higher saturation of soil with microflora, and a wide diversity of the taxonomic composition of microorganisms, first and foremost of the main litter destructors—fungi. In Estonian Scotch pine forest fungi are predominant in all decomposition stages of lichens.

Regular increase in the taxonomic diversity of microflora in the Scotch pine forest of Estonia results in the biomass content remaining practically on the same level even at a significant chemical transformation of lichens. This causes a higher decomposition rate in comparison with northern latitudes where limited taxonomic composition of microflora leads to a sharp decrease in the values of the biomass of microorganisms during the exhaustion of the available substrate.

Intensive decomposition of lichens under the environmental conditions prevailing in Estonian Scotch pine forest favours greater accumulation of humic substances and enrichment of organic matter with nitrogen.

Our findings give evidence of the zonal character of the decomposition of lichens in nature.

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