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ИНСТИТУТ СТЕПИ
INSTITUTION OF THE RUSSIAN ACADEMY OF SCIENCES THE URAL BRANCH
INSTITUTE OF STEPPE

ВОПРОСЫ СТЕПЕВЕДЕНИЯ

QUESTIONS OF STEPPE SCIENCE

IX

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ALGAL STACKS AND FUNGAL STACKS IN LICHENS AND THEIR IMPORTANCE FOR SURVIVING IN EXTREME HABITATS

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The lichen is a complex symbiotic entity, typically composed of a lichenized fungus (mycobiont) and an alga or cyanobacterium (photobiont). The «textbook lichen» has a thallus composed of an upper fungal cortex overlying an internal algal layer, which in turn overlays a fungal medullary layer. Some lichens do indeed correspond to this tidy picture, but in others the arrangement and abundance of the photobiont cells differ; even closely related species growing in different habitats may show marked differences in response to their different ecology [7]. Polluted environments also affect algal patterns [9]. Growth activity of the fungal partner can also influence patterns in the algal layer [3].

Lichen phenotypes in extreme habitats may differ considerably from those growing under mild conditions; for instance, the upper cortex in lichens living in desert areas is much thicker (up to 6 times) in comparison with average European lichens; similarly algal layer is 2 -3 times thicker in desert lichens. A «reverse» structure of thallus has been reported by Vogel [10] for a South African species of *Buellia* growing on quartzite pebbles. It has its algal partner hidden below black, light-impermeable medulla but in contact with translucent quartzite; the algal cells receive diffuse light from below, through the rock. Vogel [10] also mentioned an unusual anatomy (he introduced the term «Fensterflechten» = window lichens for it) in the South African *Psora crystallifera*, where the thick cortex is cracked into translucent crystal-like structures above the algal layer. Fensterflechten have also been reported from the Atacama Desert [2].

Since the environment can influence the pattern of algal cells, it would not be surprising if lichens from extreme habitats – those that are especially cold, hot, dry or insolated – were to show particularly unusual patterns. Our research on some lichens from the deserts of Central Asia, a region in which all four of these extreme conditions are commonly experienced, shows that algal cells in many of them are organized in vertical stacks, rather than as an even horizontal layer. These **algal stacks** are separated by what we have termed **fungal stacks**, namely regions of vertically oriented, translucent fungal plectenchyma that extends downwards from the upper cortex. Our further comparisons have shown that various lichen species from unrelated groups with both algal and fungal stacks occur in strongly insolated areas in the world.

In our project, we will focus on this **stack anatomy** in lichens, which is analogous to the South African living stones and other window-leaved plants growing partly underground to obtain light by stacks of translucent central mesophyll cells and chlorophyll containing cells are arranged below them and at margins of underground leaves [4]. This anatomy is considered to be adapted for water absorption and avoiding heat stress from the sunlight [8], but its real function is still not clarified [1].

A real stack anatomy in lichens, but slightly developed, was described by Poelt [6], who introduced the term «Kegelrinden» [cortex cones] for conical extensions of cortex tissue into the algal layer in lobate species of *Candelariella* and *Lecanora* species. Algal stacks in these species are, however, rather indistinct. Nevertheless, Malcolm [5] found a remarkable example of algal stacks in *Labyrintha implexa* (monospecific genus *Labyrintha* is endemic to New Zealand). He measured the light transmission through translucent hyphal bundles and fully hydrated algal stacks, and found that absorption rates were 8.6 times lower in the former. Malcolm did not make any further physiological measurements. He discussed possible advantages of this thallus anatomy but, other than observing that it may increase illumination of the deeper algal cells, he did not reach any clear conclusions. Although this species does occur in a rather dry, though certainly not desert-like, part of the South Island, it is also present in much more humid, oceanic areas, e.g. Campbell Island; it is a rare species throughout its range. This species does not fit the pattern shown by all the other observed lichens with stack anatomy, which occur in dry areas or alpine habitats.

We suggest that the purpose of algal stacks is to increase a period during which photosynthesis can occur. Lichens in dry habitats have a rather limited opportunity for photosynthesis, as they are not usually sufficiently hydrated, so adaptations which extend the period of photosynthesis ought to be advantageous. In lichens without algal stacks, as the thallus dries out from the surface, the photobiont cells, which are arranged in a thin horizontal layer, will stay in an optimal state of hydration for only a short period of time. On the other hand, photobiont cells in an algal stack are arranged in a tall column, which may reach right to the base of the thallus; cells at different heights are in different states of hydration as the thallus desiccates; and photosynthesis can continue for longer. The problem of cells deeper in the stack being shaded by those above may be overcome by the fungal stacks, which permit light to penetrate deep into the thallus.

Fungal stacks do, of course, reduce the proportion of the thallus surface area that is underlain by photobiont cells. This obviously reduces the amount of sunlight that can be directly intercepted by photobiont cells, and this must be disadvantageous to some extent. Lichens with algal and fungal stacks have also higher dark respiration than those with layered anatomy (see our unpublished results below).

Preliminary Results

Two hypotheses that bear on our project have already been tested: (1) during desiccation, algal stacks and fungal stacks extend the period of CO_2 uptake (photosynthetic activity) due to dynamic use of photobiont cells at different heights, and (2) under conditions of high irradiance, lichens with algal stacks and fungal stacks increase their CO_2 uptake compared with lichens from the same habitats that lack those features.

Our first hypothesis, that algal stacks and fungal stacks extend the period of CO_2 assimilation, was not supported by our experiments. On the contrary, *Aspicilia desertorum*, one of the species with tissue stacks, appeared to desiccate faster than species from the same place without stacks (our unpublished data). However, it did not disprove the hypothesis either, and further experiments are justified, as desiccation is a complex process that is affected by many variables, including relative humidity of the air, irradiance, wind speed and thermal properties of the substrate.

Our experiments do support the second hypothesis, that under light saturation lichens with tissue stacks have higher photosynthetic capacities (CO_2 uptakes under saturated light conditions) than co-occurring lichens without tissue stacks (Fig. 1).

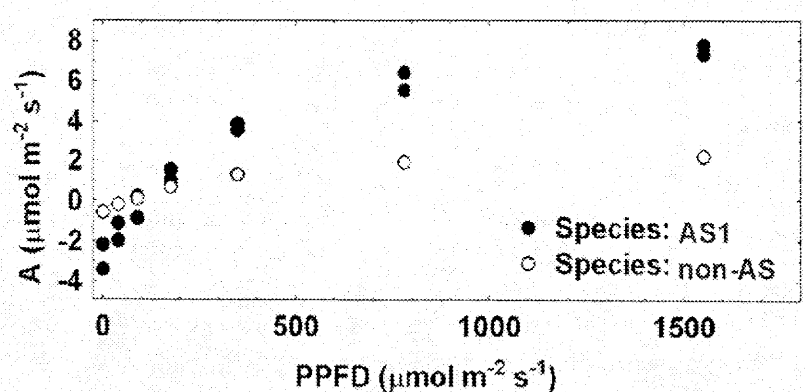

Fig. 1. Example of the light response of CO_2 assimilation (y axis; positive values = CO_2 gain) to changing irradiance (x axis; PPFD = Photosynthetic Photon Flux Density) in the rock sample from Kazakhstan bearing both species with stacks (AS1 = *Caloplaca variabilis* agg.) and other species with

layered anatomy (non-AS; various crustose lichens). Gas exchange measurements were made according the method described below. First measurement was made on whole community containing AS1 and non-AS together. Two consequent measurements were made on the same sample but after removing of non-AS species (black dots). The light response of species with layered anatomy (white dots) was calculated as differences between first and second measurement and weighted by areas of AS1 vs. non-AS.

High photosynthetic capacity would seem to be clearly advantageous in areas with high insolation, but – equally clearly – high respiration of lichens with stacks (Fig. 1; shown by negative values during low irradiation) must offset this advantage to some extent. High respiration observed in lichens with stacks is probably caused by a larger biomass per unit of area. The second hypothesis is also supported, indirectly, by the observed geographical distribution of lichens with tissue stacks. They occur in areas of high insolation and the fact that they occur in these areas in unrelated groups suggests that this is not merely a coincidence: convergent evolution in response to the same selection pressure seems to be more plausible explanation. The fact that lichens with algal stacks often dominate the communities in which they occur implies that this adaptation is a successful one.

Aims for our future research

The main hypothesis «**The stack anatomy represents ecological profit in deserts and has an impact on speciation process**» will be tested by a complex research divided into the four following areas.

1. Physiology

- Are there differences in CO_2 assimilation between lichens with layered anatomy and lichens with variously developed stacks under a changing environment?
- In which conditions do both lichen types differ in particular?

2. Genetic fixation

- Is the formation of stacks only the phenotype response to extreme conditions or is it genetically fixed?

3. Role of algae

- Are the lichens with stacks associated with specific algal lineages, different from those in lichens with tissues in horizontal layers?
- Are the algal cells in stacks morphologically different from those in lichens without stacks?

4. Ecological profits

- Which conditions make the stack anatomy advantageous?
- Do the lichens with algal stacks and fungal stacks survive more extreme conditions (e.g. light, heat, frost) than other lichens?

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ВОДОРОСЛЕВЫЕ И ГРИБНЫЕ СТОЛБЦЫ В ЛИШАЙНИКАХ И ИХ ЗНАЧЕНИЕ ДЛЯ ВЫЖИВАНИЯ В ЭКСТРЕМАЛЬНЫХ УСЛОВИЯХ

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Наши полевые исследования и изучение гербарного материала показали наличие вертикально оформленных водорослевых и грибных столбцов (вместо горизонтальных слоёв) в лишайниках из различных систематических групп, но произрастающих в сильно засушливых и/или инсолированных местообитаниях. Наши эксперименты подтверждают гипотезу, что при световом насыщении у лишайников с тканевыми столбцами есть более высокие фотосинтетические способности (поглощение CO_2), чем у лишайников без тканевых столбцов.

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ЛИШАЙНИКИ РОДА *XANTHOPARMELIA* (VAIN.) HALE В ОРЕНБУРГСКОЙ ОБЛАСТИ (РОССИЯ)

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В результате обработки собственных полевых сборов, коллекций различных лихенологов, хранящихся в крупнейших гербариях мира, нами обнаружено для территории Оренбургской области 14 видов рода *Xanthoparmelia* (Vain.) Hale, 3 из которых – новые для региона и Урала. Показаны морфологические, химические и экологические особенности видов.

We have revised herbarium specimens of *Xanthoparmelia* (Vain.) Hale from the Orenburg region including our recently collected samples. We have confirmed the occurrence of 14 species in the region; 3 of these species are new to the Ural Mts. Our appraisal of morphological, chemical and ecological characters of the species resulted.

Введение

В настоящее время Род *Xanthoparmelia* (Vain.) Hale – один из крупнейших родов кустистых и листоватых лишайников в мире [8] с центрами разнообразия в Южной Африке и Австралии. В Европе он насчитывает 33 вида [9], в Казахстане 9 [10], а в России – 18 [4], что указывает на недостаточную его изученность в пределах такой большой