New Aspects of the Reproduction by Autospores in the Lichen Alga *Trebouxia* (Microthamniales, Chlorophyta)

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Summary: Two different “zoospore to zoospore” cycles — named cell cycle A and cell cycle B — have been found in *Trebouxia* by starting cultures of different species from zoospores and following the further developmental stages under identical culture conditions. In cell cycle A the first cell divisions after zoospore settlement result in an autosporangium with few (4–32) adhering autospores (tetrads or autospore packages) and then zoosporangia and autosporangia with numerous (>32) small autospores are formed, adhering together with other cells into an autospore package. In cell cycle B, however, the zoospores first develop into almost completely differentiated vegetative cells which are transformed directly into zoosporangia or autosporangia with numerous small autospores. Autospore packages are not formed in cell cycle B. It is concluded that these differences in the reproduction by autospores are important characters for the identification of *Trebouxia* species, but that they do not justify separation of the genus into two genera or subgenera.

Key Words: Autosporulation; Cell cycle; Lichens; *Trebouxia*.

Introduction

Since early studies of the coccoid green lichen alga *Trebouxia* much attention was given to the way of asexual reproduction (e.g. FAMINTZIN & BORANETZKY 1867; WARÉN 1920). However, reproduction is a controversial aspect in the taxonomy of *Trebouxia* and has probably been overestimated while other important characters, e.g. chloroplast structures including pyrenoids (ETTL & GÄRTNER 1984; FRIEDL 1989a) were neglected. In early as well as more recent studies (REHÁKOVÁ 1968; ARCHIBALD 1975; HILDRETH & AHMADJIAN 1981) essentially two distinct types of nonmotile reproductive cells were found, namely cell packages and numerous small cells. The presence or absence of cell packages was considered as an important character and consequently *Trebouxia* was separated into two subgenera (WARÉN 1920; TSCHERMACK-WOESS 1989) or even into two genera (ARCHIBALD 1975; for review see GÄRTNER 1985a). ETTL & GÄRTNER (1984) did not find clear differences in the reproduction by nonmotile cells (autosporation according to these authors) in their investigation of *Trebouxia* strains that were obtained from culture collections and thus they did not use autosporation as a taxonomic character. In a study of numerous *Trebouxia* isolated taken from lichens of the family Parmeliaceae (FRIEDL 1989b), however, many strains could be clearly distinguished by the presence of tetrads and autospore packages from strains that lacked these stages. But on the other hand this difference did not seem to be a very reliable character since it appeared to be variable even within one strain and dependent on culture conditions (see results). Moreover, in some strains it was
not clear whether autospore packages were formed or not.
In the present investigation, complete developmental cycles (from zoospore germination to zoospore formation) in various species and strains of *Trebouxia* have been studied in culture, with the aim to find out whether distinct developmental patterns exist and if so, whether these differences are taxonomically significant. The present study revealed two different developmental cycles. These and other observations on cultured and lichenized phycobionts of the lichen family Parmeliaceae indicate that differences in the reproduction by autospores can be used as taxonomic characters.

**Material and Methods**

**Material:** For culture experiments the following strains were used: *Trebouxia asymmetrica* SAG 48.88, *T. flava* UTEX 181, *T. gelatinosa* UTEX 905, *T. gigantea* UTEX 2231, *T. crenulata* CCAP 219/2, *T. usneae* UTEX 2235, *T. irregularis* UBT-86.077 and *T. irregularis* UTEX 2236. The strains were obtained from the Culture Collection of Algae at Innsbruck (GARTNER 1985b), but were originally derived from other culture collections (see GARTNER 1985a). Additional strains were isolated from lichens of the family Parmeliaceae (species names given in brackets) and are kept at the University of Bayreuth (UBT): *T. arboricola* UBT-86.042C1 (*P. acetabulum*), *T. arboricola* UBT-87.016 (*P. flaventior*), *T. arboricola* UBT-86.107 (*P. flaventior*), *T. gelatinosa* UBT-86.108B2 (*P. caperata*), *T. gigantea* UBT-88.002B6 (*P. hottentotta*), *T. irregularis* UBT-86.077 (*Platismatia glauca*), *T. impressa* UBT-86.009E1 (*Parmelia sulcata*). For collection sites of the lichens see FRIEDEL (1989b). Fresh thalli of *Omphalora arizonica* (TUCK. ex WILLEY) NASH & HAEFELN were collected at the Santa Rita mountains, Arizona, U.S.A., sent by mail to Bayreuth and kept frozen at −20°C for several months until the phycobiont was isolated.

**Methods:** Culture conditions, isolation of the phycobiont and embedding for electron microscopy were the same as described previously (FRIEDEL 1989a). The production of zoospores was induced as described by MELKONIAN & BERN (1983). The zoospore suspension was kept in glass tubes under culture conditions until the zoospores were settled. After gentle centrifugation the pellets were placed in several portions on microtiter plates with 2 ml wells containing agarized culture medium. From that small agar pieces with just a few cells on it were used for microscopic examination at intervals of 12–24 hrs. These culture experiments were repeated twice for most strains examined. Squashed preparations of the algal layer of *Omphalora arizonica* were placed in liquid culture medium in small glass petri dishes and examined at the same intervals using an inverted microscope.

**Results**

The presence of autospore packages was a distinct character in some cultured phycobiont strains. In *T. impressa* UBT-86.009E1 and *T. arboricola* UBT-86.107 autospore packages were dominant and no zoospores or sporangia with numerous small cells were detected (Fig. 1). But when *T. impressa* UBT-86.009E1 was cultured on TOM-1 medium, zoosporangia and sporangia with small cells were present and the autospore packages disappeared. Three months after *T. arboricola* strain UBT-87.016 had been isolated from the lichen *Parmelia flaventior* it consisted only of autospore packages (Fig. 2), but after two years of culturing single vegetative cells with a fully differentiated chloroplast, zoosporangia and sporangia with numerous small cells were dominant (Fig. 3). Similar, in *T. gigantea* UBT-88.002B6 autospore packages were dominant shortly after isolation from the lichen *Parmelia hottentotta*, but were significantly less frequent after some months of culturing. *T. gelatinosa* UBT-86.108B2 is an example where no autospore packages were seen, only vegetative cells and sporangia with numerous small cells or zoospores were present (Fig. 17).

Culture experiments were performed to find out whether differences are manifested in the asexual reproduction of *Trebouxia*. Zoospores were used to start new cultures of different species and strains at a certain defined develop-

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Figs. 1–11. Different developmental stages of *Trebouxia* spp. with cell cycle A. Bar = 10 μm.
Fig. 1. *T. impressa* UBT-86.009E1, cultured phycombiont from *P. sulcata*. Small undifferentiated cells adhere into large autospore complexes.
Figs. 2, 3. *T. arboricola* UBT-87.016, cultured phycombiont of *Parmelia flaventior*. Fig. 2. Undifferentiated small cells adhere into autospore packages. Three months after separation from the lichen thallus. Fig. 3. Single, large and completely differentiated cells, cells containing numerous protoplasts (s) and single young vegetative cells. 20 months after separation from the lichen thallus.
Figs. 4–8. Zoospore to zoospore development (cell cycle A). Fig. 4. Young vegetative cells from zoospores of *T. asymmetrica* SAG 48.88 after three days. Fig. 5. Cell at protoplast division, several protoplasts. From zoospores of *T. crenulata* CCAP 219/2 after six days. Fig. 6. Autosporangia containing few autospores. v, vegetative cell. From zoospores of *T. asymmetrica* SAG 48.88 after six days.
Fig. 7. Autosporangia with few autospores starting to dissociate. From zoospores of *T. gigantea* UTEX 2231 after eight days.

Fig. 8. Adhering zoosporangia or empty walls of zoosporangia that developed from autospores adhering into an autospore package. Arrow: young vegetative cells (= autospores) developed from retained zoospores. From zoospores of *T. asymmetrica SAG* 48.88 after 12 days.

Figs. 9–11. Different developmental stages of the phycobiont of *Omphalora arizonica*. m, mycobiont hyphae. Fig. 9. Single vegetative cell with attached mycobiont hypha from a squashed preparation of the algal layer. Note finely lobed chloroplast containing a pyrenoid and nucleus with nucleolus. Figs. 10, 11. Autospore packages developed from vegetative cells as in Fig. 9 after two weeks of culturing.
Figs. 12–20. Different developmental stages of *Trebouxia* spp. with cell cycle B. Bar = 10 μm.

Figs. 12–16. Zoospore to zoospore development (cell cycle B). Figs. 12, 14–16. *T. gelatinosa* UTEX 905. Fig. 13. *T. flava* UTEX 181. Figs. 18–20. *T. irregularis* UTEX 2236. Fig. 12. Young vegetative cells (v) and settled zoospores (z) after one day. Fig. 13. Almost completely differentiated cells with chloroplasts containing numerous starch grains. From zoospores after three days. Fig. 14. Almost completely differentiated cell (v) and cell with biparted chloroplast. Note numerous starch grains in the chloroplasts. From zoospores after six days. Fig. 15. Cells at protoplast divisions, indicated by several flat chloroplasts and completely differentiated vegetative cells (v). From zoospores after eight days. Fig. 16. Empty sporangium (s), cell with numerous protoplasts and vegetative cells. From zoospores after eight days. Fig. 17. *T. gelatinosa* UBT-86. 108B2, cultured phycobiont from *Parmelia caperata*. Vegetative cells (v) and sporangia (s) containing numerous small autospores from an agar slant culture. Fig. 18. Almost completely differentiated vegetative cell. Note ovoid shape, nucleus with nucleolus, chloroplast with numerous starch grains and a pyrenoid (p). From zoospores after seven days. Fig. 19. Cells with biparted chloroplasts. From zoospores after seven days. Fig. 20. Autosporangia with numerous small autospores (s) and cells containing numerous protoplasts. From zoospores after nine days.
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Figs. 21—23. Ultrastructure of sporangia containing numerous daughter cells in different *Trebouxia* spp. c, cap-like wall thickening, w, sporangial wall. z, zoospore. small arrow, cell wall. arrow head, flagellum or flagellated cell. Bar = 2 μm. Fig. 21. Nonmotile autospores with cell walls and zoospores within the sporangial wall. *T. arboricola* UBT-86.041C2. Fig. 22. Overview of a sporangium containing numerous zoospores and some small autospores (within marked section). *T. irregularis* UBT-87.077E1. Fig. 23. Marked section of Fig. 22 shown enlarged.

mental stage. This had the advantage that the sequence of developmental stages from zoospore germination to zoospore formation could be followed under identical conditions. For these culture experiments a selection of strains representing most of the species found as phycobionts in the Parmeliaceae (FRIEDL 1989b) was used. *Trebouxia asymmetrica* SAG 48.88 and *T. gigantea* UTEX 2231 were selected because autospore packages were always present in agar slant cultures. *T. gelatinosa* UTEX 905, *T. irregularis* UBT-86.077 and *T. irregularis* UTEX 2236 were examples of those species where no autospore packages were detected (c.f. Fig. 17). *T. crenulata* CCAP 219/2, *T. flavus* UTEX 181 and *T. usneae* UTEX 2235 were representatives where it was uncertain whether autospore packages can be formed. Two different “zoospore to zoospore”-cycles were observed, here referred to as cell cycle A and cell cycle B. They are summarized in Figs. 24 and 25. In cell cycle A (Fig. 24) the zoospores developed into small vegetative cells with a cup-shaped parietal chloroplast within three days (Fig. 4). After 6—8 days vegetative cells still smaller than vegetative cells from regular agar slant colonies were observed and they already contained several simple and flat chloroplasts (Fig. 5). This indicated that protoplast division had already started in those cells prior to the development into large vegetative cells. At the same time small autospore packages of 4—32 cells occurred and one or two days later these small autosporangia were dominant in the cultures (Figs. 6, 7). From the tenth day on production of zoospores was observed (Fig. 8). At the same time sporangia containing numerous (more than 32) small cells with a simple parietal chloroplast also occurred. Both sporangia were always adhering together with other cells into a package (Fig. 8), no single zoosporangia were seen. After the zoospores were released, also a few cells remained within the sporangium and developed into young vegetative cells within the old sporangial wall (Fig. 8). These observations were identical in *T. asymmetrica* SAG 48.88, *T. crenulata* CCAP 219/2 and in *T. gigantea* UTEX 2231. In *T. crenulata* CCAP 219/2 the autospore packages became dissociated after two weeks and single vegetative cells were present. Similar to cell cycle A was the following observation in the phycobiont of *Omphalora arizonica* (Figs. 9—11). Shortly before separation from the mycobiont mainly single vegetative algal cells (Fig. 9) were detected, only very few tetrads and small autospore packages were seen in squashed preparations of the algal layer. However, two weeks after inoculation with liquid culture medium tetrads and autospore packages were dominant. Mycobiont hyphae were still attached to these autosporangia demonstrating that the single vegetative cells of the algal layer were transformed into autospore pack-
Figs. 24, 25. Diagrams summarizing both developmental cycles in *Trebouxia*. Broken lines: reproduction of *Trebouxia* within lichen thalli as interpreted from developmental stages seen in squashed preparations of algal layers of lichens.

Fig. 24. Cell cycle A. 1, zoospore. 2, young vegetative cell. 3, small undifferentiated vegetative cell. 4, protoplast division, chloroplast already divided. 5, autosporangium containing few autospores compressed within the sporangial wall. 6, autosporangium with autospores that begin to dissociate and where new protoplast divisions occur while the autospores that begin to dissociate and where new protoplast divisions occur while the autospores still adhere within the sporangial wall. 7, some autospores of stage 6 are developed into sporangia with numerous daughter cells which either escape as nonmotile autospores (a, autosporangium) or as free-swimming zoospores (z, zoosporangium) while other autospores are developed into an autosporangia (a) with few cells where new protoplast divisions occur. 8, autosporangium of 6 dissociates into single cells.

Fig. 25. Cell cycle B. 1, zoospore. 2, young vegetative cell. 3, almost completely differentiated vegetative cell. 4, protoplast division, chloroplast already divided into four. 5, cell containing numerous protoplasts. 6, development from stage 5 either into a sporangium with numerous nonmotile autospores (a) or into a zoosporangium (z).

ages in culture (Figs. 10, 11). Two days later, also zoosporangia and sporangia with numerous small cells were formed and were together with other cells in autospore packages within the sporangial wall. In cell cycle B (Fig. 25) the zoosporangia developed into small vegetative cells with a simple cup-shaped chloroplast within 2–3 days (Fig. 12). In contrast to cell cycle A, however, these cells continued growing and after 3–6 days they contained an almost fully differentiated chloroplast (e.g. in *T. usneae* with a pyrenoid with starch plates), while cell shape and size were as in vegetative cells from agar slants (Figs. 13, 18). At the same time cells occurred with biparted chloroplasts indicating that protoplast division had already started (Figs. 14, 19). After 6–8 days the single cells contained numerous (more than 32) chloroplasts (Figs. 15, 16) and production of zoospores was observed (Fig. 16). Different to cell cycle A the zoosporangia were always single and were never together with vegetative cells or other sporangia within a sporangial wall. At the same time single sporangia were also observed containing numerous (more than 32) small cells with a simple parietal chloroplast (Fig. 20). In contrast to cell cycle A, sporangia containing only four or few (less than 32) adhering autospores (autospore package) were never observed in cell cycle B, even not after several weeks. These observations were identical in *T. gelatinosa* UTEX 905, *T. flava* UTEX 181, *T. irregularis* UTEX 2236, *T. irregularis* UBT-86.077E1 and in *T. usneae* UTEX 2235. In *T. flava* UTEX 181 only few (less than 64) zoospores or small nonmotile cells were formed, while in all other strains numerous zoospores were developed.

The ultrastructure of sporangia with numerous small cells revealed non-flagellated cells at the same time within one
sporangium (Figs. 21–23). This was observed frequently, for example in *T. irregularis* UBT-86.077E1 and *T. arboricola* UBT-86.041C2.

**Discussion**

The present observations have demonstrated that the structural development of asexual reproduction in *Trebouxia* follows two different ways (named cell cycle A and cell cycle B) and that two types of sporangia with nonmotile reproductive cells are found: tetrads or cell packages with few cells (absent in cell cycle B) and sporangia with numerous small cells (present in both cell cycles). Definition and terminology of asexual reproductive cells have been a matter of controversed discussion (ETTL 1988a, b). ETTL (1988a) proposed a uniform classification of asexual reproductive cells which was critically reviewed with respect to recent ultrastructural studies by SEGAA (1991). According to these definitions, the tetrads and cell packages in *Trebouxia* are autospores since they are derived from a flagellated condition, i.e. a reduced flagellar apparatus is present in these cells (SLUIMAN & LOKHORST 1988). This ultrastructural finding confirmed previous notions based on light microscopy (e.g. TSCHERMAK-WOEß 1983; ETTL & GÄRTNER 1984; GÄRTNER 1985a). However, the identity of the sporangia with numerous small cells is still a matter of discussion. ETTL & GÄRTNER (1984) noted that no clear delimitation of both types of sporangia containing nonmotile cells is possible in *Trebouxia* since they only differ by the number of cells produced which is variable and therefore both are autosporangia. Other authors (e.g. REHÁKOVÁ 1968; TAKESHTA et al. 1989; TSCHERMAK-WOEß 1989), however, made a distinction between autosporangia (cell packages) and “aplanosporangia” containing numerous small cells. LOKHORST et al. (1989) also distinguished auto- and aplanospores in the soil alga *Friedmannia israelensis* which is closely related to *Trebouxia* (MELKONIAN & BERN 1983; MELKONIAN & PEVELING 1988). Both, numerous small nonmotile cells and zoospores, may occur in one sporangium as shown in the present study (Figs. 21–23). Therefore, it is evident that the small nonmotile cells have derived from zoospores or from cells that were almost completely differentiated as zoospores which were retained within the sporangium and developed into young vegetative cells within the sporangial wall bypassing the motile condition. This fits well into the classical definition of autospores by PASCHER (1927) and GEITLER (1934) which has also been adopted by ETTL (1988a) and SEGAA (1991). It is also congruent with ETTL’S (1988a) statement that it is rather difficult to delimitate autospores and zoospores exactly. Even the development of sporangia with numerous small cells is almost identical with that of zoosporangia (TSCHERMAK-WOEß 1989). Consequently, – in agreement with ETTL & GÄRTNER (1984) – the term autospore is used here for those cells which were sometimes described also as “aplanospores” (REHÁKOVÁ 1968; TSCHERMAK-WOEß 1989; LOKHORST et al. 1989).

ETTL & GÄRTNER (1984) stated that autospores in *Trebouxia* are quite different in size and shape, but that there is not a qualitative difference. The different development of autospores as interpreted from different stages seen in many species and strains was summarized by GÄRTNER (1985a, Fig. 3). Different to GÄRTNER the present study is based on complete developmental sequences starting with zoospores as a defined stage and has demonstrated that the structural development of reproduction by autospores follows two different ways (Figs. 24, 25). Both developmental ways were already partly mentioned by GÄRTNER (1985a, Fig. 3), but were not realized as distinct patterns.

PEVELING & KÖNIG (1985) already found differences in early developmental stages of different strains of *Trebouxia* that followed from zoospores, but they did not capture further stages. The first stages found in the complete developmental cycles in the present study (1–5 in Fig. 24 and 1–3 in Fig. 25) are congruent with the stages described by PEVELING & KÖNIG (1985).

On the basis of a detailed ultrastructural study of cell division events (sporulation) in *Friedmannia israelensis*, LOKHORST et al. (1989) explained the formation of two types of nonmotile reproductive cells (autospores and aplanospores in the authors’ sense) by the fact that the development of zoospores can be suppressed due to environmental conditions at different times in the ontogeny of the sporangium. Suppression early in the ontogeny results in few large autospores (tetrads or autospore packages) with a still undifferentiated flagellar apparatus, suppression at a very late stage in numerous small autospores with an almost complete flagellar apparatus (aplanospores of LOKHORST et al. 1989). Obviously, this may also be true for *Trebouxia* spp. with cell cycle A. The present study has shown that species with cell cycle A can start to reproduce already as young vegetative cells and can stop their transition into reproductive cells at a very early stage resulting into packages of at least four autospores (tetrads). Autosporangia with numerous small autospores and zoospores are also formed, but contrary to *Friedmannia* they are formed after autospore packages have developed and they are always adhering together with other cells within a sporangial wall.

In species with cell cycle A it may be due to culture conditions, whether autospore packages or zoosporangia and autosporangia with numerous small autospores are
found sporangia with flagellated cells of *T.* within lichen thalli. However, SLOCUM et al. (1980) phycobionts from the lichen family Parmeliaceae (FRIEDL packages. *T. gigantea* *T. crenulata* *T. impressa* "reproduction by zoospores is usual small autospore packages were detected in lichen thalli having *T. showmanii* (cell cycle A) as a phycobiont (FRIEDL & GÄRTNER 1988). It is quite plausible for a lichen alga in its character for the identification of *Trebouxia* species. However, the cell cycle feature does not correlate with other taxonomic characters. For example, *T. impressa* and *T. flava* are different in their cell cycles, but share a common pyrenoid ultrastructure and a common chloroplast morphology (FRIEDL 1989a, b). Furthermore, *T. usneae* and *T. irregularis* differ in characters of their vegetative cells and their zoospores (FRIEDL, unpubl. results), but they have in common reproduction by cell cycle B. Thus, in the author’s opinion there is no reason to regard the character cell cycle as more important than other characters and therefore a separation of *Trebouxia* species into two subgenera (e.g. TSCHERMAK-WOESS 1989) or even genera (ARCHIBALD 1975; PEVELING & KÖNIG 1985) is not justified.

### Acknowledgements

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### References


— (1988b): Zellteilung und Sporulation als wichtige Unter-

| *T. aggregata* | *T. anticipata* |
| *T. arboricola* | *T. erici* |
| *T. assimetrica* | *T. excentrica* |
| *T. corticola* | *T. flava* |
| *T. crenulata* | *T. gelatinosa* |
| *T. decolorans* | *T. glomerata* |
| *T. galapagensis* | *T. irregularis* |
| *T. gigantea* | *T. italiana* |
| *T. higginsiae* | *T. magna* |
| *T. impressa* | *T. pyriformis* |
| *T. incrustata* | *T. usneae* |
| *T. jamesii* |
| *T. potteri* |
| *T. showmanii* |
| *T. simplex* |

phycobionts from the lichen family Parmeliaceae (FRIEDL 1989b) no free swimming zoospores were detected within lichen thalli. However, SLOCUM et al. (1980) found sporangia with flagellated cells of *T. gelatinosa* with thalli of *Parmelia caperata* and they interpreted this as a potential for zoospore release, but free swimming zoospores were not seen. SLOCUM et al. (1980) obviously depicted autosporangia which are characteristic for *Trebouxia* spp. with cell cycle B.

It is concluded that *Trebouxia* species which exhibit tetrads and autospore packages reproduce according to cell cycle A and those which do not form autospore packages perform reproduction as in cell cycle B. In Table 1 the *Trebouxia* species are allocated to both cell cycles. This distinction, together with other features (e.g. chloroplast morphology and pyrenoid structures) is an important character for the identification of *Trebouxia* species.

Table 1. *Trebouxia* spp. with cell cycle A and *Trebouxia* spp. with cell cycle B. *", species where zoospore to zoospore cycle was studied (see results). In all other species the allocation to a certain cell cycle is concluded by the presence (cell cycle A) or absence (cell cycle B) of autospore packages.

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It is also due to culture conditions or it may even be species-specific how early autospore packages become dissociated and then single cells are present in the cultures (e.g. in *T. crenulata* CCAP 219/2, see results) or the autospores adhere into large complexes of several generations of autospores (e.g. in *T. impressa* UBT-86.009E1, Fig. 1). In species with cell cycle B, however, almost completely differentiated vegetative cells are transformed directly into single zoosporangia or single autosporangia with numerous small autospores without the formation of tetrads or autospore packages. Those species are different from *Friedmannia* with respect to their reproduction.

The specific differences in the reproduction by autospores may also be expressed within lichen thalli. For example, *T. irregularis*, with cell cycle B, was found to reproduce only by numerous small autospores within a lichen thallus while only tetrads and small autospore packages were detected in lichen thalli having *T. showmanii* (cell cycle A) as a phycobiont (FRIEDL & GÄRTNER 1988). It is quite plausible for a lichen alga in its dry environment that mechanisms of reproduction that do not involve motile cells are advantageous. SLOCUM et al. (1980) reported that "reproduction by zoospores is usually suppressed in the lichen association" (p. 163; see also AHMADJIAN 1970). Similarly, during a study of


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